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CORAL GROWTH[1]

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INTRODUCTION

The study of coral biology in general, and coral skeletal growth in particular has a special fascination because it reaches back even beyond the origin of classical biology to the studies and collections of the earliest naturalists. Yet, in spite of the antiquity and continuity of scientific attention, many of the problems considered by these investigators are still under active study today, together with a wide variety of more recently formulated questions.

Because of its long past and modern diversity the subject of coral growth has a large and scattered literature and a comparably diverse following. As in any broadly interdisciplinary research area, communication and assimilation of results and concepts in the field as a whole often lag far behind the level of sophistication of specific sub-disciplines. Our intention in this review is to assemble and compare the questions and results of various studies of coral skeletal accretion in order to disseminate as widely as possible information about mutually relevant investigations with different purposes and methodologies.

It should be clearly understood that 'coral growth studies' are in reality methods or experimental approaches to larger fields of interest, each with its own literature and terminology. We will summarize briefly the different reasons for investigation of coral growth before integrating these into a review of methods and results.

REASONS FOR STUDYING CORAL GROWTH

Reef and atoll development

Beginning with Darwin's (1842) theory of reef development much work focused on the 'coral reef problem' (Davis, 1928): i.e., how could coral reefs reach the surface of the ocean in areas of great depth and, once at the surface,

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how could they maintain themselves against the ravages of the erosional forces of the waves? Stoddart (1969) reviews the history of this controversy. Darwin as early as 1842 and Dana in 1875 advanced the idea that the main constructional elements of the reefs were the coral polyps and colonies; for this reason many workers interested in the 'coral reef problem' sought the answer in the study of the rate of growth of coral colonies themselves. In spite of our greater knowledge of reef structure and dynamics, this information is still pertinent to discussions of rates of reef growth (Hoffmeister and Multer, 1964; Chave, Smith and Roy, 1972).

Biological description

The obvious biological question resulting from an interest in the growth of reefs was, how fast do corals grow? Closely related to this is the question of variability of growth rate and that of whether corals exhibit determinate or indeterminate growth. The fact that, of all animals, corals leave the most massive skeletal remains was no doubt an incentive for the extensive formulation, by whatever means available, of estimates of coral growth rates even though Vaughan, as early as 1915, pointed out that corals are poor systems for the study of 'the laws of growth'. In addition to some piecemeal information of limited value on growth, early studies of coral growth developed two concepts which still determine the approaches to coral research. One was that corals could be divided into reef-building and non-reef-building forms, and that of the reef-building forms some were of much more importance in building the actual framework of the reefs while others were of more importance in contributing carbonate sediment to the reef structure (Wells, 1957). The second concept was that any scatter in observed growth rates could be attributed to environmental factors as well as differences between species and growth forms.

Ecological controls

An understanding of coral growth rates, growth forms, and longevity is basic to the study of coral reef ecosystems or their components. Ecological controls over coral survival and distribution are reviewed by Wells (1957), Stoddart (1969), Connell (1973), Glynn (1973b), and Yonge (1963). Light, clear water, sufficient water movement, and relatively stable temperature and salinity (both within fairly narrow ranges) have long been recognized as important for reef and coral growth. The question of what conditions are optimal for growth has, however, only been subject to quantitative, experimental study within the past few decades.

Environmental indicators

Along with the realization that the growth rate of corals was affected by aspects of the local environment came the realization that the skeleton recorded indications of significant ecological events or conditions during the life of the coral. LeConte (1875), Krempf (1934, 1935), and Ma (1934a,b, 1937, 1957, 1959) were among the earliest to suggest that environmental changes left traces in the skeletons of modern corals. More recently, workers

on modern corals have attempted to find records of environmental events in the chemistry, isotopic content, and structure of coral skeletons; these studies are reviewed below. Although this type of investigation is closely related to the ecological issues mentioned earlier, most attention to these topics has come from geologists, geochemists, and geophysicists rather than from biologists or ecologists.

