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Factors Affecting Calcification Processes in the Hermatypic Corals POCILLOPORA DAMICORNIS and PORITES COMPRESSA

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FACTORS AFFECTING CALCIFICATION PROCESSES IN THE HERMATYPIC CORALS *POCILLOPORA DAMICORNIS* AND *PORITES COMPRESSA*

by

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Each person whose signature appears below certifies that he has read this dissertation and that in his opinion it is adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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CHAPTER I

INTRODUCTION

The origin, formation and distribution of coral reefs are determined by the biology of the reef biota. This biota includes a wide assortment of organisms, the most obvious of which are the corals and the calcareous algae. Corals ordinarily contribute the greatest mass of material while algae serve as cementing agents. Literature on coral biology and reef structure is reviewed by Stoddart (1969), Yonge (1963), Wiens (1962), Wells (1957a, b), and Vaughan and Wells (1943).

The corals mainly responsible for the reef structure are the hermatypic (reef-building) corals, which are distinguished from the ahermatypic (non-reef-building) corals by the presence (in hermatypic corals) of intracellular zooxanthellae (dinoflagellate symbionts). The formation of most organic reefs is greatly dependent on ecological factors. The hermatypic corals are very sensitive to environmental conditions, and in contrast to the ahermatypic corals (which are widely distributed in the world oceans) they are restricted to a narrow latitudinal and vertical band in the ocean. They are found growing only in shallow, well lighted water (continental shelves, submarine banks, atolls, etc.) and in the tropics or subtropics (ordinarily within the 20°C minimum temperature isotherm). Within this band other factors further restricting their occurrence are salinity,

circulation, sedimentation, type of substrate, and nutrition. For reef formation these factors must by adequate to support vigorous coral growth. To form a thriving reef the rate of limestone accumulation through coral (or other $CaCO_3$ depositing organisms) growth must exceed the rate of loss through organic (boring organisms) and inorganic (solution, wave erosion) attrition.

An understanding of such factors is important when considering reef origins, in particular the atolls of the Indo-Pacific (see Ladd, 1961, and Stoddard, 1969, for a review of theories on reef origins). Where reef formation involved submergence (in some instances apparently 1500 m) coral growth rate must have been high enough so that the rate of upward reef formation was equal to the rate of submergence. That the ecological factors were not always satisfactory is suggested by the occurrence of guyots (flat-topped seamounts) and drowned atolls typically at a depth of 1000-1500 m in the Indo-Pacific Basin (Menard, 1964).

Although a considerable number of growth rate studies have been made the studies have usually lacked either control of, or quantitative data on, the ecological factors. Most of this previous research has been done under natural conditions where growth rates were determined by height, weight, or diameter measurements made on coral colonies over a period of months or years. A review of these methods and their results is given in Chapter II.

A laboratory method recently developed by Goreau (1959) uses rate of ^{45}Ca incorporation as a relative measure of calcification rate of corals under various ecological conditions. This method has the distinct advantage of permitting quantitative study of calcification

rates during short periods of time (one hour or less) under strictly controlled conditions. It has the disadvantages of study under the unnatural laboratory conditions including the possibility of giving relative calcification rates rather than absolute growth rates. However, despite these disadvantages this method seems to be the most practical quantitative approach.

In my research the effect of temperature on coral growth rate was studied using Goreau's basic method. The Q_{10} and the temperature adaptation of the calcification process in corals was investigated (Chapter VI). In conjunction with this some of the factors were analyzed which might introduce errors in estimates of natural growth rates from the laboratory obtained calcification rates (Chapters IV and V). An attempt is made to translate the laboratory rates into growth rates. The results are compared with natural growth rate measurements (Chapter V).

CHAPTER II

REVIEW OF CORAL GROWTH RATE INVESTIGATIONS

Early observations on growth rates are reported by Darwin (1889), Dana (1879), Guppy (1889), Agassiz (1890), Gardiner (1901, 1903) and Wood-Jones (1910). These reports were generally based on casual observations; for example, of the accumulation of corals growing on ship bottoms, cables, anchors, etc., or in channels that were periodically dredged. The time periods involved were generally somewhat indefinite. Some of the rates obtained from these initial observations were considerably higher than those indicated by more recent work.

Since 1900 several investigators have applied more rigorous methods. Measurements (height, weight, diameter, length) were made over a period of time varying from several months to several years. The corals were ordinarily grown in a more or less normal habitat for the species, and were either left naturally attached or were attached to cement blocks, tiles, etc. Often a large number of samples (colonies) were used. These studies have provided valuable estimates of growth rates and a summary is provided in Tables 1-3.

The choice of a particular category or species to be included in these tables was based either on its usefulness (due to its wide distribution) in making comparisons between two geographical areas, or because of its particular significance as a dominant reef-building

coral. Additional selection of data was necessary to make the results from all the sources as comparable as possible. Thus colonies that died or were damaged during a study were omitted from the analysis. (Because of this selection and certain recalculations the values given in the tables do not always exactly agree with the original values.)

The data in the tables were arranged approximately in ascending order according to the surface water temperatures found in the respective areas with the intent of determining whether a higher growth rate accompanies a higher natural water temperature. However, a direct comparison of the results obtained by the different investigators in their respective areas is of doubtful validity, since a diversity of techniques, species, habitats, lengths of observations, and conditions of the corals (size, age, apparent health) were involved. Even in those categories with the most complete data (Acropora, massive Porites, branched Porites, Pocillopora damicornis, Montastrea annularis) it is difficult to detect a trend.

More meaningful comparisons are between the growth rates of different species or categories found in the same locality. Thus Montastrea annularis (called Orbicella annularis by Vaughan), according to Vaughan (1916) the dominant reef species in the West Indies (at times however replaced by Acropora palmata), has a relatively slow growth rate compared with Porites and Acropora species which are dominant reef corals in the Indo-Pacific. Of the major Indo-Pacific reef corals the Acropora are quite consistently the fastest growing in all areas, followed by the branched and then the massive Porites species. The meager data available on Montipora and Pocillopora--also important

reef corals--places their growth rate between that of Acropora and the branched Porites.

During these investigations the capriciousness of growth rate (Wood-Jones, 1910; Mayor, 1924; Edmondson, 1929) was noted. Rapid growth alternates with inactivity in no apparent pattern. Mayor (1924) mentions a massive Porites in Samoa which grew 37 mm in diameter in one year, made no growth the next and grew 54 mm the last year. Edmondson's measurements (1929) showed great variation between different colonies of the same species all growing under apparently identical conditions.

Since most of the values in Tables 1-3 are averages based on a fairly large number of observations the variation is not so evident nor is there any indication of some of the maximum rates recorded. Annual growth rates of several exceptionally fast growing colonies are listed below:

SPECIES	DIAMETER (mm/yr)	HEIGHT (mm/yr)	WEIGHT (%/yr)	INVESTIGATOR
Acropora cervicornis		264		Lewis et al.(1968)
Acropora teres	268	133	2786	Mayor (1924)
Pocillopora damicornis	62	40	974	Mayor (1924)
Montipora ramosa			1197	Boschma (1936)

Those data expressed as weight (%/yr) contain some of the most rapid apparent growth rates as well as the greatest variability. This is evidently a reflection of the effect of initial colony size on measurements expressed as percent. For this reason the height, length, diameter measurements are more meaningful when different size colonies

are compared. They are however inadequate for comparing actual $CaCO_3$ deposition between different species or growth forms because coral skeletons vary so greatly in shape and density.

ESTIMATES OF THE RATE OF REEF FORMATION

Estimates of the rate of reef formation have been made by several investigators. A summary is given in Table 4.

The rate of reef formation is more than an extension of coral growth rates. It is also determined by percent coverage of the coral on the reef, contributions from various other reef organisms (mollusks, calcareous algae, bryozoans, etc.) and several physical and chemical factors. In Table 4 when the basis of the estimate is given as "Coral Growth Rate" the investigator may have included physical or chemical components of reef formation, but ordinarily contributions from corals other than the ones listed, or from other organisms, or corrections for percent coverage of the coral, were not included. When the basis of the estimate is given as "Coral Growth Rates Averaged", the growth rates of several prominent coral species or categories and various of the other components (depending on the investigator) determining the rate of reef formation were used. The original papers should be consulted for the various components used and the assumptions made in each estimate. The large variation in estimates is a reflection of the different methods of computation used.

Most of the rate measurements were made on coral colonies growing on the surface of the reef in what may be less favorable shallow water (Yonge, 1940); therefore many of the estimates given in Table 4 may be minimum rather than average or maximum. Little quantitative work

has been done on the effect of depth on coral growth and reef formation, but from casual observation, Gardiner (1903) assumed a rate of 45.7 mm/yr for reefs at a depth of 9-27 m, and Verstelle's data on soundings made in the Dutch East Indian Archipelago suggest even faster growth in depths exceeding 5 m. His data suggest some of the highest rates of reef formation; however, they should be accepted with caution. He reports both "rising" and "sinking" reefs (only his data on "rising" reefs is given in Table 4), the significance of which is not known. Kuenen (1950) questions the reliability of using soundings.

INVESTIGATIONS OF FACTORS AFFECTING CORAL GROWTH RATES

Some of the factors thought to affect rates are: sexual activity and planulation (Vaughan and Wells, 1943), age and size of the colony (Goreau and Goreau, 1960a), availability of planktonic food (Vaughan and Wells, 1943), light (Goreau, 1959; Goreau and Goreau, 1959), silt (Shinn, 1966), temperature (Shinn, 1966; Ma, 1937), and perhaps salinity and water turbulence. Initial investigations on these factors were mainly casual observations of those habitats in which growth appeared most vigorous and luxuriant. Thus Gardiner (1903) and Yonge (1940) suggested greater growth rates for corals at moderate depths than for those in shallow water. The correlation between temperature and coral distribution has suggested an effect of temperature on growth.

Using a more experimental approach Stephenson and Stephenson (1933) and Mayor (1924) observed differences in the growth of two halves of the same initial coral colony when the halves were placed

in different habitats. With a similar technique Shinn (1966) showed that extreme temperatures and excessive silt inhibit growth. Seasonal fluctuations in rate were suggested by the work of Shinn (1966), but were not found by Lewis et al. (1968) or Edmondson (1929). Geographical differences in growth rate are probable (Lewis et al., 1968), but difficult to verify.

Experimental evidence for the effect of size and age of a colony on its growth or calcification rate is given by Stephenson and Stephenson (1933) and Goreau and Goreau (1960a). For many corals there is an exponential decrease of rate with size. Using ^{45}Ca Goreau and Goreau (1959) obtained no conclusive evidence that depth affects calcification rate, but they did show a drastic effect of light on the rate. For several species the light:dark calcification ratio was greater than 10. A relation between nutrition and growth is not obvious. Some evidence suggests that concentrated feeding slows calcification rate (A. A. Roth and D. Crabtree, personal communication).

CHAPTER III

BASIC MATERIALS AND METHODS

INTRODUCTION

Methods common to most of the experiments are described in this chapter. Major variations are also discussed here and are summarized for each experiment in Table 5. Methods restricted to a particular type of experiment are discussed in later chapters.

The basic method used was a modification of that developed by Goreau (1959). It involved the growth or incubation of corals in sea water containing the radioactive isotope ^{45}Ca, and permitted the determination of calcification rates over short periods of time under laboratory conditions. Coral collected on the reef was brought to the laboratory, put into an incubation vessel containing the radioactive sea water, and incubated or grown under controlled light and temperature conditions for some period of time--never more than 24 hours and often 1 hour or less. At the end of the incubation period, samples were taken to determine the quantity of ^{45}Ca incorporated into the coral skeleton. Preparation of the samples for ^{45}Ca assay involved tissue removal (by alkaline hydrolysis), size determination (by either weight or surface area), and solution of the skeleton in HCl. Activity of the ^{45}Ca in this acid solution was measured using a liquid scintillation spectrometer. The quantity of ^{45}Ca incorporated was used to determine the relative or absolute growth rate.

RESEARCH LOCALITIES

Research was done at two localities in the Indo-Pacific. Most was done at the Hawaii Institute of Marine Biology (HIMB) located on Coconut Island in Kaneohe Bay, Oahu, Hawaii. The specimens were collected at several of the more luxuriant patch reefs found in Kaneohe Bay. At the other locality, Eniwetok Atoll, the corals were collected in the lagoon just offshore from the Eniwetok Marine Biology Laboratory (EMBL). These corals were found attached to various pipes and cables occurring in this area on the shallow sandy bench that forms the periphery of the lagoon. Corals at both localities were collected from depths of less than 12 m.

EXPERIMENTAL ORGANISMS

Two species were used--Pocillopora damicornis (Linnaeus) and Porites compressa Dana. P. damicornis (Fig. 1) was chosen because it is widely distributed throughout the Indo-Pacific tropical ocean, its growth form permits a simple method of sample taking, and a considerable amount of physiological and ecological research has involved this species. P. compressa (Fig. 2) was used because the genus Porites is a major reef builder throughout the tropical oceans, and the species P. compressa is the dominant coral (composing perhaps 80% or more of the coral on many of the patch reefs) in Kaneohe Bay. P. compressa was also easily sampled. P. damicornis is an imperforate highly branched coral with relatively small colonies (usually not more than 20-25 cm in diameter), whereas P. compressa is a perforate coral with finger-like branches and colonies often a meter or more in diameter.

Different colonies of a single species of coral are morphologically variable. With P. damicornis colonies I generally avoided extremes of pigmentation and size. Although very large colonies were not ordinarily selected because of evidence (Goreau and Goreau, 1960a) which correlates reduction of growth rates with increased colony size in some coral species, they were sufficiently large to supply the number of samples required for the experiment. The growth form of P. damicornis varies from a fragile, finely branched form to a robust form with thick branches. Both forms were used but usually only one form within any one experiment. No evidence of a correlation between colony morphology and calcification rate was obvious in the colonies used, although large variations in calcification rate between colonies were observed.

Colonies of P. compressa were selected if they had a sufficient number of large branches with flattened (rather than rounded or hemispherical) ends. This enabled the taking of core samples (from the branch end) with uniform surface areas.

PREPARATION OF CORAL FOR INCUBATION

Corals were collected not more than 12 hours (usually less than 4 hours) prior to an experiment. Whole colonies were too large to use in the incubation vessel; therefore, portions or branches were removed with a pair of wire cutters. These were held upright in the incubation vessel by use of an acetate and plexiglas rack or holder (Fig. 3). In "Collection Method 1" complete colonies were brought to the laboratory where the branches were removed, placed in the racks, and incubation was begun. This method, however, was found to

be unsatisfactory when different sections of an experiment (such as the temperature experiments) had to be done on consecutive days, since different colonies had to be used for different parts of the same experiment (nested experimental design), introducing an extra variable. Neither could this method be used for P. compressa, since these colonies are too large to bring to the laboratory. In "Collection Method 2" branches were removed from colonies remaining on the reef, placed in the racks, and brought to the laboratory. When using this method colonies being used several times for different parts of an experiment were marked with a buoy or tag prior to the initial collection. Care was taken to avoid damage through mechanical abrasion, unnecessary exposure to air, or exposure to extremes of light and temperature during collection and handling.

SEA WATER PREPARATION

Several hours prior to an experiment the sea water for the incubation was prepared by adding ^{45}Ca to 500 or 900 ml (depending on the experiment) of sea water contained in the incubation vessel. The water was stirred thoroughly and then allowed to stand until the experiment began to permit complete mixing and any short-term chemical equilibrium changes to occur. The sea water was obtained from the laboratory sea water system (an open system using natural sea water) and the ^{45}Ca from New England Nuclear or International Chemical and Nuclear in the form of $^{45}CaCl_2$ in a 0.5 N HCl acid solution. Usual concentrations of ^{45}Ca were 0.5-1.0 μc per ml of sea water. The total amount of calcium added never exceeded 1% of the natural calcium in

sea water. Samples (50 λ) of the sea water were taken for an accurate determination of its radioactivity using a liquid scintillation spectrometer.

INCUBATION

At this point the rack of coral branches was either placed directly into the radioactive sea water and the incubation begun, or it was passed through a period of acclimation in non-radioactive sea water. This period was generally for either 0.5 or 1.0 hour and was to acclimate the corals to the incubation conditions and particularly to avoid any overshoot artifact (Grainger, 1958) or other anomalies due to sudden stress such as temperature shock. The acclimation period was used mainly in the temperature experiments where extreme temperatures were involved. Conditions during this acclimation period were identical to the incubation conditions, except that during this period the temperature was changed gradually to that of the incubation temperature. At the end of the acclimation period the rack containing the experimental organism was transferred to the incubation vessel containing the radioactive sea water. Incubation time was quite variable depending on the experiment, but often was 0.5 or 1.0 hour. Incubations were usually conducted between 10:30 AM and 2:30 PM to avoid possible diurnal rhythms in calcification rate (see Chapter V). Physical conditions under which an experiment was performed were determined by the incubation system. Three types of systems were employed.

In the first system (Incubation System 1, Fig. 4) a glass staining dish was used for the incubation vessel. It was fitted with a plexiglas top, bored with two holes and fitted with rubber stoppers. One held a

thermometer, the other a glass tube through which air was bubbled into the incubation sea water to aid circulation and maintain constant pH and a high oxygen tension. For temperature control the incubation vessel was placed in a temperature regulated water bath. The corals in the vessel had 360° illumination from ambient light, but the main light source was situated 23 cm below the bottom of the incubation vessel and consisted of four cool 40 watt fluorescent bulbs covered with a translucent plastic shield. A major criticism of this system was the position of the light.

In "Incubation System 2" (Fig. 5) the light source was situated in a semicircle above the incubation vessel and consisted of ten 20 watt fluorescent bulbs. A piece of white cardboard behind the bulbs served as a reflector. The downward irradiance was 6,700 $\mu w/cm^2$. Incubation vessels, aeration, circulation, and temperature regulation were identical to "Incubation System 1".

The third system (Incubation System 3, Fig. 6) was designed to be portable and provided a method for doing experiments under identical conditions at different geographical locations. From the top of an incubation housing (constructed from corrugated cardboard) was suspended the light source--a General Electric 300 watt Cool-Beam lamp (PAR56/2MFL) situated 42 cm away from the coral in the incubation vessel. The white interior of the housing gave reflection from all directions. Light intensity was controlled with a variable transformer. The current was maintained at 2.5 amps. For these experiments the downward irradiance was 30,000 $\mu w/cm^2$. Temperature was controlled by means of a water bath the temperature of which was regulated manually by working the heat of the GE light source (supplemented with hot water

for high temperature incubations) against cooling with ice cubes. The plexiglas incubation vessels were of two sizes and sufficient respectively to hold the 500 ml and 900 ml quantities of sea water used. Holes bored in the tops held a glass tube for aeration and circulation and a thermometer. A magnetic stirrer provided additional circulation in the incubation vessel plus circulation of the bath water.

POST-INCUBATION PROCESSING OF CORAL

The processing and analysis of both P. damicornis and P. compressa involved rapid termination of ^{45}Ca incorporation and sampling followed by removal of tissue from the samples and the rinsing, drying, solution, and ^{45}Ca activity determination of the samples. In addition the samples of P. damicornis were weighed.

Incubation was terminated by immersing the coral in fresh water. This usually involved a large quantity of water (1200 ml or more) for at least 1 min to dilute that ^{45}Ca adhering to the surface of the coral which had not been incorporated into the coral skeleton.

Samples of P. damicornis were taken by cutting tips from branches with wire cutters. Efforts were made to make the tips uniform. Although the size varied from 3-72 mg, the range for any one experiment was smaller. In P. compressa only one sample from each branch was taken. This was in the form of a 5.8 mm diameter core taken from the end of the branch with a # 2 cork borer. The cores taken were long enough to penetrate the tissue on the end surface of the branch.

In P. compressa after samples were taken the tissue was removed, while in P. damicornis the samples were ordinarily dried and weighed first. Samples dried at 105° C for 1 hr gave a constant weight.

Tissue removal was by alkaline hydrolysis. Usually the sample was treated for 7 min in 5.0 ml of 0.5 or 1.0 N NaOH in a boiling water bath. (Hydrolysate was saved if a protein determination was to be made; see Chapter IV.) This was sufficient for tissue removal in the imperforate species P. damicornis, but P. compressa needed more rigorous treatment. The procedure was the same except that it was performed twice, and after each treatment it was thoroughly shaken with a Vortex Jr. Mixer. Tissue removal was followed by a thorough rinsing of the samples 2-5 times with approximately 2 ml of water. With P. compressa this was done after each treatment with the NaOH. (Monitoring of the final rinses always indicated low levels of radioactivity.) The skeletal samples were then dried.

For assay of the incorporated ^{45}Ca a Packard TriCarb Liquid Scintillation Spectrometer, Model 2002, was used. The skeletal samples were prepared for assay by being completely dissolved in 0.5 ml of 3 N HCl for the P. damicornis samples and 1.0 or 2.0 ml (depending on the length of the cores) for the P. compressa samples. Aliquots of 0.20, 0.25, and 0.50 ml respectively were taken from these solutions and put in liquid scintillation vials along with the scintillation system. This system was of two types. The first (Counting System 1), developed by Lutwak (1959) for counting ^{45}Ca samples, was composed of 4.0 ml ethyl alcohol to 6.0 ml of a 0.4% diphenyloxazole solution in toluene. Five ml of this fluid were added to each vial. The other system (Counting System 2) involved adding 4.0 ml of distilled water to the sample and 10 ml of Insta-Gel (Packard Instrument Co., Inc.). This was shaken (forming a thick gel) and counted. All coral samples were counted to 10,000 counts (except for samples of low activity which were

counted for 100 min) to give equivalent statistical accuracy for all samples. Because of high activity the sea water samples were usually counted to 50,000 counts. Final counts on each sample were corrected for background and radioactive decay.

CALCULATIONS

Most of the results were expressed in terms of the quantity of $CaCO_3$ deposited per unit of surface area per hour (ng $CaCO_3/mm^2/hr$). (The conversion of weight measurements in P. damicornis to surface area is discussed in the next chapter.) The equation

$$\text{ng } CaCO_3 \text{ (coral)} = \frac{\text{ng } CaCO_3 \text{ (sea water)}}{\text{CPM (sea water)}} \cdot \text{CPM (coral)}$$

was used to convert the relative CPM (counts per minute) to absolute ng $CaCO_3$ units. The term ng $CaCO_3$ (sea water)/CPM (sea water) is the ratio of $CaCO_3$ to CPM in the incubation sea water (sw), CPM (coral) is the activity of the coral sample, and ng $CaCO_3$ (coral) is the quantity of $CaCO_3$ deposited in the coral sample.

The sea water $CaCO_3$ concentration was calculated from standard values of Ca concentration in sea water with a salinity of 35°/oo (Culkin, 1965). This was 0.413 mg Ca/g sw giving 1.056 mg $CaCO_3$/ml sw. (It is assumed that all Ca is either in the form of $CaCO_3$ or is readily available in such form through equilibrium reactions.)

The determination of CPM (sw) and CPM (coral) was with the liquid scintillation spectrometer as already described. Sea water causes more quenching than the coral samples. In Counting System 1 the counting efficiency ratio, sea water:coral, was 0.890. In Counting System 2 it was 0.984.

SAMPLING TECHNIQUES

Sampling of the coral occurred at three points--the selection of colonies, branches within colonies, and tips or cores from the branches. The colonies used for these experiments were not a random sample of the colonies of either of the two species. Whether using Collection Method 1 or 2 the colonies used in an experiment were ordinarily the first colonies found that best fit the previously described morphological criteria.

The branches from P. damicornis colonies selected for testing were those that had a sufficient number of tips (for later sampling) and that were not obviously damaged or unhealthy. Tips were chosen for their uniformity of shape--stubby and odd shapes were avoided when possible. After studies investigating growth gradients in P. damicornis colonies (Chapter V), more careful selection was made. Branches for a given experiment were ordinarily removed from similar positions in a colony and only the most apical tips were chosen. It was hoped that this selection would decrease variability.

In P. compressa the position within the colony was not considered so important as the shape and size of the branch. This was important in obtaining cores with uniform surface areas. All cores were taken from the end of branches since side cores showed significantly lower calcification rates (see Chapter V).

LIGHT MEASUREMENTS

Downward irradiance (at the approximate position of the corals during an incubation) was determined in Incubation Systems 2 and 3 using a Spectroradiometer Model SR (Instrumentation Specialities

Company) with a remote fiber optic probe attachment. The results are plotted in Fig. 7 along with measurements made of direct sunlight (1:30-2:00 PM on August 6, 1970) and underwater at 1 m depth (A. A. Roth, personal communication). Integration of the curves from 400 mμ to 750 mμ gave downward irradiance (in $\mu w/cm^2$) of 44,000 (direct sunlight); 26,000 (underwater at 1 m); 6,700 (Incubation System 2); and 30,000 (Incubation System 3).

The wavelength of maximum intensity for Incubation System 2 (fluorescent lights) more closely coincides with sunlight than does System 3 (GE Cool-Beam lamp), but the total intensity of System 3 is more comparable to natural daytime maximum light levels. No adequate measure was made for System 1. Its intensity would have been less than either Systems 2 or 3. The optimum light intensity for photosynthesis (of the zooxanthellae) and calcification processes in corals is not known; Halldal (1968) did show saturation of oxygen production (with monochromatic light--440 mμ) at 95,000 $ergs/cm^2/sec$ (9,500 $\mu w/cm^2$) but no inhibition up to at least 225,000 $ergs/cm^2/sec$ (22,500 $\mu w/cm^2$).

Ideally the light intensity of System 2 could have been increased in System 3 by using more fluorescent bulbs rather than changing to an incandescent light. This was not done because it would have made the system too bulky for easy transportation.

CHAPTER IV

INVESTIGATION OF PARAMETERS FOR EXPRESSING CALCIFICATION

INTRODUCTION

Both field and laboratory studies of growth rates in corals lack precision because of inadequate methods of measuring and expressing growth rates. Discounting such phenomena as growth gradients within colonies (see Chapter V) calcification is probably a linear function of surface area; hence, it may often be best expressed in terms of surface area. The irregular surfaces and shapes however, make the direct measurement of surface area difficult; therefore other parameters have usually been used (Goreau, 1959). Goreau considered organic nitrogen (determined by the micro-Kjeldahl method) to be the most satisfactory.

The surface area of P. compressa was simple to measure and it was used as the parameter for expressing calcification rates in all experiments with P. compressa. For P. damicornis, however, it initially seemed that there was no adequate method for obtaining surface area directly; therefore, other parameters were investigated as possible alternative methods of expressing calcification. These were total sample weight, skeletal weight, tissue weight (total sample weight minus skeletal weight) and tissue protein weight. These weight measurements were compared with a "computed" surface area

(based on the total sample weight measurement). The method for expressing calcification was considered best that gave the least variable results.

MATERIALS AND METHODS

Folin-Ciocalteau Method for Protein Determination

A modification of the Folin-Ciocalteau method (Lowry et al., 1951) was used for protein determination. Reagents consisted of: I. 0.12% sodium (or potassium) tartrate solution made up in a 0.06% $CuSO_4 \cdot 5H_2O$ solution; II. 8.0% Na_2CO_3 solution; III. Folin reagent (1 Phenol:2 H_2O). At the time of an assay, solutions I and II were combined in equal parts to form the Protein Reagent. A protein standard stock solution was prepared from Bovine Albumin Powder (Fraction V) and had a final concentration of 200-400 μg protein/ml--depending on the preparation. During an assay this standard solution was ordinarily treated with NaOH in the same manner as the samples and three concentrations of this alkaline treated stock solution were prepared by dilution:

1 part stock solution : 4 parts water
3 " " " : 2 " "
5 " " " : 0 " "

These three dilutions were used to prepare a standard curve.

The solutions to be assayed were prepared by solution of the coral tissue through alkaline hydrolysis, and 5 ml of Protein Reagent was added to 0.5 ml aliquots of both standards and samples. Incubation for one hour at room temperature was followed by the addition of 0.5 ml of Folin reagent and immediate thorough mixing. Thirty minutes

later the optical densities of the solutions were read at 650 nm on a Beckman DU or DBG spectrophotometer. Protein concentrations for the tissue solutions were read from the standard curve.

Since prolonged treatment with strong alkali may reduce the apparent protein concentration (as measured by the Folin-Ciocalteau method), when hydrolyzing the coral tissue a sufficiently rigorous treatment to completely remove and solubilize the coral tissue was necessary, but not so rigorous as to significantly decrease the measureable protein. A treatment with 5 ml of 1 N or 0.5 N NaOH for 7 min in a boiling water bath was the typical procedure used. To verify the effectiveness of this procedure six sample tips from a P. damicornis colony were dried and weighed. Weights ranged from 11.8 to 75.1 mg. Tissue was removed with 5 ml of 0.5 N NaOH in a boiling water bath. Aliquots of the hydrolysate were removed at 4, 7, 14, and 21 min of such treatment. Standards had identical treatment. Protein assays of the hydrolysate were made.

The tissue or protein content is not necessarily an accurate indicator of surface area or an adequate parameter for expressing calcification rate, since some corals (particularly the perforate corals) have tissue that penetrates into the corallum ("internal" tissue) as well as covering its surface. The extent of this internal tissue in P. damicornis was investigated. In experiment P2 samples removed from a P. damicornis colony were dried and treated with 9 ml of 0.5 N NaOH in a boiling water bath. Ten samples were treated for 7 min, nine samples for 14 min, and seven for 28 min. Skeletal weights for each sample were determined. To expose any remaining internal tissue several of the samples from each time group were pul-

verized to a powder with mortar and pestle (see Table 6). The weights of the pulverized samples were determined and all samples were treated with 0.5 N NaOH for 10 min in a boiling water bath. After centrifugation of the powdered samples aliquots of each sample solution were removed for protein assay. In a similar experiment (experiment P3) the tissue was initially removed by mechanical abrasion (using an emery disk on a Dremel Moto Tool Model 270)--rather than by alkaline hydrolysis. The procedure for each experiment is summarized in Table 6.

Comparison of Various Parameters for Expressing Calcification Rate

Other parameters--more rapidly measured than tissue protein weight--were investigated. Measurements were made on coral samples that had been incubated in ^{45}Ca enriched sea water. In experiments P4 and P5 total sample weight, skeletal weight, dry tissue weight, and protein weight were measured; in experiment P6 only total sample weight and protein weight. All samples in P5 were from a single colony. Six sample tips from each of three colonies were used in P4 and eight samples from each of three colonies in experiment P6. Incubation procedure for each experiment is summarized in Table 5. The variability of the calcification rates expressed in terms of each of these parameters was used as the basis of comparison between the different parameters.

Estimation of Surface Area from Total Sample Weight

From these experiments (P4-P6) it seemed that total sample weight was as satisfactory a parameter for expressing calcification as any of the other methods when using samples of similar size and shape. It was noticed though that with increasing sample weight calcification rate

per unit weight decreased slightly. This could be because of growth gradient phenomena along the axis of a tip, and/or because calcification rate is a function of surface area rather than weight. The latter was investigated by developing a relation between the weight and surface area of P. damicornis samples. To do this, weight, length, and diameter measurements made by A. A. Roth (personal communication) on 304 P. damicornis coral samples were used. The idealized shape of these samples was considered to be a hemisphere (distal portion of the tip sample) plus a cylinder (proximal portion) and the surface area was calculated as:

$$\begin{aligned}\text{Surface area of sample} &= \text{Surface area of cylinder} + \\ &\quad \text{Surface area of hemisphere} \\ &= 2\pi rh + 2\pi r^2 \\ &= 2\pi r(h + r) \\ &= 2\pi rl \\ &= \pi dl\end{aligned}$$

(where r = radius of cylinder and hemisphere, h = height of cylinder, l = length of sample, and d = diameter of sample).

The relation between the surface area (as calculated by the above formula) and weight of these samples is expressed by the equation:

$$\text{Surface area} = 62.3(1.0 - e^{-0.0298 \cdot \text{weight}}).$$

This relation is shown in Fig. 8. Obviously this relation is not valid for sample sizes much beyond the range (57 mg) of the sample sizes on which it is based since surface area is not limited to 62.3 mm^2 as the equation implies. Surface area as calculated from this equation is

compared in Table 7 with the other parameters as a method for expressing calcification.

RESULTS AND DISCUSSION

Results of experiments P1, P2, and P3 are given in Table 6. A small difference between apparent protein content of the hydrolysates from the four different treatment times is seen in P1. About 95% of the maximum value is obtained after the 4 min treatment, and continued treatment beyond 7 min seems to cause a small decrease in the apparent protein content. Of the four treatment times investigated the 7 min treatment appeared the most satisfactory.

Experiment P2 also indicates that little if any additional protein is accessible (non-pulverized samples) to hydroxide treatment beyond 7 min. Since the mechanical abrasion removed only surface tissue (and hence surface protein) experiment P3 showed that most of the protein accessible in the non-pulverized samples is surface protein--the alkaline hydrolysate contained little protein when there was prior tissue removal by abrasion. Pulverizing the skeletal samples does apparently release small amounts of additional (internal) protein which may be a constituent of the organic matrix. Since surface protein in P. damicornis composes probably more than 95% of the total protein (compare protein content of P1 samples with protein content of pulverized samples in P2) and in any case the internal protein is not readily accessible to the alkaline hydrolysis, the protein content of a sample should be a reliable estimate of its surface area. In Table 7 it is compared with other parameters as a method for expressing calcification.

Table 7 gives the results for experiments P4, P5, and P6. The Coefficient of Variation [C. V. = (Standard Deviation/Mean) · 100] is used as an index of the suitability of a parameter. The results indicate that the particular parameter used makes relatively little difference in the C. V. values. This evidently results from growth rate gradients existing along the axis of a tip sample. Growth occurs so much more rapidly in the distal (hemispherical) portion of the tip than in the proximal (almost cylindrical) portion that $CaCO_3$ deposition occurring in the cylindrical portion has relatively little effect on the total calcification rate of the tip. Thus the size (weight or surface area) of the tip--as long as the fast growing distal portion is completely included--is not of major significance in determining the amount of $CaCO_3$ deposited. The growth gradient masks the effect that size has on the quantity of $CaCO_3$ deposited per tip. Since the choice of a parameter makes relatively little difference in the C. V. values the variability of the results appears not to be an artifact of the method of expression but rather an inherent property of the coral. This agrees with the results of Goreau (1959) who got similarly high variability using protein nitrogen as the method of expression.