Physiological questions

Closely involved in the relationship between the skeletal record and the environment is the mechanism of calcification and its environmental controls. This aspect of coral growth centres on the close symbiosis between corals and their intracellular algae, zooxanthellae, and in particular on the relationship of photosynthesis to calcification. Muscatine (1973), Taylor (1974), and Vandermuelen and Muscatine (1974) give the most recent reviews of this field; more recent publications are reviewed below. Finally, the question of the chemical and biochemical relationships of corals to the other organisms on the reef as well as within individual corals leads back to a refined version of the question that first focused attention on these organisms: How do coral reefs function and grow?

DEFINITIONS

Much of our inability to compare the results of different studies and to apply the observations of one investigator to the problems of another arises from inadequate or inappropriate definition of the terms and measurements used. We wish, therefore, to establish some basic working definitions which will be expanded upon later as needed.

For the purpose of this review we define corals as cnidarians which deposit massive skeletons. Our attention will be focused on the scleractinian corals, with special emphasis on the hermatypic scleractinians. While we recognize that many writers have come to identify 'hermatypic' with 'zooxanthellae-containing', we will restrict the former to its original sense of 'reef-building'. We consider 'symbiotic' those corals which contain zooxanthellae, 'aposymbiotic' those corals which normally contain zooxanthellae but whose symbionts are missing, and 'non-symbiotic' those corals which do not normally contain symbiotic zooxanthellae. The term 'ahermatypic' has frequently been improperly equated with this last group.

The definition of growth presents substantially greater problems. The sense in which we wish to discuss the subject is that of net skeletal accretion. Growth must, however, inevitably be operationally defined by the method of measurement adopted, so that a review and comparison of all types of skeletal accretion measurements is necessary—increase in mass, volume, area, or a variety of linear dimensions, and the flux or rate of uptake of skeletal components such as calcium will be discussed. In addition to the dimensional characters measured, the time base of the rate is also important; the relationship, or lack thereof, between hourly, daily, seasonal and annual growth rates will be one of the definitional problems presented later.

Some of the more pervasive difficulties in growth definition and comparison must be discussed in connection with specific examples; at the outset the

reader is exhorted to remember that the nature of growth is a conglomeration of human concepts and is by no means graven on the limestone tablets of the corals themselves.

ORGANIZATION

It is our intention to provide a thorough and critical review of quantitative work on the skeletal growth of symbiotic scleractinian corals. Related studies, such as those focused on tissue metabolism, growth morphology, or the growth of non-symbiotic or non-scleractinian corals, will be discussed insofar as they seem relevant to the mechanisms of coral growth in the above sense.

We first present a review of the literature organized on the basis of the growth measurement method(s) employed; where feasible, we also identify the species and geographical locations in order to provide both reference information and the context of the measurements. We divide the methods into categories of real-time observations (measurements of dimensional or mass increase or of chemical uptake over a discrete time interval initiated and terminated by the investigator) and retrospective observations (in most cases radiographic or radiometric) where the skeletal structure, composition or substratum provides the time base. These methods are discussed and compared on the basis of the types of data produced and their relative advantages and disadvantages.

We then integrate and summarize the results of these various studies in terms of current knowledge about the skeletal accretion rates of corals. Finally, we return to a consideration of the questions which have motivated the various growth studies in an effort to point out the methods and directions of research which seem to show the most promise for the future.

METHODS

REAL TIME

Direct measurement of corallum size

The most direct way to measure coral growth is to record some dimension of the corallum and, after a time interval, to repeat the measurement. The dimension measured may be: (a) linear, e.g., the length of branch, the diameter or circumference of a colony or the height of a colony above the substratum; (b) areal, e.g., the surface area of a colony in the case of encrusting, massive or plate-like growth forms, or the projected area in the case of branching forms; (c) volume, e.g., the volume occupied by the colony—either the true volume of the colony (usually equivalent to displacement volume) or the total volume of the colony including the spaces between branches; or (d) weight, e.g., measured in air as the live wet weight or in water as the buoyant weight.