In the following experiments calcification rate results for P. damicornis experiments will be expressed in terms of the "computed" surface area. The C. V. values for "Surface Area" were as low as, if not slightly lower than, for any of the other parameters, and it made comparisons between P. damicornis experiments and P. compressa experiments convenient if both were expressed in terms of surface area. Goreau (1959) expressed calcification rate in μg Ca/mg N/hr units. To compare his values with my results, values expressed in ng $CaCO_3/mm^2/hr$

units can be converted approximately to μg Ca/mg N/hr units by dividing by 4 for P. damicornis and by 60 for P. compressa. There is approximately 1.5 μg N/mm^2 in the P. damicornis samples and 24 μg N/mm^2 in P. compressa samples, assuming that the nitrogen weight is 16% of the total protein weight. The typically lower rates of calcification obtained by Goreau probably resulted from his larger sample sizes (100 mg vs. approx. 15 mg) and longer incubation periods (see Chapter V).

CHAPTER V

ESTIMATION OF GROWTH RATES FROM CALCIFICATION RATES

INTRODUCTION

Errors introduced by the laboratory situation could result in misleading calcification rates and inaccurate estimates of growth rates. They might be caused by changes in the intrinsic (or real) calcification rate due to handling or by abrupt (and possibly unsatisfactory) changes in the growth environment on transfer to the laboratory. Growth gradients within a coral colony, ^{45}Ca deposition through inorganic exchange, and inappropriate methods of expressing calcification (discussed in Chapter IV) may cause errors in the apparent calcification rates or in growth rates derived from them. Diurnal fluctuation in calcification rate is an additional potential source of error when estimating long-term growth rates from short-term calcification rates. Practically, knowledge of diurnal fluctuations is also necessary if incubations are to be performed at several times of the day.

MATERIALS AND METHODS

To investigate changes that occur in the intrinsic calcification rate due to the experimental method the correlation between $CaCO_3$ deposition and incubation time was examined. Degree of linearity of a rate-time curve should provide information on the magnitude of any

change that occurs in the intrinsic calcification rate during an incubation. Four experiments were performed. In the first (experiment L1), rates in samples removed (from branches of a P. damicornis colony) at various incubation times (from 1 to 24 hours) were compared. Experiment L2 was similar. Calcification rates in P. compressa samples taken at different incubation times (from 5 to 60 min) were compared to see if any initial lag in ^{45}Ca incorporation might be observed. In experiments L3 and L4 the corals were exposed to a sudden stress or drastic change in environmental conditions at the commencement of the incubation. The effect of this stress was observed in the calcification rate of samples taken at different incubation times. The stress in experiment L3 was the sudden exposure to light of branches of P. compressa which had been kept in the dark for 8 hours (6:30 PM-2:40 AM) previous to the incubation. In L4 the stress (using P. damicornis) consisted of an immediate increase of 6°C from the reef temperature to the incubation temperature.

Unless the living coenosarc forms an effective barrier to exchange, ^{45}Ca deposition by inorganic exchange may produce apparent calcification rates that are greater than the real rates since ^{45}Ca may be deposited in the corallum without net growth occurring. The amount of exchange across both the living and dead coenosarc was studied. The quantity of exchange across the living coenosarc was investigated by initially incubating (calcification incubation) the coral in ^{45}Ca enriched sea water (3.0 hr incubation in E1; 0.5 hr in E2). At the termination of this incubation some corals were removed as samples (controls) and the rest were transferred to a vessel containing non-radioactive sea water for a second incubation (exchange incubation).

^{45}Ca content of the samples taken after the exchange incubation was compared with that of the control samples.

Exchange across the dead coenosarc was examined by initially killing the coral in cold water--at least 0.5 hour at 5°C or colder. According to Edmondson (1928) this is sufficient to kill these coral species. The dead coral was transferred to an incubation vessel containing radioactive sea water. Branches were removed and samples taken after 0.5 hour of incubation.

Growth gradient experiments involved comparing calcification rates in samples removed from several positions within a colony or along a branch. Within branches of P. compressa, gradients were examined (experiment G1) by comparing calcification rates in core samples taken from the side of a branch (Position I) with rates in core samples taken from the end of a branch (Position II). Four types of sampling positions within P. damicornis colonies were designated: Type IA--lateral tips from peripheral branches (i.e., branches around the outside margin of a colony), Type IB--terminal tips from peripheral branches, Type IIA--lateral tips from central branches, Type IIB--terminal tips from central branches. In experiment G2 calcification rates of samples removed from each of these four positions were compared.

Diurnal changes in calcification rate were studied by comparing rates obtained during incubations at various times of the day. Identical 0.5 hour incubations of P. damicornis were performed in duplicate (on consecutive days) at 9:00 AM, 12:00 noon, and 3:00 PM in experiment D1. In experiment D2 0.5 hour incubations under conditions of both light and dark were performed at both noon and midnight. An incubation vessel darkened with black paint and tape was used for the dark incubations. For all incubations the corals were maintained under

ordinary natural light conditions until the incubation. No period of acclimation prior to the incubation was provided. Corals in the dark incubation at noon and the light incubation at night were suddenly exposed to new light conditions at incubation commencement. Corals used in the dark midnight incubation were protected from light when transferred to the incubation vessel and throughout the incubation.

With P. compressa light and dark incubations at night were performed (experiment D3). Six branches were used in the dark incubation, three in the light. All branches were from the same colony. The dark incubation was from 12:40 AM to 1:10 AM, the light incubation from 2:40 AM to 3:10 AM. Otherwise the procedure was the same as that for the dark and light midnight incubations of P. damicornis (experiment D2).

RESULTS AND DISCUSSION

Results of experiments L1-L4 are given in Figs. 9-12 respectively. All experiments show at least a small change in calcification rate with incubation time (positive or negative slopes of the dashed lines) but only in the case of L1 is this change (slope $\neq 0$) statistically significant ($P < 0.001$). At 24 hours the calcification rate (as read from the regression line) was only about 1/4 of its one hour value. Apparently a reduction of calcification rate may occur during long incubation periods under laboratory conditions. Some of Goreau's (1959) results showed a similar reduction. The reason may be pH changes in the incubation water, waste product buildup, reduced oxygen tension, or unsatisfactory circulation, light, and temperature conditions.

In short incubations there is no indication of a decrease in rate with time nor of an initial lag in ^{45}Ca deposition, in P. compressa

(Fig. 10). In another experiment (not further discussed) similar results were obtained with P. damicornis. This evidence indicates that the ^{45}Ca is transported very rapidly (within one minute) across the coenosarc and deposited in the skeleton, thus making very short incubations feasible--and preferable to the long incubations.

The absence of any apparent effect of "light" stress on calcification rate in P. compressa (experiment L3, Fig. 11) agrees with other data (Goreau, 1959) that indicate the independence of calcification rate from light in this species. In experiment L4 (Fig. 12) no overshoot artifact due to the application of high temperature stress was obvious, though it has been reported for other organisms (Grainger, 1958). Any anomalies due to temperature stress if present were either masked by the variability of the results or occurred so rapidly that their results were not apparent.

The results of the exchange experiments are given in Table 8. The exchange rate values for experiments E2-E5 are based on results of 0.5 hour exchange incubations. In E1, however, the exchange rate is an estimate, read from a regression line, based on samples (67 samples altogether) taken over a period of eight hours. (This was necessary because the variability of the samples was such that by itself the 0.5 hour incubation was not meaningful.) For those experiments involving exchange across the live coenosarc the values given under "Calcification Rate" are the rates obtained during the calcification incubation (controls). The "Exchange Rate" is the observed reduction (from this calcification rate) that occurred in the experimental samples during the exchange incubation. In neither case, however, was the reduction statistically significant ($P < 0.25$ for E1; $P < 0.75$ for E2).

The calcification rates given for the rest of the exchange experiments were rates obtained during other experiments but under incubation conditions similar to those of the exchange incubation with which they are compared. Probably experiment E4 gives the most reliable value for exchange across the dead coenosarc in P. damicornis. In this experiment the same colonies were used to obtain both the calcification and exchange rate. The results agree with the work of Goreau and Goreau (1960b) on other species. They showed that while considerable exchange occurred in bare coral skeletons and across the dead coenosarc, it is slight across the living coenosarc. No corrections for inorganic exchange were deemed necessary in any of the following experiments.

The growth form of a coral colony indicates the nature of the growth rate gradients existing within the colony. A branched colony should have the highest growth rate at the tip of a branch; in fan, leaf-shaped, or encrusting colonies, the greatest rates are around the periphery of the colony; and massive or spheroidal colonies should show little or no growth rate gradients. The growth rate gradient experiment (G1) using P. compressa does show a difference ($P < 0.005$) between the calcification rate of sample cores taken from the end of a branch as opposed to cores taken from the side (Table 9). End cores calcified five times more rapidly than the side cores. In P. damicornis (experiment G2) no significant difference ($P < 0.25$) was observed between calcification rates in sample tips removed from peripheral branches and those removed from central branches (i.e., IA and IB vs. IIA and IIB), but a difference ($P < 0.0005$) did exist between the lateral sample tips and the terminal tips (IA and IIA vs. IB and IIB,

see Table 10). Samples from the terminal position calcified almost six times as rapidly as those from the lateral position.

Diurnal fluctuations in calcification rate in P. damicornis are summarized in Tables 11 and 12. In experiment D1 variability tends to mask any changes in calcification rate that may occur from 9:00 AM to 3:00 PM (Table 11). There was a tendency ($P < 0.10$) towards a decrease in rate from 9:00 AM to 3:00 PM. Since this experiment was done, work by J. Vandermeulen (personal communication) has verified this interpretation, and A. A. Roth (personal communication) has shown similar diurnal fluctuations in Acropora. In experiment D2 (Table 12) there was a difference ($P < 0.0005$) between rates at noon and midnight, those at noon being twice as rapid as those at night. The difference between light and dark calcification rates was not significant ($P < 0.25$).

There was no significant difference ($P < 0.90$) between dark and light incubations at night in P. compressa (1680 $\pm$ 150 ng $CaCO_3/mm^2/hr$ $\pm$ SEM for the dark incubation compared with 1739 $\pm$ 108 for the light incubation). Neither did the difference between these night rates and the day rates appear significant. P. compressa is evidently more independent of the daily cycle and the light conditions than is P. damicornis.

Except for the diurnal fluctuations in rate in P. damicornis no significant errors appear to be introduced by the laboratory situation if the incubation period is short and if samples are removed from appropriate positions within the colony or branch. It should be possible then with appropriate calculations to estimate coral growth rates from the calcification rates. The calculations are simple for P. compressa. Density of the P. compressa skeleton is 1 mg/mm^3 or 1 mg $CaCO_3/mm^3$

assuming that the skeleton is composed only of $CaCO_3$. Using 2250 ng $CaCO_3/mm^2/hr$ as a typical calcification rate for an end core sample from a branch of P. compressa (see Table 9) the growth rate of that branch is calculated as:

$$\text{Growth Rate} = \frac{2.25 \times 10^3 \text{ ng } CaCO_3/mm^2/hr}{1.0 \times 10^6 \text{ ng } CaCO_3/mm^3}$$

$$= 2.25 \times 10^{-3} \text{ mm/hr}$$

$$= 19.7 \text{ mm/yr}$$

At the same time the laboratory experiments were being done, natural growth rates of 23 branches on five different colonies of P. compressa in Kaneohe Bay were measured using a method developed by Shinn (1966). The rates obtained for the individual branches during the four months of the study ranged from 8-33 mm/yr. The mean was 24 mm/yr. Previously obtained values for natural growth rates in branched Porites (Table 2) give comparable results. The growth rate of 19.7 mm/yr estimated from the calcification rate appears to be in good agreement with the natural growth rates.

Similar calculations can be made for P. damicornis. Calcification rates of P. damicornis must first be converted so that they are expressed in terms of the cross-sectional area of the sample tip rather than in terms of the surface area. A typical rate of calcification obtained with Incubation System 3 (rates obtained when using this system were 2-3 times higher than in Incubation System 2) at incubation temperatures of 25°C-27°C was 500 ng $CaCO_3/mm^2/hr$ (where mm^2 is surface area). Surface area averaged about 18 mm^2 per tip and cross-sectional area is

estimated at approximately 3 mm^2. Calcification rate in terms of the cross-sectional area would be:

$$\text{Calcification Rate} = (500 \text{ ng } CaCO_3/mm^2/hr) \cdot \frac{18 \text{ } mm^2}{3 \text{ } mm^2}$$
$$= 3.0 \times 10^3 \text{ ng } CaCO_3/mm^2/hr$$

Density of the P. damicornis skeleton is 1.7 mg/mm^3 or approximately 1.7 mg $CaCO_3/mm^3$. The growth rate is calculated as:

$$\text{Growth Rate} = \frac{3.0 \times 10^3 \text{ ng } CaCO_3/mm^2/hr}{1.7 \times 10^6 \text{ ng } CaCO_3/mm^3}$$
$$= 1.76 \times 10^{-3} \text{ mm/hr}$$
$$= 15.4 \text{ mm/yr}$$

If growth rate at night is 1/2 of its day value (experiment D2):

$$\text{Growth Rate} = 2/3 \cdot 15.4 \text{ mm/yr}$$
$$= 10.3 \text{ mm/yr}$$

This value is somewhat low compared with P. compressa or with previous measurements on growth rates in P. damicornis (Table 2). Edmondson (1929) got 14 mm/yr based on six samples from Hawaii. Mayor (1924) got somewhat higher values in Samoa. Nonetheless the calcification rates obtained in the laboratory for both P. compressa and P. damicornis do give reasonably good estimates of the natural growth rates.

CHAPTER VI

TEMPERATURE AND CALCIFICATION RATE

INTRODUCTION

Observations on the distribution of hermatypic corals have long suggested a relation between temperature and the distribution or luxuriousness of reefs (Vaughan, 1919). Although some hermatypic coral species can survive short exposures to low temperatures (Mayer, 1914, 1918; Edmondson, 1928) and some coral head patches or patch reefs may form at colder temperatures (Yabe and Sugiyama, 1932; MacIntyre and Pilkey, 1969), vigorous reef formation does not occur in areas where the minimum annual temperature drops below 18°C (Wells, 1957a). The maximum endurable temperature has usually been considered as approximately 36°C (Wells, 1957b), but it varies with species (Edmondson, 1928; Mayer, 1914), and under certain conditions it may be somewhat higher (Kinsman, 1964).

Several components may be responsible for the effect of temperature on coral distribution. It may result from a direct effect on the rates of physiological processes. In this way it could affect reproduction (Yonge, 1940), feeding responses (Edmondson, 1928), and calcification. A second way it might affect calcification is through its effect on the solubilities of CO_2 and $CaCO_3$. Relatively little is known about the effect of temperature on the rate of physiological processes in coral. Field observations (Shinn, 1966) and growth ring

annulations (Ma, 1937) have shown that temperature does affect growth rate. Only recently (Cox, 1971; Clausen, 1971), however, have any controlled laboratory experiments been performed.

Even less is known about temperature adaptation in corals, although it may be assumed from their distribution pattern that they do not adapt well to different temperature regimes (particularly low temperatures). Mayer (1918) did observe that in general those corals taken from warm water (Samoa) resisted hot water no better than, and tolerated cold water as well as, those taken from cooler water (Florida). However, according to Mayer (1914) the degree of resistance of a particular coral species to extreme temperature is correlated with its microhabitat, while Edmondson (1928) showed no such correlation with habitat.

Because of the obvious importance of temperature in the distribution of hermatypic corals it seemed significant to examine the effect of temperature on physiological rate processes. The calcification process was chosen because of the basic importance of $CaCO_3$ deposition in reef formation.

MATERIALS AND METHODS

Five temperature experiments were done using P. damicornis and two with P. compressa. Table 5 summarizes the materials and methods used. Each experiment contained from 5 to 12 different incubations representing as many different temperatures. Because of limitations of equipment only one incubation (at one temperature) could be performed each day. That meant that with Collection Method 1 (experiments T1 and T4) different colonies were used for each temperature

of an experiment (nested design). Thus, in experiments T1 and T4 the three colonies used at one incubation temperature were not the same as those used at another temperature. With Collection Method 2 all incubations within one experiment were on the same colonies.

In experiment T1 samples were removed at three different incubation times. To do this, a branch was taken from the incubation vessel, sample tips rapidly removed, and the branch returned to the vessel for further incubation.

The incubation temperatures are given in the graphs of the results. The sequence of temperatures used for each experiment was randomized using random number tables. This was done to avoid possible correlation of the results with any uncontrollable natural environmental variables (e.g., moon phase, and changes in natural water temperature), unconscious changes in technique, or selection of coral colonies or branches.

The experiments were performed at several different times of the year and (for P. damicornis) at different geographical localities (Hawaii and Eniwetok). The natural surface water temperature at the time and locality of collection is indicated for each experiment in Fig. 13.

RESULTS

The calcification rates are given in Fig. 14 for P. damicornis and in Fig. 15 for P. compressa. Only the results of 0.5 hour incubations are plotted. In experiment T1 incubations were for 1.0 hour and 1.5 hours as well (Table 13). In Figs. 14 and 15 and in Table 13 the large standard errors represent variation both between colonies and between replicates within colonies.

The calcification rates observed in experiment T1 are much lower (Fig. 14) than in the other P. damicornis experiments. This might be a result of the different counting procedure (see Chapter III), the larger size used (surface area averaged 33 mm^2, vs. 18 mm^2 in the other temperature experiments), or the different incubation system. Appropriate corrections should have eliminated the difference in counting procedure as a source of error. The difference in size could significantly reduce the apparent calcification rate if calcification occurs only or mainly in the distal hemispherical portion of a sample tip (see Chapter IV). The major difference in the incubation system involved the type, intensity, and position of the light source (see Chapter III) and this may be responsible for the low values.

The interpretation of the results depends on an analysis of variance (anova) study. The main objectives of this analysis were: 1) to compare responses (rates) at different temperatures, 2) to define and localize "peaks" or temperature optima, and 3) to compare responses of coral populations with different histories (the temperature history, which differed due to season and/or location, is the immediate concern, but other aspects cannot be eliminated). To reduce the differences between the variances (an assumption of anova is that variances are equal) the logarithms of the data were used. The fixed effects anova model (Model I, see Steel and Torrie, 1960) was used for all comparisons; hence, inferences can be made only for the particular temperatures, colonies, etc., used in an experiment.

An anova was performed separately on each temperature experiment. In all experiments there was a significant difference in calcification rates between temperatures ($P < 0.0005$). Ordinarily a difference (at

least $P < 0.05$) between colonies was found. No significant difference between lengths of incubation time ($P < 0.10$) was found in T1. Significance of the colony x temperature interaction was tested in those experiments where the same colonies were used at all temperatures. It was not significant ($P < 0.1$ for T6; $P < 0.25$ for T7) for either of the P. compressa experiments but was significant ($P < 0.0005$) for all the P. damicornis experiments (T2, T3, and T5). The significant interaction term means that the curves of the individual colonies did not agree closely with each other.

An anova study within each temperature of T1 (treatments = times, blocks = colonies) was also made. These P values are given in Table 13. Typically there is a reduction of calcification rate with increasing incubation time but this is significant (sixth column) only for the more extreme temperatures. This may result either from an adjustment of the coral to the new temperature (not completed during the 1.0 hour acclimation period) or--more likely--from deterioration of the coral physiology perhaps leading eventually to death.

Within each of the temperature experiments one or more "peaks" or maxima are present. Some are prominent while others are little more than plateaus. A multiple comparisons test--Duncan's New Multiple Range Test (Duncan, 1955; Steel and Torrie, 1960)--is used to define and localize the significant maxima, i.e., those maxima which result from other than colony and replicate variation.

Figs. 16 and 17 give the results of this test. From these results each maximum can be given a temperature range which includes all temperatures immediately to either side of the apparent temperature optimum whose rates are not significantly different from the rate at the

apparent maximum. Those rates not significantly different from the apparent maximum but separated from it by rates that are significantly different are not included. Any two maxima so separated are assumed to be two discrete maxima.

Temperature ranges of maxima so defined are given in Table 14. Two fairly discrete regions of optimum temperature exist, one centering around 27°C the other around 31°C, one or the other being dominant depending on the natural water temperature to which the coral is adapted. No maxima were separable in this fashion in experiment T4, although inspection of the graph (Fig. 14) suggests maxima in these same two temperature regions.

These results suggest that coral populations with different histories respond differently to temperature. To verify this an anova study was done between experiments performed at different seasons or localities. In this analysis T2, T3, and T5 of the P. damicornis experiments were used (it was not feasible to use experiments with the nested design, i.e., T1 and T4). Both of the P. compressa experiments were used. A number of different comparisons were made (Table 15). For each comparison only data from temperatures used in all experiments being compared were included.

The anova results are given in Table 15. The P values of importance are those for "History" and "History x Temperature" interaction. A significant P value for "History" indicates a significant difference between the mean responses (mean of calcification rates at all temperatures given) of corals with different histories. Significant "History x Temperature" interaction indicates in addition a difference in slopes--

between histories--of the lines connecting the mean rates at different temperatures, i.e., a greater history response at one temperature than at another.

For P. damicornis both the "History" difference and "History x Temperature" interaction are significant in Comparison I. Evidently this is a result mainly of the significant difference occurring at the higher temperatures (Comparison III) since no difference is shown from 25°C to 29°C (Comparison II) for either "History" (mean rates) or "History x Temperature" interaction (slopes). That is, in the temperature region of the 27°C optimum no difference is shown between Hawaii and Eniwetok. At the higher temperatures significant differences are indicated for all comparisons (III, IV, V); however, no Hawaii summer experiment is available for contrast. Experiment T4 (Fig. 14) suggests that during summer in Hawaii the response to temperature may be quite similar to Eniwetok.

P. compressa showed a marked reduction in mean calcification rate (note "History" for Comparison VI, Table 15) between summer and winter experiments, but the two temperature optima are less obvious (reflected in the less significant P value for "History x Temperature" interaction, Comparison VI) than in P. damicornis. This is perhaps an artifact resulting from too few sample temperatures.

Q_{10} is often used in expressing the results of temperature experiments. In these experiments the presence of the two optima and the variability of the results make Q_{10} values less meaningful and more difficult to calculate. The Q_{10}'s for those temperature ranges that seemed most significant in the interpretation of the results are given in Table 16. From the lower temperatures up to 27°C the trend (in P.

damicornis experiments) is increasing Q_{10}'s with increasing natural water temperature. Likewise, from the 31°C optimum to higher temperatures (T3 and T5) the Q_{10} increases (here signifying a decreasing slope) with increasing natural water temperature.

Although the data for P. compressa are not as conclusive, the results indicate that it as well as P. damicornis may have two optimum temperatures. The calcification rate for P. compressa is several times greater than for P. damicornis; however the effect of temperature on the calcification rate of P. compressa is apparently less (in Table 16 compare experiment T7 with experiments T1 and T2 over the 17°C to 27°C range). The low rates obtained in the winter suggest that P. compressa does not adapt as well to low temperatures as does P. damicornis.

DISCUSSION

The optimum temperature range given for the formation of coral reefs is 25°C to 29°C (Wells, 1957b). Using annual growth lines Ma (1937) showed an increase in growth rate with temperature at least up to 27°C. Shinn (1966) reported fastest growth in Acropora cervicornis at 28°C to 30°C--both higher and lower temperatures retarded growth.

From laboratory studies in Hawaii, Cox (1971) obtained an optimum temperature of 30°C for Montipora verrucosa. L. H. Fisk (personal communication) in Eniwetok showed an optimum at 31°C to 33°C for Acropora formosa. Preliminary studies in Hawaii (Clausen, 1971) showed a temperature optimum at approximately 25°C for P. damicornis. The more recent work reported here suggests that it is closer to 27°C and that a second optimum may occur at 31°C. P. compressa shows a

similar pattern. These laboratory studies suggest a possibly higher temperature optimum than has previously been accepted.

Since the optimum temperature range reported here was based on the study of a single physiological process using a very short incubation period it may not represent an optimum for physiological processes in general or over longer growth periods. Corals kept on a water table may die after long exposure (several weeks) to 31°C (P. Jokiel, personal communication). Edmondson (1928) reported the death of P. damicornis (called by him P. cespitosa) after 60 min exposure to 35°C and after 5 hr at 32°C. P. compressa was dead after 8 hr at 32°C. However the experimental situation under which these results were obtained may not reflect the natural situation either. Edmondson in his study evidently did not take into consideration the natural temperature regime to which his corals were adapted. Kinsman (1964) has found corals growing in the Persian Gulf in areas where the water temperature at times exceeds 40°C. Corals adapted to high temperatures may be able to survive considerably higher temperatures than previously recorded.

Adaptation to a changing environmental component (such as temperature) may be short-term (phenotypic adaptation--applied to an individual organism) or long-term (genotypic adaptation--applied to a population). The former would be induced by daily and seasonal changes in the environment, the latter by geographic or latitudinal environmental changes. During adaptation the rate-temperature curve may be translated (to the right or left, or up or down) or rotated (clockwise or counterclockwise). Thus the optimum temperature, the rate at the optimum temperature, and the Q_{10} may be altered.

The significant History x Temperature interaction indicates that adaptation occurs in both coral species. In P. damicornis the existence of a counterclockwise rotation (increasing Q_{10}) of the rate-temperature curve (from lower temperatures up to the 27°C optimum) in going from cold to warm adapted coral colonies is indicated (experiments T1, T2, T4, and T5 in Table 16). In the higher temperature range (from 27°C to higher temperatures) there is both a discrete shift in optimum temperature and a counterclockwise rotation of the rate-temperature curve when going from cold to warm adapted corals. The counterclockwise rotation (increasing Q_{10}) can be observed (in Table 16) when comparing T1 and T2 (from 27°C up in experiments without the 31°C optimum) and T3 and T5 (from 31°C up in experiments with the 31°C optimum). Because of insufficient data the nature of adaptation in P. compressa is not as obvious. A discrete shift in optimum temperature may occur--further conclusions are unwarranted at this point.

Although a shift in the rate-temperature curve (translation) is a usual method of adaptation, a discrete shift of the temperature optimum is unusual. Isoenzymes may be involved. Baldwin and Hochachka (1970) found two acetylcholinesterases (isoenzymes) in the trout Salmo gairdnerii. The "warm" variant of the enzyme is found in warm adapted trout and it functions optimally at 17°C, whereas the "cold" variant is found in cold adapted trout and functions best at 2°C. There is a temperature-dependent transition of the enzyme between the two variants.

A comparable system in P. damicornis would require two enzymes that function most efficiently at 27°C and 31°C respectively. The

optimum temperature for each enzyme would be sharply defined, thus giving discrete maxima. At moderate natural water temperatures both enzymes would be present and two maxima would be observed. At extreme natural water temperatures only a single enzyme and maximum would be present.

Multiple metabolic pathways sometimes exist for performing the same function. Discrete shifts in metabolic processes might result from two such pathways that function optimally at two different temperatures. Either with isoenzymes or alternate pathways enzymes with different temperature maxima are involved.

It cannot be stated from the results exactly how long it takes for these corals to adapt to a new temperature regime. It is probably several weeks (compare T3 with T2 in Figs. 13 and 14). Short-term adaptation usually occurs in days or weeks (Prosser, 1958). In these experiments long-term changes in natural water temperature due to geographic location (experiment T5) have effects comparable to the short-term seasonal natural water temperature changes. From these data the effects of genotypic adaptation cannot be separated from those of phenotypic adaptation.

Low temperature is an obvious limiting factor in coral distribution. High temperature, however, may only rarely be limiting in the present oceans if the 31°C optimum is generally valid. However, calcification rates obtained at 31°C are not much greater than those at 27°C. While the corals may survive (and thrive) at high temperatures the growth rate is not greatly enhanced. On the other hand, if the ocean temperature were to remain close to <u>either</u> of the two optima, reef formation might be somewhat faster than it commonly is.

In the past an equatorial belt may have existed where the water regularly exceeded 30°C. Unless corals can adapt to higher temperatures than those represented in T5 such high water temperatures would be deleterious to coral growth and reef formation. The absence of Paleozoic reef corals (not the same as present reef corals) from the tropics has in fact been attributed to excessive water temperatures (Cailleux, 1951).

The present existence of corals in areas of uncommonly high temperature (Persian Gulf and Red Sea), though, suggests that tolerance to high temperatures (>32°C) may develop. Corals from these areas should be studied to provide a complete picture of adaptation to high temperatures.

CHAPTER VII

SUMMARY AND CONCLUSIONS

From field studies various environmental factors are known to affect the growth of corals. Only recently though has a laboratory method been developed which permits a quantitative study under controlled conditions. Corals are incubated for short periods of time in sea water containing ^{45}Ca. The rate of ^{45}Ca incorporation is used as a measure of calcification rate. This method has the disadvantage of study under the unnatural laboratory conditions but appears to be the most practical quantitative approach.

Temperature affects coral distribution. It also affects rates of physiological processes. Little attention has been given to the relation between coral distribution and effect of temperature on reaction rates. Using the laboratory method mentioned above I studied the effects of temperature on calcification rate in the two species of coral P. damicornis and P. compressa. $CaCO^3$ deposition was chosen because of its basic importance in reef formation. Immediate effects of temperature on calcification rate were studied, as well as temperature adaptation to seasonal and geographic changes in natural water temperature. The results can be summarized as follows:

1. Growth rates (calculated from the calcification rates) obtained in the laboratory during short incubation periods were comparable to those obtained in the field. This

suggests that the laboratory method is adequate to provide reliable data on calcification processes.

2. Significant errors may be introduced during long incubations (significant decrease in rate with time), but very short incubations (even less than 15 min) are feasible. No apparent lag in ^{45}Ca deposition was observed at the commencement of an experiment.
3. Inorganic exchange of ^{45}Ca across the living coenosarc was not significant.
4. A significant difference in calcification rate occurred between samples taken from different positions along a coral branch. For both species, samples from terminal (distal) positions calcified several times more rapidly than samples from lateral positions.
5. The calcification rates obtained for P. damicornis seemed relatively independent of any size parameters (surface area, weight, etc.) of the samples. This probably is a result of growth gradient phenomena.
6. In P. damicornis no significant difference was observed between rates obtained at 9:00 AM, 12:00 noon, and 3:00 PM. However, rates obtained at 12:00 noon and 12:00 midnight were significantly different.
7. Temperature has a marked effect on the rate. This effect varies depending on the history of the coral (i.e., temperature adaptation occurs). P. damicornis showed both a 27°C and a 31°C optimum temperature--one or the other being dominant depending on the natural water temperature to which

TABLE 1

Annual increase in diameter of different corals at several locations as reported by various investigators. All growth rates have been converted to mm/yr units. The number of samples on which the values are based is given in parentheses.

Coral	Edmondson, 1929 Hawaii	Stephenson & Stephenson, 1933 Great Barrier Reef	Vaughan, 1916 Bahamas & Tortugas	Mayor, 1924 Samoa	Lewis et al., 1968 Jamaica	Tamura & Hada, 1932 Yap & Palau
Acropora spp.		102 (35)	54 (77)	79 (35)		
A. cervicornis			52 (27)			
A. hyacinthus		145 (1)		110 (8)		
A. digitifera						11 (15)
A. palmata			61 (32)			
Porites (branched)			26 (207)	44 (5)		
Porites (massive)		23 (5)	13 (120)			
Porites porites[a]			20 (126)			
P. lutea				34 (19)		6 (9)
Pocillopora				41 (14)		6 (6)
P. damicornis[b]		69 (13)		47 (10)		
Montipora verrucosa						7 (10)
Fungia	14 (38)	7 (2)		17 (1)		6 (9)
Montastrea annularis[c]			8 (120)		24	

a Called by some authors *Porites clavaria*.
b " " " " *Pocillopora cespitosa* or *P. bulbosa*.
c " " " " *Orbicella annularis*.

TABLE 2

Annual increase in height of different corals at several locations as reported by various investigators. All growth rates have been converted to mm/yr units. The number of samples on which the values are based is given in parentheses.

Coral	Edmondson, 1929 Hawaii	Vaughan, 1916 Bahamas & Tortugas	Mayor, 1924 Samoa	Lewis et al., 1968 Barbadoes	Lewis et al., 1968 Jamaica	Tamura & Hada, 1932 Yap & Palau
Acropora spp.		35 (42)	27 (35)			
A. cervicornis		42 (18)		144	264	122 (24)
A. hyacinthus			40 (8)			
A. palmata		27 (18)				
Porites (branched)	7 (35)	19 (106)	30 (5)	36	36	19 (10)
Porites (massive)	9 (21)	7 (44)				
Porites porites[a]		19 (67)		36	36	
P. lobata	8 (12)					
Pocillopora spp.			28 (13)			
P. damicornis[a]	14 (6)		28 (10)			
Montipora verrucosa	14 (1)					
Fungia			3 (1)			
Montastrea annularis[a]		6 (47)		24	24	

[a]See footnotes for Table 1.

TABLE 3

Annual increase in weight (%) of different corals at several locations as reported by various investigators. The number of samples on which the values are based is given in parentheses.

Coral	Edmondson, 1929 Hawaii	Vaughan, 1916 Bahamas & Tortugas	Mayor, 1924 Samoa	Boschma, 1936 Bay of Batavia	Tamura & Hada, 1932 Yap & Palau
Acropora spp.			375 (15)	390 (9)	79 (33)
A. hyacinthus			293 (5)		
A. digitifera				121 (2)	90 (15)
A. palmata		134 (5)			
Porites (branched)	84 (29)		360 (4)	130 (3)	116 (10)
Porites (massive)	57 (24)		49 (5)	84 (3)	56 (9)
P. lobata	64 (15)			131 (1)	
P. compressa				159 (1)	
Pocillopora spp.			194 (8)	132 (4)	61 (6)
P. damicornis[a]	125 (12)		270 (5)	73 (1)	
Montipora verrucosa	60 (8)				23 (10)
Fungia	21 (3)		37 (1)		16 (9)
Montastrea annularis[a]		36 (5)			

[a]See footnotes for Table 1.