Length. While most of the real time estimates of growth rate have the initial and final measurements made by the same investigator, Mayer (1918) reports growth measurements spanning 23 years on Great Barrier Reef corals which

were first measured by Saville-Kent (1893). The colonies were relocated by reference to photographs in Saville-Kent's report. While it seems likely that the same corals were remeasured in this case, photographic relocation studies must take into account the difficulty in identifying individual corals with certainty. Furthermore, it must be recognized that the rate obtained is a long-term net value and may include destruction of parts of the surviving colonies, position alterations or effects of changes in the environment.

Linear measures of corallum size were used by Abe (1940) who made extensive growth studies on the solitary coral *Fungia actiniformis* var. *palawensis* in Palau. In addition to measuring increases in length of the corals he also measured weight and made extensive experimental and transplant studies to determine the environmental factors affecting the growth and distribution of this coral (Abe, 1937). Linear measurements of fungiid corals were also reported by Edmondson (1929) and Bosch (1967) in Hawaii, Tamura and Hada (1932) in the Carolines, and Stephenson and Stephenson (1933) on the Great Barrier Reef.

Mayor (1924) measured the increase in height and two diameters of a number of species of Samoan corals. In addition he took a series of 'before and after' photographs to illustrate the changes in colony size and form with time, and carried out a series of transplant studies in different parts of the reef. Notably he made some observations with a diving hood in Samoa and clearly pointed out the differences between conditions on the reef flat, where most early growth studies were carried out, and the deeper reef areas—a point too often forgotten or ignored even today.

Edmondson (1929) reviewed much of the earlier work on coral growth as well as conducting experimental studies on Hawaiian corals. He measured linear growth increments in species of *Porites* and *Pocillopora* in a number of localities on Oahu and recorded linear growth measures for species of *Cyphastrea*, *Montipora*, *Stephanaria* (= *Psammacora*), *Pavona*, *Leptastrea* and, as noted above, *Fungia*. Manton (1932) measured increase in length of branch tips of *Pocillopora bulbosa* (= *P. damicornis*) on the Great Barrier Reef, but was more concerned with the mode of addition of new polyps (see below, p. 189). Vaughan (1915a,b) summarized four years' records on diameters and heights of Florida corals, both transplants and controls. Shinn (1966) measured the increase in length of the tips of the branching coral, *Acropora cervicornis*, in the Florida region in an effort to use differences in growth rate as an environmental indicator. He also (1972) drove spikes into heads of the massive corals *Diploria strigosa* and *Montastrea annularis* and measured growth over a period of ten years by the rate of coral encroachment on the spikes. Lewis, Axelson, Goodbody, Page and Chislett (1968) made comparative measurements of the growth of transplanted fragments of four species of corals in Jamaica and Barbados.

The use of Alizarin Red S to stain the skeleton deposited by living corals was developed by Barnes (1970, 1972). Incubation of the growing coral in a container in which the dye has been dissolved in sea water can be done in the laboratory; in the field, the use of plastic bags permits staining the coral without detaching it from the substratum. This technique provides a visible skeletal time base against which subsequent growth may be measured when the coral is sacrificed and sectioned. Glynn and Stewart (1973) have used this method to study environmental controls over the growth of *Pocillopora*

damicornis in the Gulf of Panama. Macintyre and Smith (1974) report some general observations based on this technique, and Buddemeier and Kinzie (1975) used it to study short-term growth variations of *Porites lobata* in Hawaii. Lewis (1974b) used the method in controlled growth laboratory experiments on *Favia fragum* in Barbados. The use of dye uptake as a calcification tracer is discussed in a later section.

Barnes (1971) has investigated the potential use of tetracycline as a possible calcification stain or tracer in corals and found it unsuitable.

In subsequent discussions of the applicability and reliability of various methods, a number of considerations will repeatedly appear; we will discuss them in some detail in connection with length measurements and amplify them only insofar as is necessary in the other discussions.

One major point of concern is the modification of 'normal' growth rates by manipulation of the coral during the course of the experiment. There is widespread agreement that injury or shock may retard calcification although little documentation of effects exists; however, Wood-Jones (1907) has advanced the opinion that localized injuries may activate a more rapid "repair growth" response. This hypothesis finds some support in recent radiographic studies (see the section on radiography, p. 199); many coral X-rays suggest the presence of denser and/or more rapid linear growth adjacent to damaged areas.