TABLE 4

Estimates of the rate of reef formation. All values have been converted to mm/yr units. For additional explanation of the basis of the estimates see text.

Basis of Estimate	Estimate (mm/yr)	Investigator	Location
Coral Growth Rate			
Montastrea annularis[a]	7	Vaughan, 1916	Golding Cay, Bahamas & Tortugas, Florida
Acropora palmata	25.4	"	Golding Cay, Bahamas
Acropora (arborescent spp.)	3.0	Guppy, 1889	Cocos-Keeling Atoll
Porites (branched)	9.1	"	"
Porites (massive)	9.1	"	"
Montipora (branched)	10.7	"	"
Stylophora & *Pocillopora*	5.2	Gardiner, 1901	Fiji
Acropora	18.3	Mayor, 1924	Samoa
Porites (branched)	7.6	"	"
Porites (massive)	16.8	"	"
Montastrea annularis	8.5	Hoffmeister & Multer, 1964	Key Largo Key, Florida
Coral Growth Rates Averaged	3.0	Guppy, 1889	Cocos-Keeling Atoll
"	30.5	Gardiner, 1903	Maldive & Laccadive Archipelagoes
Est. at 9-27 m	45.7	"	"
Coral Growth Rates Averaged	8	Mayor, 1924	Samoa
"	<14.0	Ladd, 1961	Reefs in general
"	16.0	Odum & Odum, 1955	Eniwetok

[a]Called *Orbicella annularis* by Vaughan.

TABLE 4 (Continued)

Basis of Estimate			Estimate (mm/yr)	Investigator	Location
Soundings					
Reef Depth	<3 meters		47.0	Verstelle, 1932	Togian Islands
" "	3-5 "		103.0	"	"
" "	>5 "		146.0	"	"
" "	<3 "		41.1	"	Bight of Tomini
" "	3-5 "		65.2	"	"
" "	>5 "		98.3	"	"
" "	<3 "		17.0	"	Kei Islands
" "	3-5 "		14.0	"	"
" "	>5 "		55.0	"	"
Terrace Depth			1.1	Emery et al., 1954	Eniwetok, Rongelap & Bikini Atolls
Carbon Dating			>3.8	"	Bikini Atoll
Organic Production			14	Sargent & Austin, 1949	Rongelap Atoll

TABLE 5

A summary of the procedures used in the experiments described in later chapters.

Exp.	Chapter	Date	Organism	Collection Method	Incubation System	Acclimation Time (min)	Incubation Time (min)	Temperature (°C)	Counting System
P3	IV	Jan 21, 1970	P. damicornis	1	2	60	30	27	1
P4	IV	Feb 9, 1970	"	1	2	0	a	27	2
P5	IV	Jul 23, 1970	"	1	3[b]	42	30	27.4	2
L1	V	Feb 9, 1970	"	1	2	0	a	27	2
L2	V	Sep 7, 1970	P. compressa	2	3	0	a	26.9	2
L3	V	Oct 14, 1970	"	2	3	0	a	26.5	2
L4	V	Oct 22, 1970	P. damicornis	1	3	0	a	31.2	2
E1	V	Mar 8, 1970	"	1	2	a	a	a	2
E2	V	Oct 7, 1970	P. compressa	2	3	a	a	a	2
E3	V	Mar 4, 1970	P. damicornis	1	2	a	a	a	2
E4	V	Jan 28, 1971	"	2	3	a	a	a	2
E5	V	Oct 6, 1970	P. compressa	2	3	a	a	a	2
D1	V	May 20-21, 1970	P. damicornis	2	2	0	30	27	2
D2	V	May 10-11, 1970	"	2	2	0	30	27	2
D3	V	Oct 13-14, 1970	P. compressa	2	3	0	30	26.4	2
G1	V	Sep 8, 1970	"	2	3	0	60	28.1	2
G2	V	Jul 23, 1970	P. damicornis	1	3[b]	42	30	27.4	2
T1	VI	Mar 17-28, 1968	"	1	1	60	a	a	1
T2	VI	Dec 18-30, 1970	"	2	3	30	30	a	2
T3	VI	Nov 11-23, 1970	"	2	3	30	30	a	2
T4	VI	Aug 17-27, 1970	"	1	3[b]	30	30	a	2
T5	VI	Jan 7-27, 1971	"	2	3	30	30	a	2
T6	VI	Dec 7-16, 1970	P. compressa	2	3	30	30	a	2
T7	VI	Sep 14-22, 1970	"	2	3	30	30	a	2

[a]See chapter listed.

[b]The magnetic stirrer was not used.

TABLE 6

Effects of various treatments on the apparent protein content (both of the coenosarc and of the internal tissue) of P. damicornis samples. Type of treatment and results of each treatment are given.

Exp.	Treatments I	Treatments II	Treatments III	Number of Samples	Average Sample Wt	µg Protein / mg Wt
P1			4 min 0.5 N NaOH	6	33.38	15.90
			7 min "	"	"	16.72
			14 min "	"	"	16.18
			21 min "	"	"	16.09
P2	7 min 0.5 N NaOH	Not Pulverized	10 min 0.5 N NaOH	4	210.75	0.0174
	"	Pulverized	"	6	115.43	0.5200
	14 min 0.5 N NaOH	Not Pulverized	"	3	278.77	0.0000
	"	Pulverized	"	6	77.15	0.5950
	28 min 0.5 N NaOH	Not Pulverized	"	2	271.20	0.0085
	"	Pulverized	"	5	87.70	0.5200
P3	Mechanical Abrasion	Not Pulverized	10 min 0.5 N NaOH	2	332.75	0.175
	" "	Pulverized	"	7	102.14	1.517

TABLE 7

The Coefficients of Variation [C. V. = (Standard Deviation/Mean) · 100] of calcification rates (of P. damicornis) expressed as rate/sample tip (Column 3) compared with the C. V. of the same rates expressed in terms of several different parameters (Columns 4-8).

Experiment	Number of Samples	Coefficient of Variation Using Various Parameters					
		Rate	Total Weight	Skeletal Weight	Tissue Weight	Protein Weight	Surface Area
P4	18	58	70	70	76	76	64
P5	68	131	110	110	120	116	112
P6	24	98	105			97	98

TABLE 8

^{45}Ca inorganic exchange rates in P. damicornis and P. compressa compared with calcification rates under comparable incubation conditions.

Exp.	Organism	Organism Condition	Exchange Incubation Temp. (°C)	Exchange Rate (ng $CaCO_3/mm^2/hr$)	Calcification Rate (ng $CaCO_3/mm^2/hr$)	% Exchange	Number of Samples
E1	P. damicornis	Alive	27	3.1	41	7.6	a
E2	P. compressa	Alive	29	140	2581	5.4	6
E3	P. damicornis	Dead	27	26	150	17.3	10
E4	P. damicornis	Dead	28.5	41	480	8.5	24
E5	P. compressa	Dead	26.9	212	1700	12.5	6

[a]See text.

TABLE 9

Experiment G1. Calcification rates at two different positions on branches of P. compressa. Values are given for each colony separately and for the means of both colonies. Values are based on three branches from each colony. A single core was taken from each position on each branch (total samples per position = 6).

Position	Rate (ng $CaCO_3/mm^2/hr$) ± SEM		
	Colony 1	Colony 2	Mean
I (Side Cores)	464 ± 29	503 ± 141	483 ± 72
II (End Cores)	2352 ± 168	2257 ± 126	2304 ± 105

TABLE 10

Experiment G2. Calcification rates at different positions (defined in text) in colonies of P. damicornis. Values are given for each colony separately and for the means of all colonies. Values are based on two samples removed from each colony at each position (total samples per position = 6).

Position	Rate (ng $CaCO_3/mm^2/hr$) ± SEM			
	Colony 1	Colony 2	Colony 3	Mean
IA	44 ± 12	82 ± 21	62 ± 5	63 ± 8
IB	414 ± 143	140 ± 86	561 ± 257	372 ± 102
IIA	108 ± 0.3	101 ± 19	39 ± 5	83 ± 6
IIB	385 ± 56	275 ± 29	711 ± 32	457 ± 24

TABLE 11

Experiment D1. Calcification rates obtained at three different times of the day with P. damicornis. Values are given for each colony separately and for the means of all colonies. Values are based on eight samples removed from each colony (four samples on each of two days) at each time (total samples per time = 24).

	Rate (ng $CaCO_3/mm^2/hr$) ± SEM			
Time	Colony 1	Colony 2	Colony 3	Mean
9:00 AM	58 ± 15	179 ± 70	367 ± 47	201 ± 29
12:00 Noon	59 ± 17	149 ± 42	210 ± 52	140 ± 23
3:00 PM	61 ± 13	133 ± 32	139 ± 55	111 ± 22

TABLE 12

Experiment D2. Calcification rates obtained at two different times of day and under two different light conditions with P. damicornis. Values are given for each colony separately and for the means of all colonies. Values are based on six samples removed from each colony within each time-condition category (total samples within each catetory = 18).

		Rate (ng $CaCO_3/mm^2/hr$) ± SEM			
Time	Condition	Colony 1	Colony 2	Colony 3	Mean
Noon	Light	77 ± 11	211 ± 37	117 ± 17	135 ± 14
"	Dark	40 ± 11	122 ± 19	128 ± 26	97 ± 11
Midnight	Light	43 ± 8	75 ± 25	29 ± 7	49 ± 9
"	Dark	13 ± 4	120 ± 44	60 ± 12	64 ± 15

TABLE 13

Calcification rates (± 1 standard error of the mean) at different temperatures and for different incubation lengths of time in P. damicornis (experiment T1). Twelve samples were removed at each incubation time (four samples each from branches of three colonies) within each temperature (total samples per temperature = 36). All data for the 0.5 hour incubation at 23°C were lost. P values (anova) in the last two columns show whether a significant difference exists between the three different times and the three different colonies within each temperature. Colonies used at one temperature were not the same as those used at another temperature. This series of incubations was done in March 1968 in Hawaii. Natural surface water temperature was 22.6°C.

Incubation Temp. (°C)	Rate (ng $CaCO_3/mm^2/hr$) ± SEM				P <	
	0.5 Hour	1.0 Hour	1.5 Hour	Mean	Time	Colonies
17	26 ± 8	15 ± 4	17 ± 5	19 ± 2	0.025	0.10
20	62 ± 36	40 ± 23	16 ± 3	39 ± 7	0.005	0.0005
23		90 ± 41	50 ± 22	70 ± 12		
25	58 ± 46	33 ± 14	53 ± 34	48 ± 10	0.75	0.90
27	154 ± 57	195 ± 95	127 ± 76	158 ± 22	0.50	0.005
29	68 ± 34	69 ± 40	49 ± 27	62 ± 10	0.50	0.50
32	38 ± 9	33 ± 11	21 ± 8	31 ± 3	0.025	0.025
34	16 ± 3	12 ± 3	8 ± 2	12 ± 1	0.0005	0.0005

TABLE 14

Temperature ranges of significant maxima in *P. damicornis* (T1-T5) and *P. compressa* (T6-T7). See text for details on method of determination.

Experiment	Temperature Range (°C)	
	First Maximum	Second Maximum
T1	>25-29	
T2	24-28	
T3		30- <32
T5	26-28	30-34
T6	>26- <29	
T7		29- >32

TABLE 15

Anova comparisons of temperature experiments. F values are calculated with the error mean square as denominator.

Comparison	I (T2 and T5)			II (T2 and T5)			III (T2, T3, and T5)		
Temperatures Used (°C)	25, 26, 27, 28, 29, 30, 32			25, 26, 27, 28, 29			29, 30, 32		
Source of Variation	D.F.	F	P<	D.F.	F	P<	D.F.	F	P<
History	1	14.1	0.0005	1	2.0	0.25	2	28.5	0.0005
Temperature	6	6.3		4	8.5		2	4.8	
Colony	10	20.1		10	15.7		15	13.6	
History x Temperature	6	14.3	0.0005	4	2.4	0.10	4	7.9	0.0005
Error	312			220			192		

Comparison	IV (T3 and T5)			V (T3 and T5)			VI (T6 and T7)		
Temperatures Used (°C)	29, 30, 31, 32, 33			31, 32, 33			26, 28, 29, 30, 32		
Source of Variation	D.F.	F	P<	D.F.	F	P<	D.F.	F	P<
History	1	57.7	0.0005	1	70.9	0.0005	1	169.1	0.0005
Temperature	4	10.7		2	15.0		4	8.7	
Colony	10	18.1		10	10.6				
History x Temperature	4	4.8	0.005	2	4.9	0.01	4	3.3	0.025
Error	220			128			76		

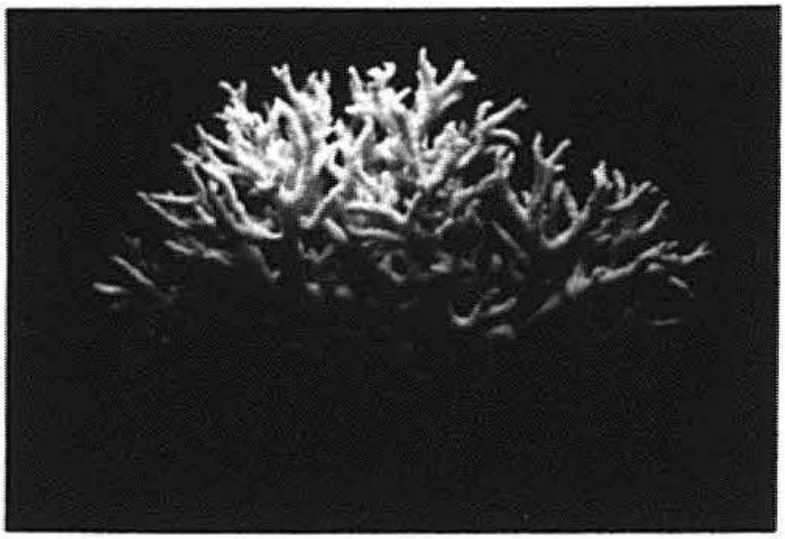
TABLE 16

The Q_{10} values over various temperature ranges in the different temperature experiments. In each case all points within the temperature range given were used as the basis of the Q_{10} estimates. Q_{10} was calculated from the slopes of straight lines --fitted by the least squares method to temperature-log rate plots --of the data given in Figs. 14 and 15 ($\log Q_{10} = 10 \cdot \frac{\log K_2 - \log K_1}{T_2 - T_1}$). The average natural surface water temperature during the time of each experiment is given.

Experiment	Natural Water Temp. (°C)	Temp. Range (°C)	Q_{10}
T1	22.6	17.0 - 27.0	4.1
T2	22.8	22.0 - 27.0	3.1
T4	26.3	25.1 - 27.0	7.4
T5	28.0	25.0 - 27.1	24.7
T1	22.6	27.0 - 34.0	0.048
T2	22.8	27.0 - 32.0	0.24
T3	24.4	31.1 - 33.2	0.017
T5	28.0	31.0 - 36.0	0.40
T7	26.0	19.1 - 30.0	1.8

Figure 1. Skeleton of a P. damicornis colony.

Figure 2. A portion of a living P. compressa colony.



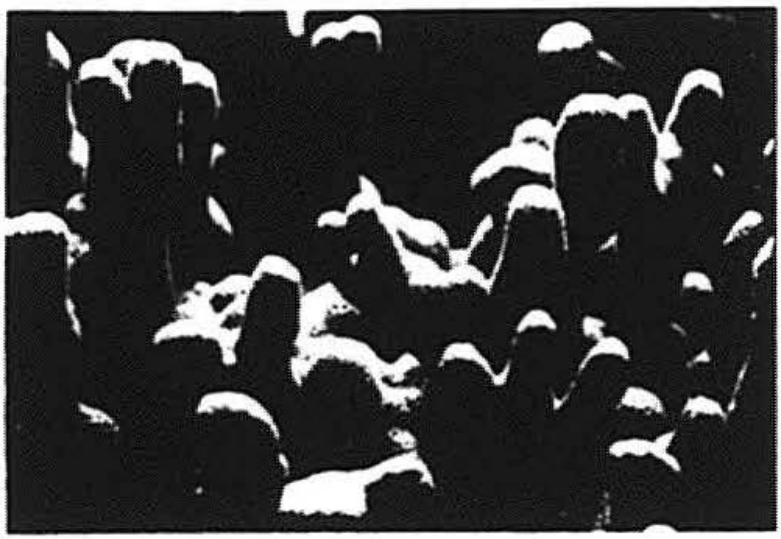
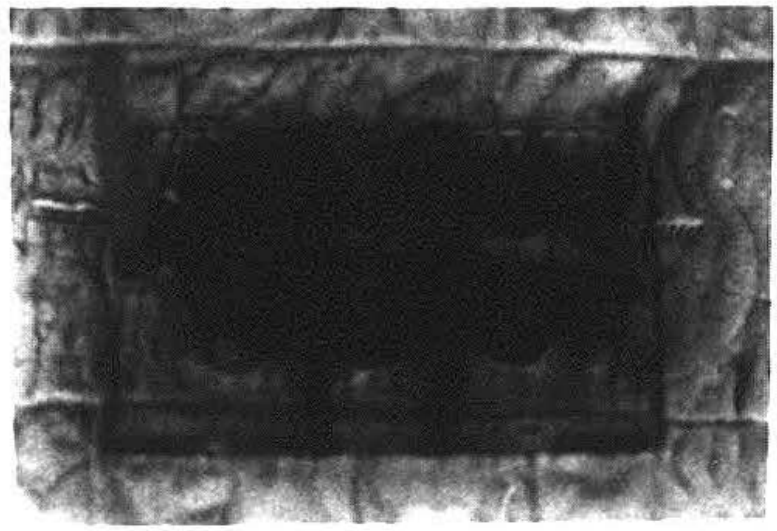


Figure 3. Rack (containing branches of P. damicornis) used to maintain the coral branches in an upright position during incubation.

Figure 4. Incubation System 1. Light source is directly under the water bath tank. Branches of P. damicornis are visible in the incubation vessel on the left. See text for further details.



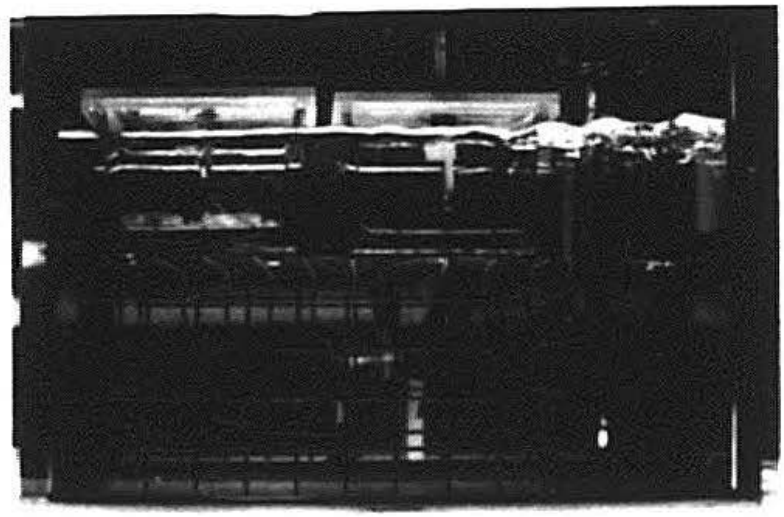
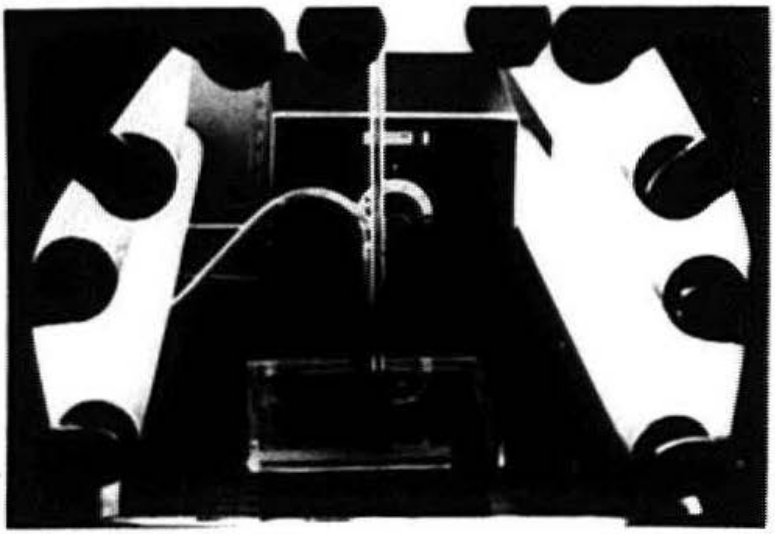
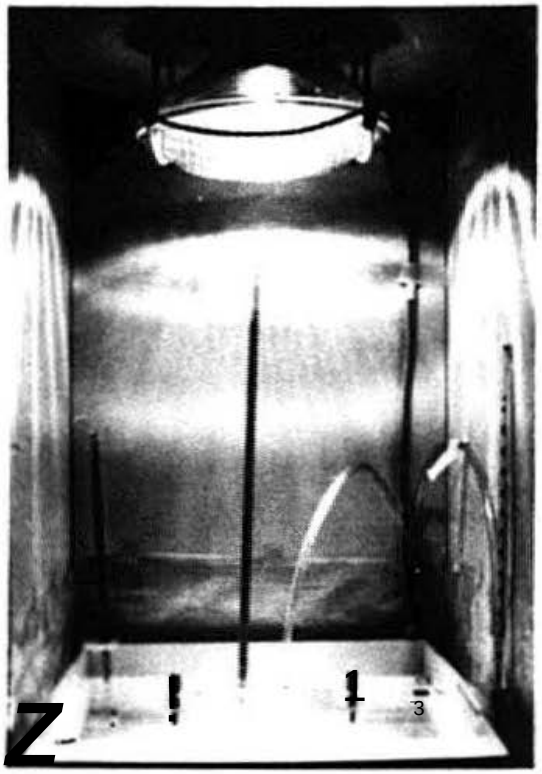


Figure 5. Incubation System 2. See text for details.

Figure 6. Incubation System 3. See text for details.




Z

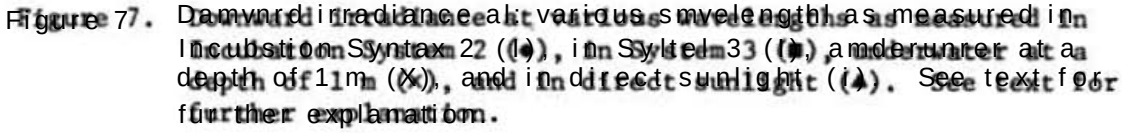


Figure 7. Downward irradiance at various wavelength as measured in Incubation System 22 (●), in System 33 (○), underwater at a depth of 1m (X), and in direct sunlight (▲). See text for further explanation.

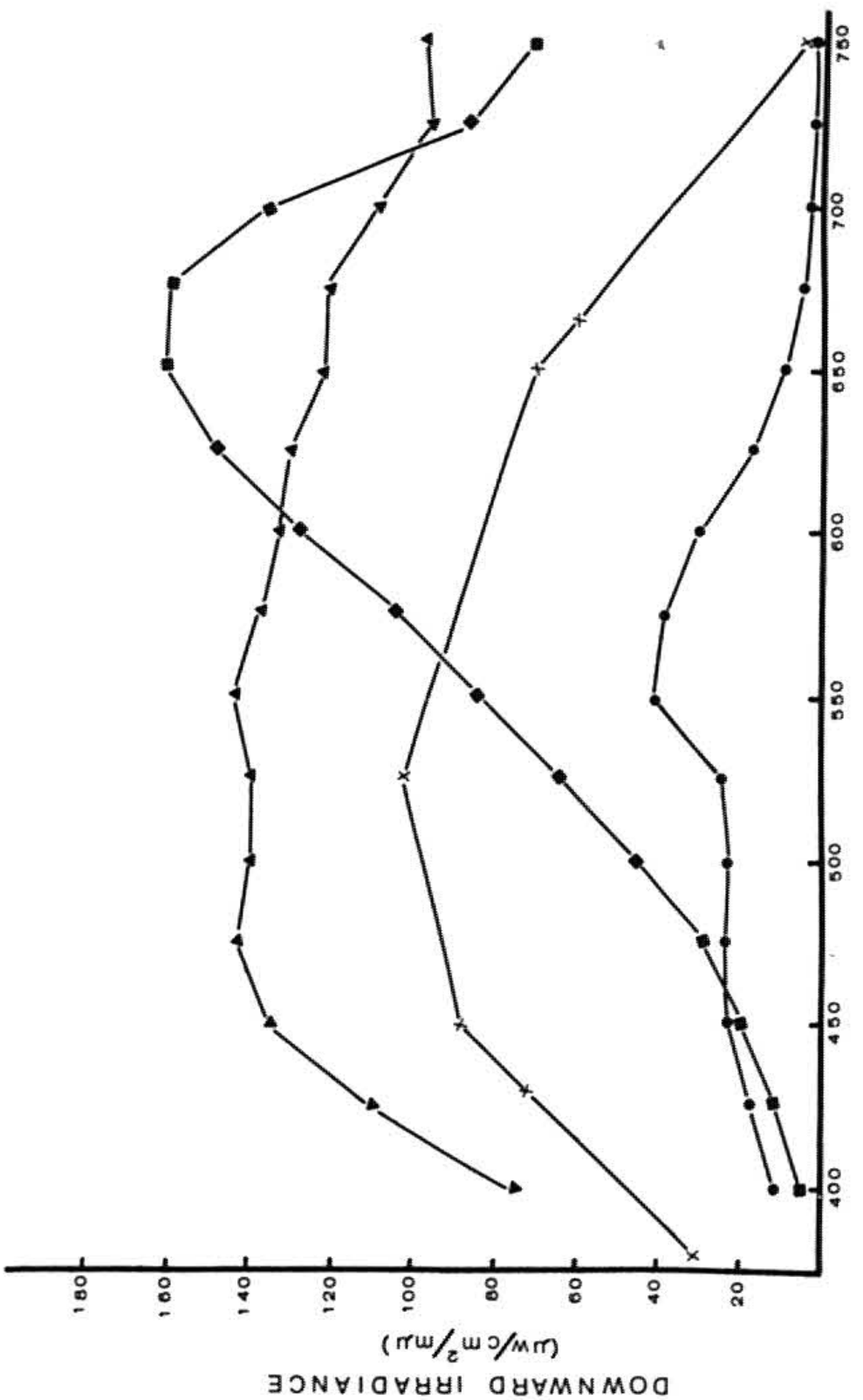

DOWNWARD IRRADIANCE
(μw/cm²/mμ)
180
160
140
120
100
80
60
40
20
400
450
500
550
600
650
700
750
WAVELENGTH (mμ)

Figure 8. Relation between weight and surface area in P. damicornis sample tips. Plot based on 304 samples--each plotted point (except for the last) is the mean of 10 adjacent samples. The smooth curve drawn through the points is described by the equation:

$$\text{Surface area} = 62.3(1.0 - e^{-0.0298 \cdot \text{weight}}).$$

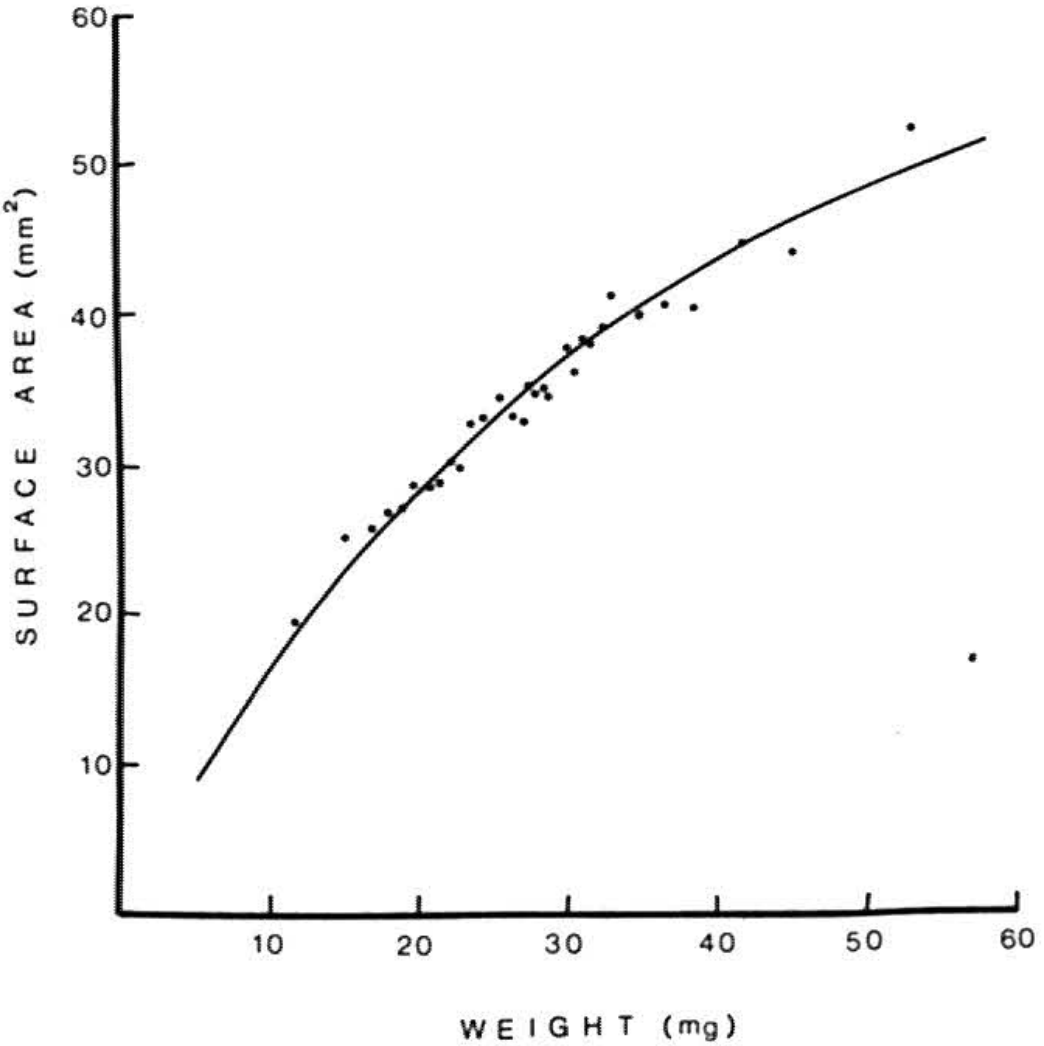
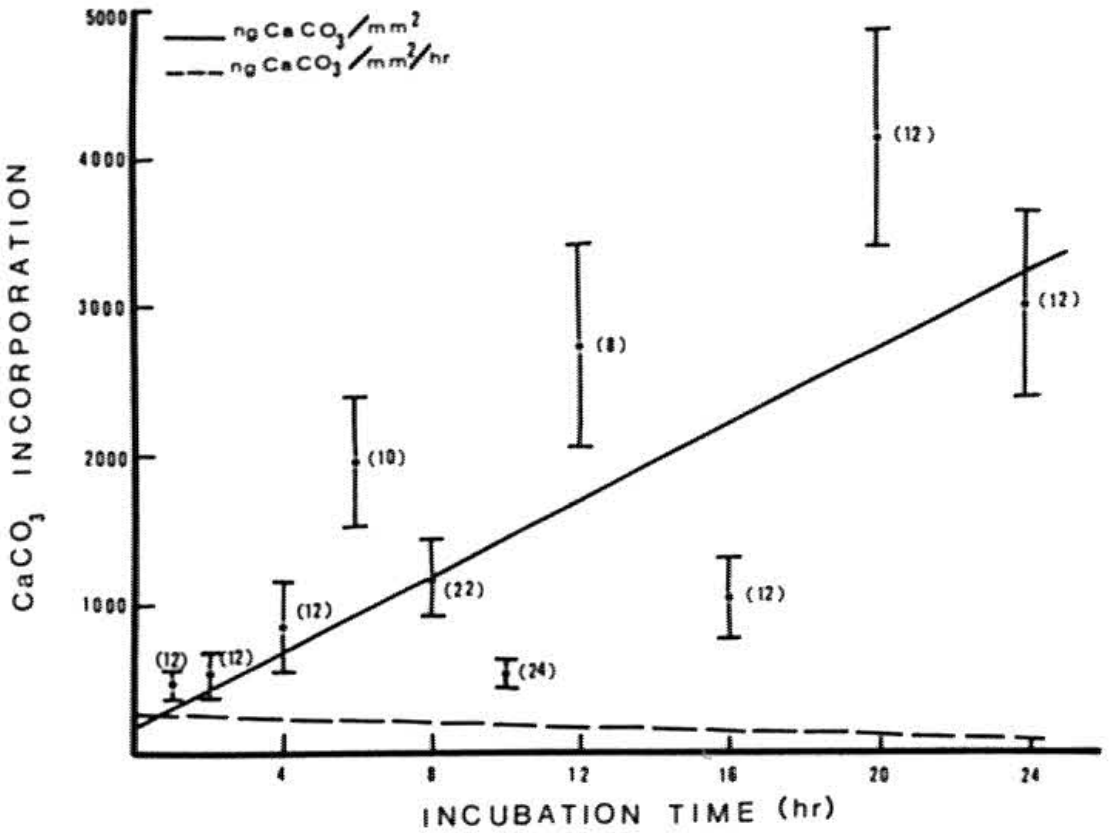

SURFACE AREA (mm^2)
60
50
40
30
20
10
10
20
30
40
50
60
WEIGHT (mg)

Figure 9. Experiment L1. Quantity of $CaCO_3$ incorporated into P. damicornis samples at different incubation times. Vertical bars represent ± 1 standard error of the mean. Lines fitted by the least squares method. Numbers in parentheses are the number of samples on which that point is based.