The duration of any such alteration of growth rate is unpredictable. This is also relevant to transplant studies where growth changes are deliberately sought in order to test environmental effects; it is not known to what extent corals may exhibit an induction or adaptation period before fully equilibrating with their new environment. Controls employed in the transplant studies of Maragos (1972) suggest that effects of re-location and weighing were negligible, but most studies do not include these points in their experimental design.

All other factors being equal (a situation which never obtains in coral research) the method of choice should be accurate and precise, would require the least frequent and least intensive specimen manipulation or damage, and would produce data on a sequential series of growth increments in order to test for temporal trends. Methods which are less theoretically desirable may produce perfectly valid data, but require more external validation or caution in acceptance.

Length measurements vary widely in the extent of specimen manipulation. Lewis et al. (1968) excised portions of colonies and transplanted them to artificial substrata before initiating growth measurements, Shinn (1966, 1972) implanted growth base-lines by banding or spiking corals in situ, while the long-term photographic study reported by Mayer (1918) required no direct manipulation of the colonies.

Advantages of length measurements include the simplicity of equipment and design, the direct relationship between the rate of linear extension and many questions in all fields of coral study, and the fact that there are more linear growth data than any other kind, permitting comparison with other results and the use of a respectable base to formulate further questions. Disadvantages include the difficulty and ambiguity of selecting and measuring the relevant corallum dimension(s), and the limitations of accuracy and precision. Measurement uncertainties are probably no less than a few milli-

meters in most cases so that relatively long-term studies (or large uncertainties) must be tolerated.

The data produced are usually for measurements of radial increase in colony size or the rate of branch extension (which sets the upper limit for colony expansion in branching corals). For the maximum significance and utility, it is essential that the direction of measurement (e.g., vertical or horizontal) be specified, as well as whether the measurements are of maximum, 'typical', or average colony dimensions. Estimates of the uncertainties associated with the rate measurements and identification of their sources are extremely useful and all too often lacking from published reports.

The use of skeletal stains to provide an included time base for growth measurements has much in common with other labelling techniques, but has some special features which merit attention. Its disadvantages include the necessary manipulation (including treatment with an acknowledged crystal poison) at the time of staining, and the fact that the measurement itself requires killing the animal, so that successive growth increments can be measured only by repeated staining before sectioning. Its unique advantage, however, is the identification of the entire growth surface at the time of staining so that growth in any direction may be measured or compared when the sample is retrieved and sectioned. This relative freedom from entrapment in one's initial choice of character to be measured is both rare and desirable.

Area. The measurement of the increase in area covered by the coral or in projected area is of particular importance to ecologists interested in the ability of different species to occupy space on the reef substratum. Connell (1973) and Maragos (1974) have studied areal increase of coral size from the point of view of reef occupancy and to determine coral age in order to estimate coral population dynamics. Lewis (1974a) measured the increase in coverage by living coral in 1 m^2 quadrats. He studied three species of Barbados corals, plotting changes in colony size and shape over a one-year period. Lewis (1974b) also studied controls over the areal increase of newly settled colonies of *F. fragum*.

Another area-related measurement of coral growth depends on an assumed relative uniformity of polyp size. If the maximum size of polyps is constant for a given species in a given locality then the change in the number of polyps in a period of time is a measure of the change in amount of living coral. A number of workers have followed changes in polyp numbers with time; this is especially easy when newly settled corals are studied. Abe (1937) and Atoda (1947, 1951a,b) studied newly settled colonies at Palau. Boschma (1929) studied structural development of *Meandrina* (= *Manicina*) *areolata* colonies, which develop by polystomadael budding. Stephenson (1931) studied a species of *Pocillopora* and one of *Porites* from the Great Barrier Reef, and gave detailed diagrams showing the addition of new polyps. Edmondson (1929) and Reed (1971) describe the settling and initial corallum development of some Hawaiian corals. Jokiel, Maragos and Franzisket (in press) describe the rates of polyp addition by newly-settled *Pocillopora damicornis* colonies in a series of controlled-environment growth and reproduction studies.