Figure 10. Experiment L2. Quantity of $CaCO_3$ incorporated into P. compressa samples at different incubation times. Plotted points are based on three sample cores for each incubation time. Vertical bars represent ± 1 standard error of the mean. Lines fitted by the least squares method.


ng CaCO3/mm2
ng CaCO3/mm2/hr
CaCO3 INCORPORATION
5000
4000
3000
2000
1000
(12)
(12)
(12)
(10)
(22)
(24)
(8)
(12)
(12)
(12)
4
8
12
16
20
24
INCUBATION TIME (hr)

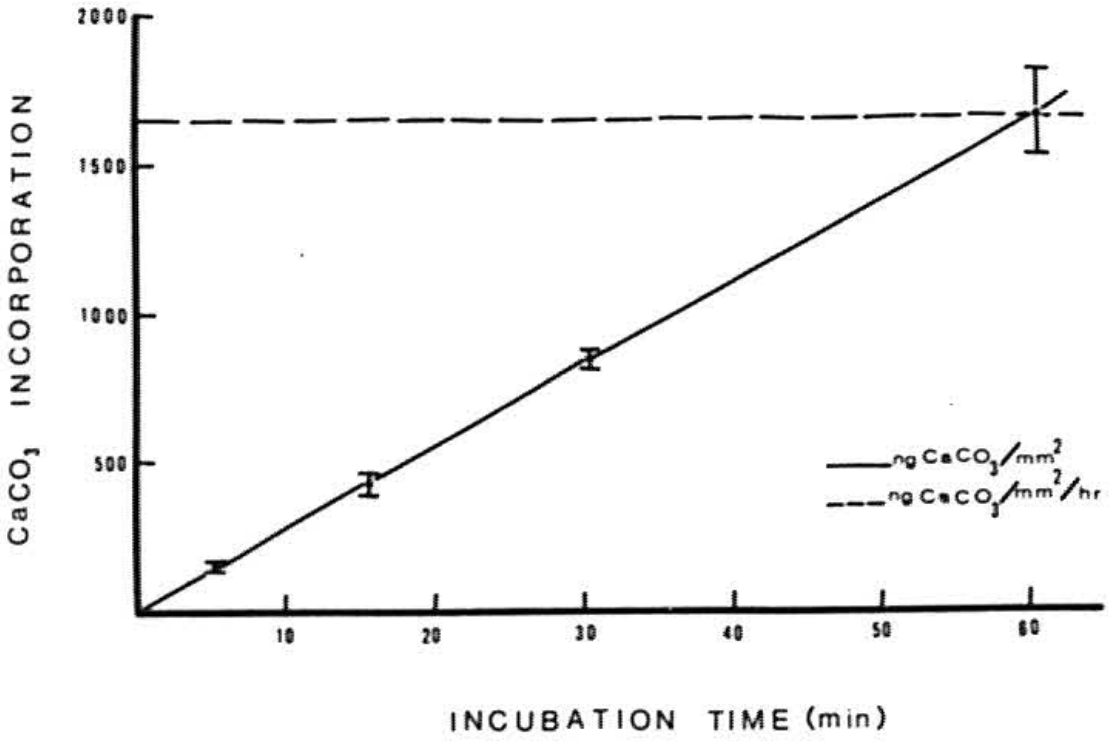
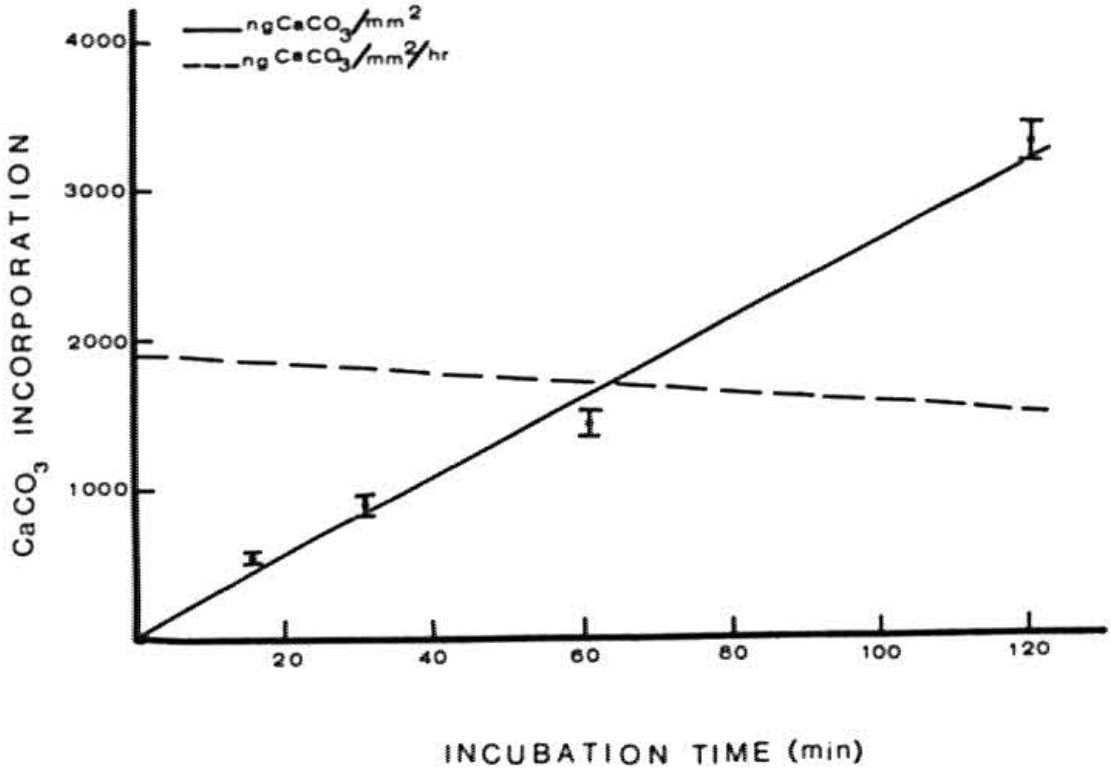

CaCO3 INCORPORATION
2000
1500
1000
500
ng CaCO3/mm2
ng CaCO3/mm2/hr
10
20
30
40
50
60
INCUBATION TIME (min)

Figure 11. Experiment L3. Quantity of $CaCO_3$ incorporated into P. compressa samples at different incubation times during exposure to "light" stress. The plotted points are based on three sample cores for each incubation time. The vertical bars represent ± 1 standard error of the mean. Lines fitted by the least squares method.

Figure 12. Experiment L4. Quantity of $CaCO_3$ incorporated into P. damicornis samples at different incubation times during exposure to temperature stress. The plotted points are based on 12 samples (six from each of two colonies) for each incubation time. The vertical bars represent ± 1 standard error of the mean. Lines fitted by the least squares method.


ngCaCO3/mm2
ngCaCO3/mm2/hr
4000
3000
2000
1000
CaCO3 INCORPORATION
20
40
60
80
100
120
INCUBATION TIME (min)

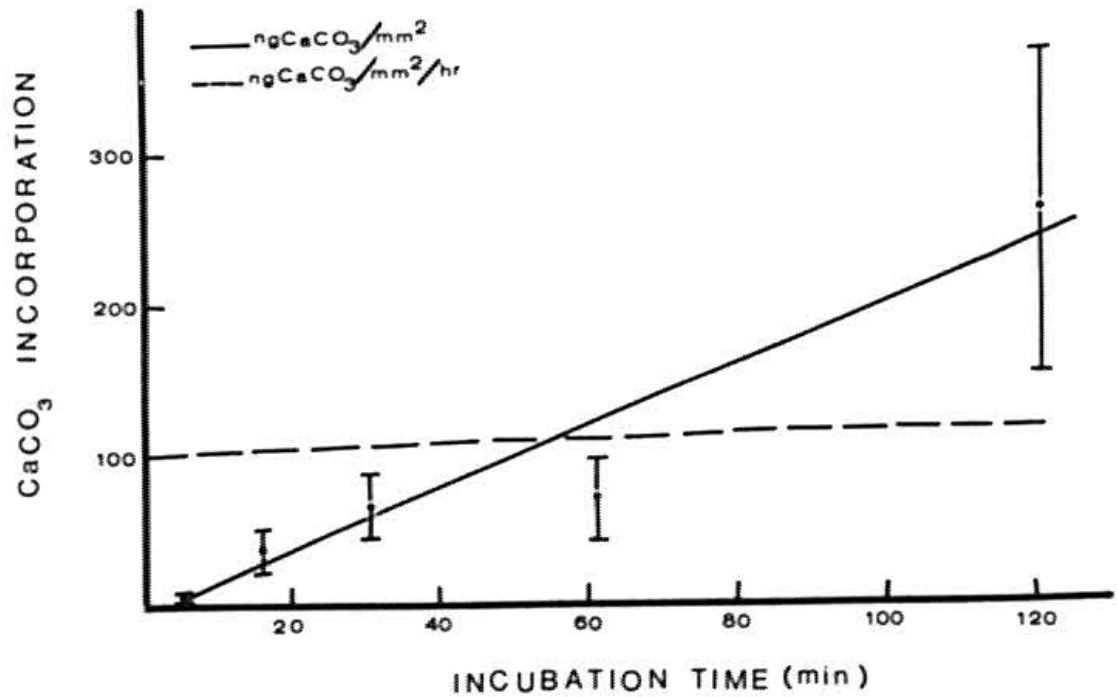

ngCaCO3/mm2
ngCaCO3/mm2/hr
300
200
100
CaCO3 INCORPORATION
20
40
60
80
100
120
INCUBATION TIME (min)

Figure 13. Natural surface water temperature at the time and place of collection of the corals. The solid line represents water measurements made in Kaneohe Bay, Hawaii, during 1970; the dashed line, Eniwetok lagoon in January, 1971, at the time of experiment T5. Only one temperature measurement (the single point ⊕) was made during experiment T1 in March, 1968. The dates of the different temperature experiments are indicated along the bottom edge of the figure.

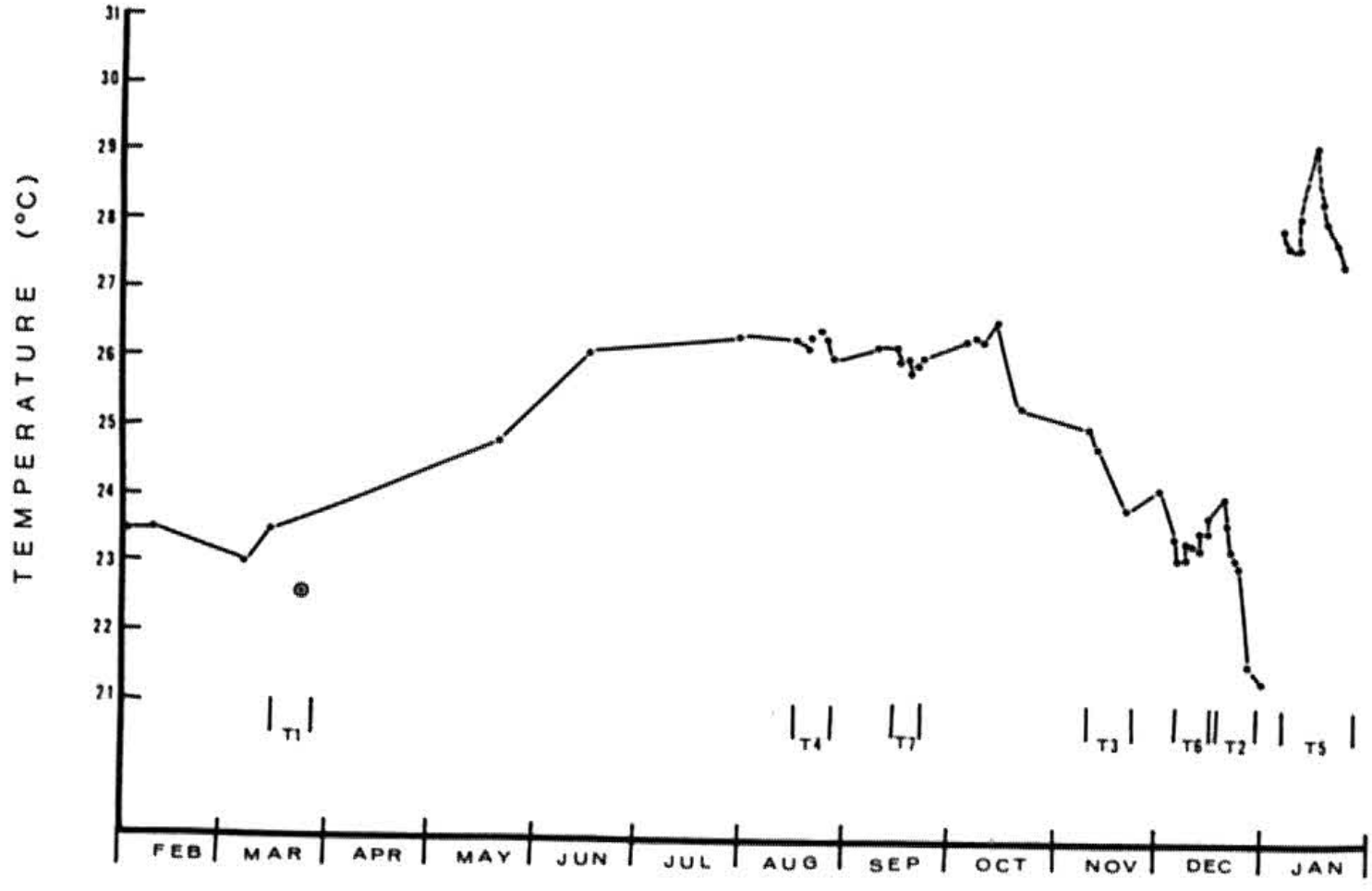

TEMPERATURE (°C)
31
30
29
28
27
26
25
24
23
22
21
T1
T4
T7
T3
T6
T2
T5
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
MONTH

Figure 14. Relation between incubation temperatures and mean calcification rates in the five temperature experiments with P. damicornis. All incubations were for 0.5 hour. Error bars equal ± 1 standard error of the mean. Average natural water temperature during the time of the experiment is given in parentheses. Experiment T5 was done at Eniwetok, the others in Hawaii. In experiments T2, T3, and T5 each point is based on four sample tips removed from each of six colonies (total samples per incubation = 24). The same six colonies were used for all incubations within one experiment. In experiments T1 and T4 the three colonies used at one temperature were not the same as those three used at another temperature. In experiment T1 and T4 points are based on four and six samples respectively from each of the three colonies (total samples per incubation in experiment T1 = 12, and in experiment T4 = 18). All data for the 0.5 hour incubation at 23°C in experiment T1 were lost. The point plotted is an estimate calculated from the rest of the data (including the 1.0 and 1.5 hour data) by a statistical method.

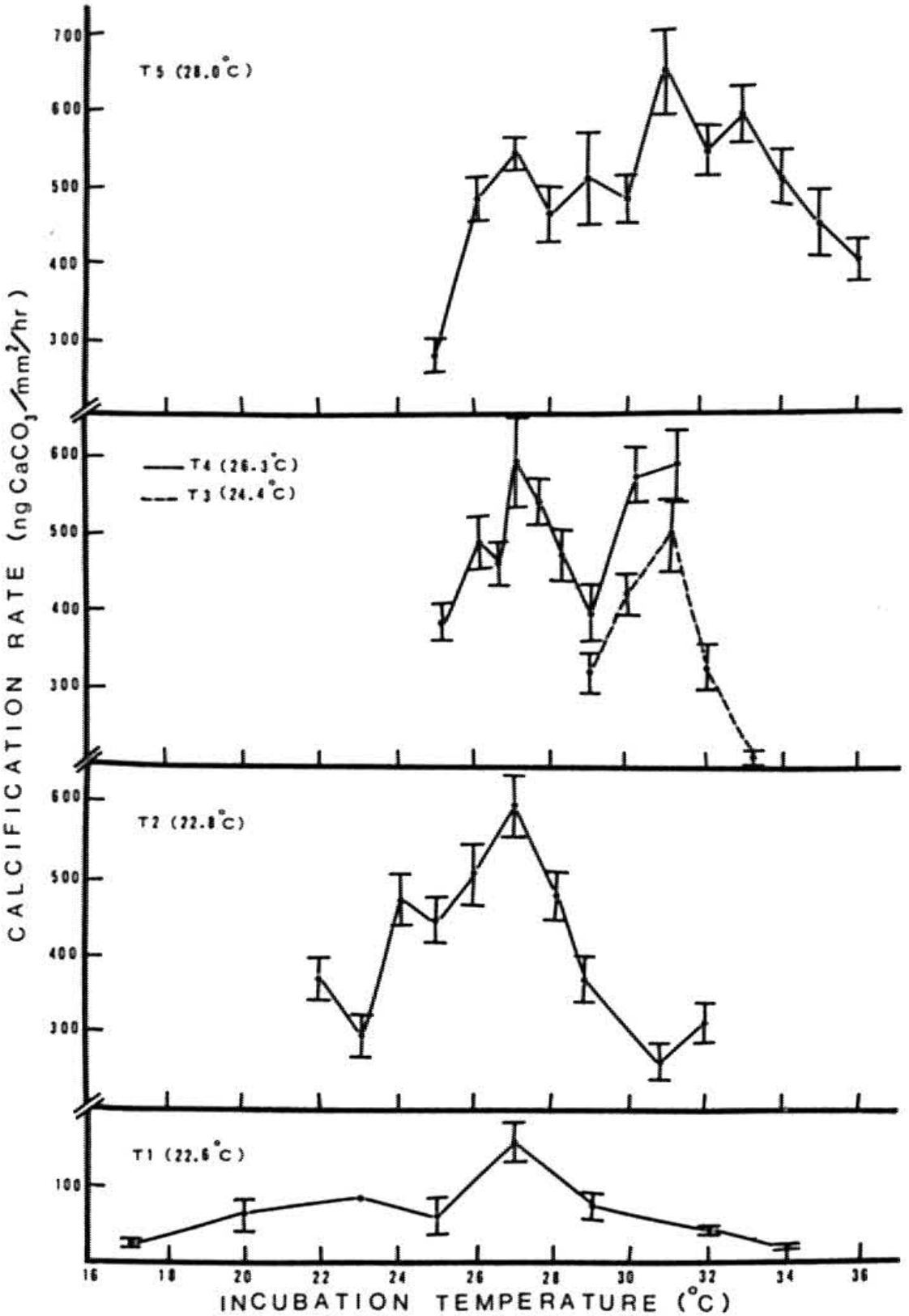

T5 (28.0°C)
T4 (26.3°C)
T3 (24.4°C)
T2 (22.8°C)
T1 (22.6°C)
CALCIFICATION RATE (ng CaCO3/mm2/hr)
INCUBATION TEMPERATURE (°C)
700
600
500
400
300
100
16
18
20
22
24
26
28
30
32
34
36

Figure 15. Relation between incubation temperatures and mean calcification rates in the two temperature experiments with *P. compressa*. Incubations were for 0.5 hour. Error bars equal ± 1 standard error of the mean. Average natural surface water temperature during the time of the experiment is given in parentheses. In experiment T6 each point is based on three core samples removed from each of four colonies (total samples per incubation = 12). Each point in experiment T7 is based on three core samples removed from each of two colonies (total samples per incubation = 6). The same colonies were used for all incubations within one experiment.

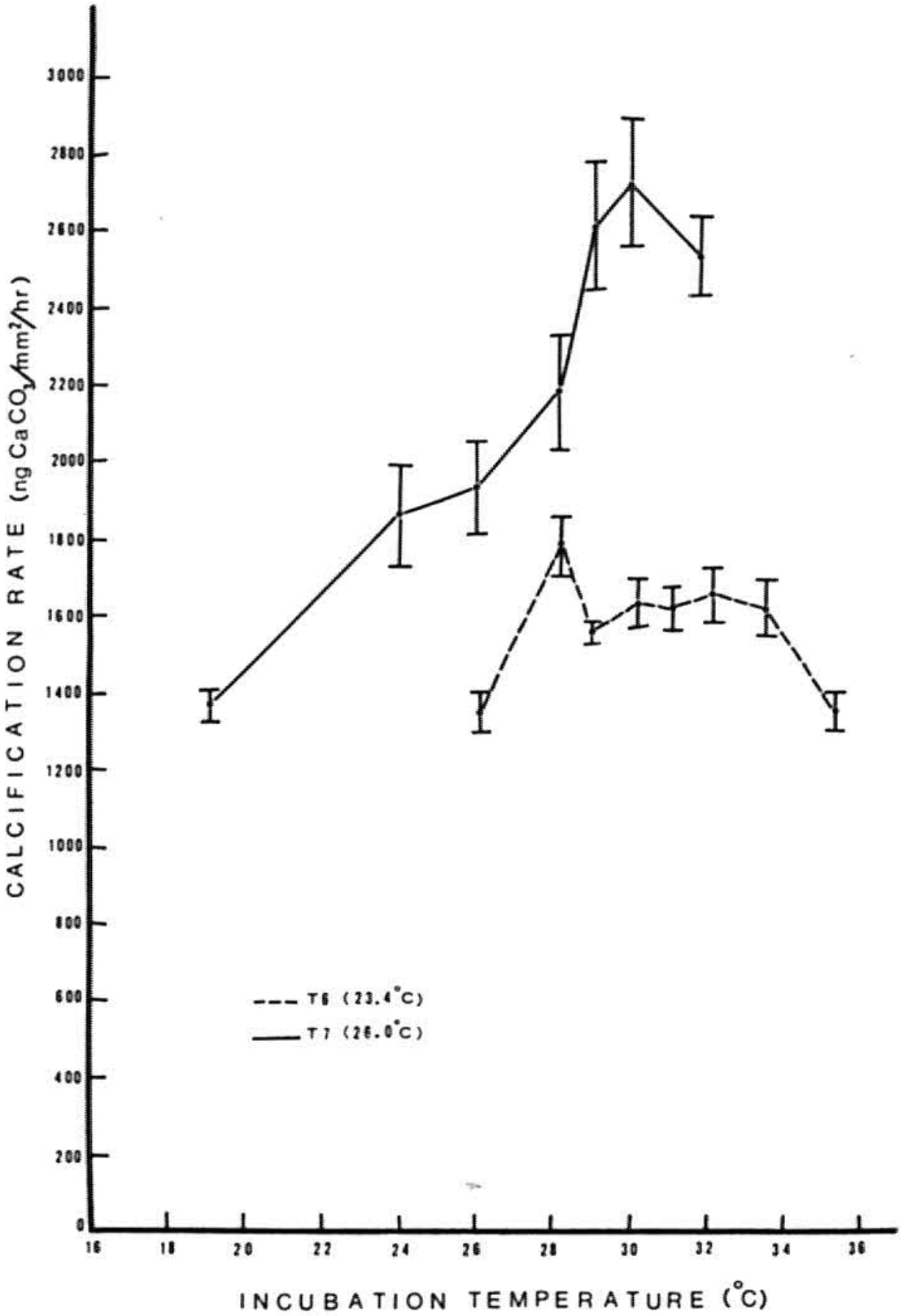

CALCIFICATION RATE (ng $CaCO_3$/mm²/hr)
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
16
18
20
22
24
26
28
30
32
34
36
INCUBATION TEMPERATURE (°C)
T6 (23.4°C)
T7 (26.0°C)

Figure 16. Results of the application of Duncan's New Multiple Range Test to the P. damicornis temperature experiments. Graphs are based on the same data as used in Fig. 14. The dashed lines are ranges computed in Duncan's Test--not confidence intervals. The logarithms (natural) of the rates are plotted here because they were required in the statistical analysis on which the ranges are based. Means not included within the range of a dashed line are significantly different ($P < 0.05$) from the mean through which that dashed line passes. Notice different scale on ordinate for experiment T1.

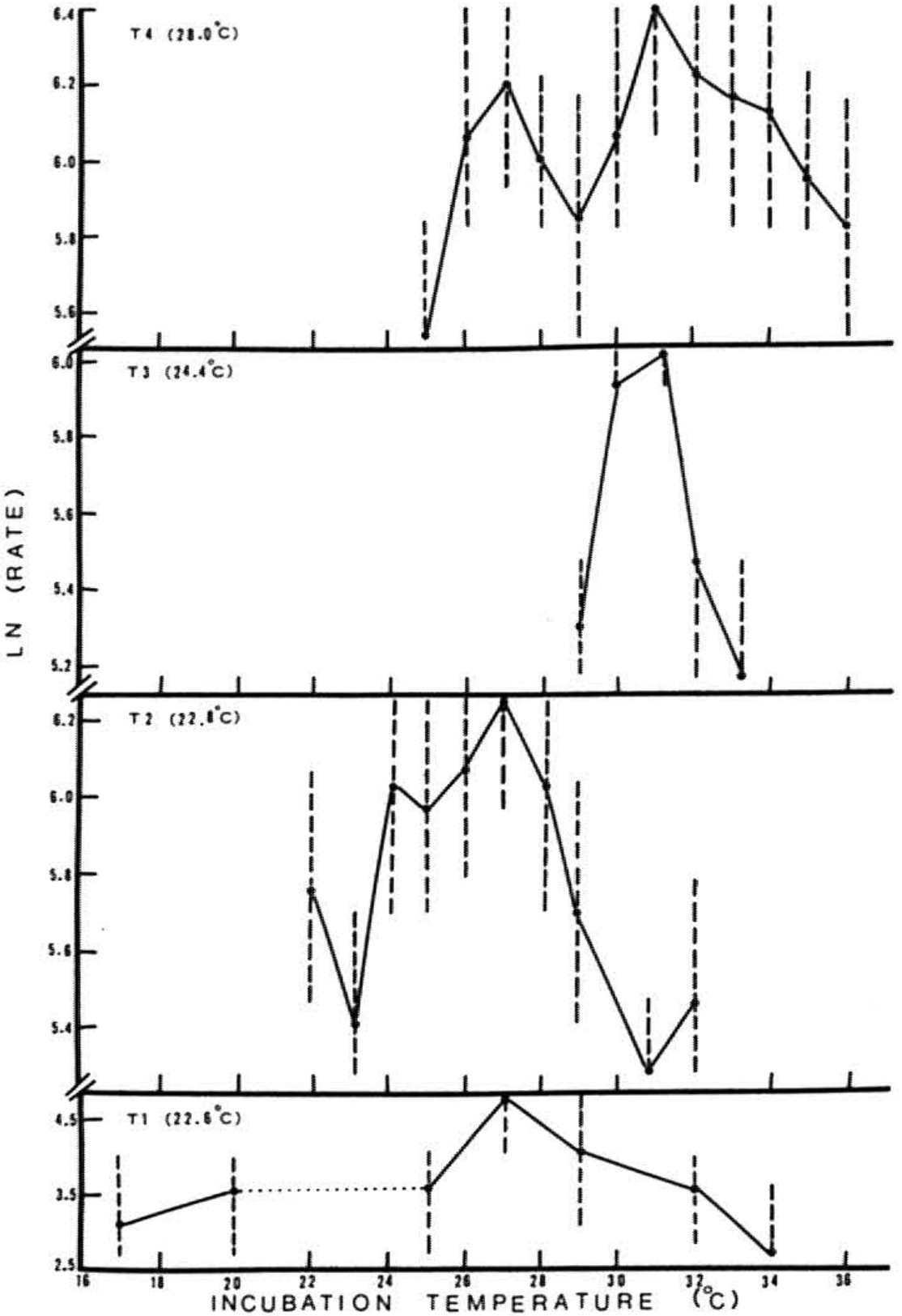
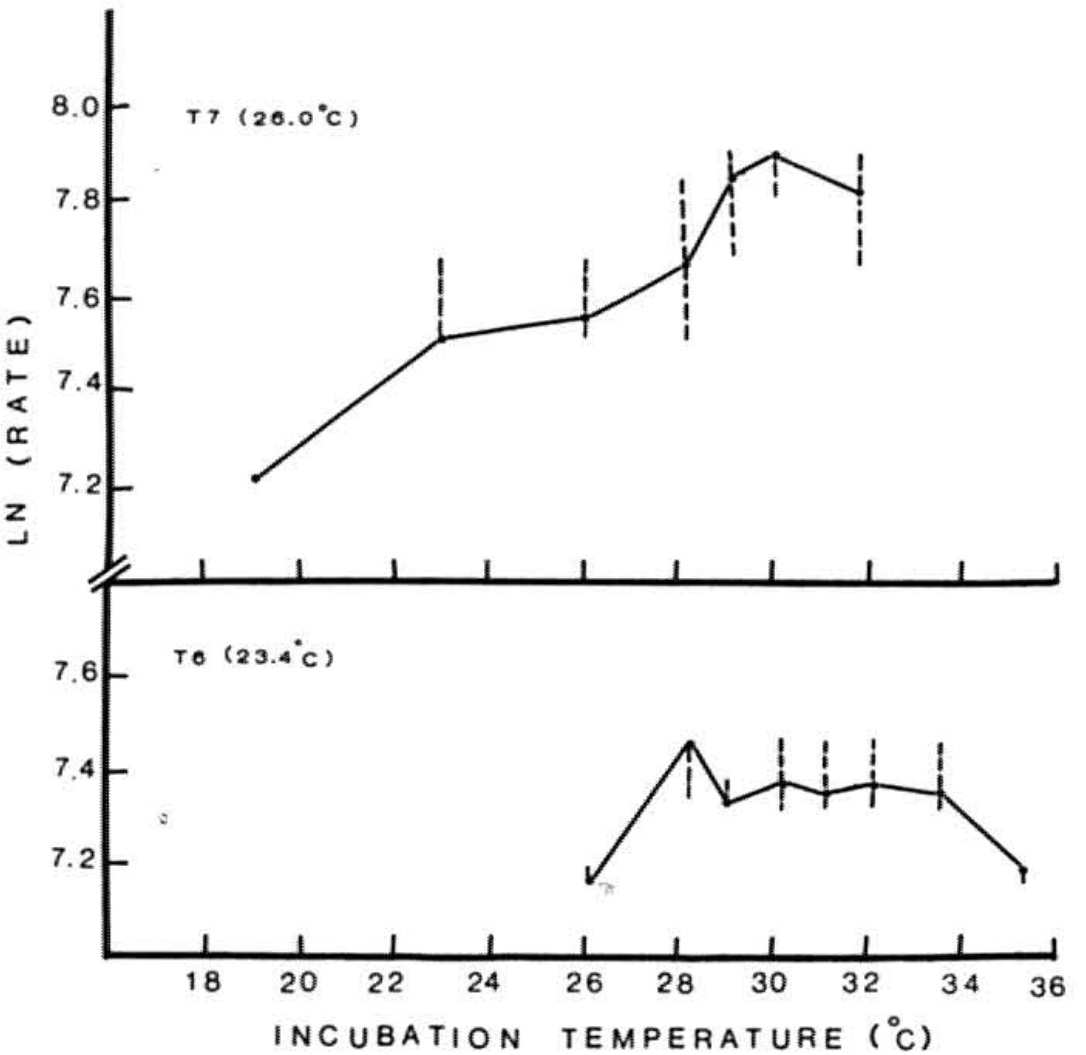

T4 (28.0°C)
T3 (24.4°C)
T2 (22.8°C)
T1 (22.6°C)
LN (RATE)
INCUBATION TEMPERATURE (°C)

Figure 17. Results of the application of Duncan's New Multiple Range Test to the P. compressa temperature experiments. Graphs are based on the same data as used in Fig. 15. Interpretation of these graphs is the same as in Fig. 16.


8.0
7.8
7.6
7.4
7.2
T7 (26.0°C)
LN (RATE)
7.6
7.4
7.2
T6 (23.4°C)
18
20
22
24
26
28
30
32
34
36
INCUBATION TEMPERATURE (°C)

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FACTORS AFFECTING CALCIFICATION PROCESSES IN THE HERMATYPIC CORALS POCILLOPORA DAMICORNIS AND PORITES COMPRESSA

by

Conrad D. Clausen

An Abstract of a Dissertation

in Partial Fulfillment of the Requirements

for the Degree Doctor of Philosophy

in the Field of Biology

June 1972

ABSTRACT

Temperature affects coral distribution and it also affects rates of physiological processes. Little attention has been given though, to the relation between the basic effect of temperature on reaction rates at the molecular level and its effect on coral distribution at the organismic level. Incubating coral samples in sea water containing ^{45}Ca and using rate of ^{45}Ca incorporation as a measure of calcification rate, I studied the effects of temperature on calcification in two coral species, P. damicornis and P. compressa. $CaCO_3$ deposition was chosen because of its basic importance in reef formation. Immediate effects of temperature on calcification rate were studied, as well as temperature adaptation to seasonal and geographic changes in natural temperature.

Temperature has a marked effect on rate--an effect that varies depending on the temperature history of the coral (i.e., temperature adaptation occurs). P. damicornis showed both a 27°C and a 31°C temperature optimum--one or the other being dominant depending on the natural water temperature to which the coral was adapted. P. compressa may also have two optima but the data are not as conclusive. The optimum temperatures may indicate two isoenzymes or two alternate metabolic pathways involved in the calcification process.

The laboratory method for study of growth in corals seems to be the most practical quantitative approach. A possible disadvantage of

this method however, is that calcification rates obtained in the laboratory may not be comparable to natural rates. Possible sources of error in estimating growth rates from the laboratory calcification rates were investigated. During long incubations (several hours or more) a significant decrease in rate was observed. However, very short incubations proved feasible and were used. Inorganic exchange of ^{45}Ca across the living coenosarc was not significant. Time of day, light conditions, and position of samples within the colony may affect calcification rate. Terminal parts of branches calcified several times more rapidly than lateral parts. P. damicornis calcified less rapidly at night than in the day. The calcification rate of P. damicornis seemed more sensitive to ecological factors than P. compressa.

Being aware of these factors I estimated growth from the calcification rates and found that rates obtained in the laboratory were comparable to those in the field.