Because of the very large number of polyps on adult corals the addition of new polyps to the entire colony is very difficult to follow. Nevertheless, Manton (1932) has described the division of polyps on the growing tips of

P. bulbosa (= *P. damicornis*). Stephenson and Stephenson (1933) used photographs to count changes in the number of polyps in several Great Barrier Reef species. Kawakami (1941) studied budding processes in five species from Palau while Kawaguti (1941) and Motoda (1940) have studied the increase in polyp numbers as related to surface area in *Goniastrea.*

The manner of addition of new polyps is an important taxonomic character of corals (Vaughan and Wells, 1943; Wells, 1956, 1973) and there is a very extensive literature regarding this aspect of coral growth. Most of the studies are morphological giving little or no temporal information and will not be discussed here.

A major difficulty in using the increase in the number of polyps as a measure of growth is that this aspect of coral morphology and growth, like so many others, is exceedingly variable. Wijsman-Best (1974) studied the ecological factors influencing the structure of the calices and the number of polyps per unit area of coral surface. She found that in faviid corals both characters are affected by depth, light, and sediment, so that polyp numbers or dimensions may be relevant to colony development or environmental effects, but are unlikely to be directly proportional to surface area, especially on an inter-colony basis.

There are relatively few direct measurements of coral growth by areal increase; several reasons for this may be given. Most simply, the uncertainties inherent in length (or any linear dimension) are compounded when the data are used to produce results relating to $(\text{length})^2$. In addition, as Vaughan (1915a) said, "Stony corals are not suitable subjects for a critical study of the laws of growth rate." This caution is especially important in areal studies where the shape of the living colony may change independently of changes in the surface area of the colony.

The most critical problems are, however, the definition of what area is to be used and its reproducible measurement. The projected area of a colony may be several orders of magnitude smaller than the square-centimetre-by-square-centimetre area of the true corallum surface; measurements of this kind have been made by cutting aluminum foil to fit the complex surface and relating the weight of foil to that of the surface area (Webb, DuPaul, Wiebe, Sottile and Johannes, 1975). This value may in turn be several orders of magnitude smaller than the 'true' surface area measured by gas adsorption or isotopic exchange. An inability to decide which measurements are feasible and relevant together with the probable damage to the coral tissue caused by very detailed surface measurement, combine to ensure that virtually all of the areal measurements made are projected areas on a macroscopic (mm^2 or larger) scale. Some workers (see flux measurement discussion below) have adopted the idea that the quantity of tissue, or of some component such as protein nitrogen, is proportional to surface area. Since it requires destructive analysis, this is not suitable for macroscopic analysis of areal growth.

Volume. While the volume of a coral colony has been measured by displacement of the colony itself or of the colony plus included (between branches) space (Barry, 1965), and by calculation of the volume of calcium carbonate from colony weight and density (see below), it has not been used in specifically growth-oriented studies; this is in part due to the sample manipulation required to measure volume by displacement.

Some examples of volume production estimates for reef rather than coral colony growth studies may be found in Chave, Smith and Roy (1972), where projected areas of coral cover were combined with average vertical coral growth rates to calculate the rate of $CaCO_3$ volume production in order to calculate the budget of carbonate production and reef growth.

Weight. Due to the variability in the shape of coral colonies, their non-uniform growth, and the difficulties in obtaining repeatable measurements from the same colony, all measures of coral growth based on some power of length are subject to various errors. Measurements of weight increase are potentially the most precise and repeatable measures of corallum growth, but until recently the techniques used often caused, or were suspected of causing, some damage to the living coral.

Vaughan (1915a) discusses some of the problems involved in measuring increase in weight; early studies employing this technique include those of Gardiner (1901), Mayor (1924), Edmondson (1929), and Abe (1940). Bak (1973, 1974) reviews this earlier work, describes a system of underwater weight determination, and gives the results of his studies in Curaçao.

Jokiel, Maragos and Franzisket (in press) also review and give descriptions of a series of weighing techniques which may be applied in the field or in laboratory experiments. Depending on the particular technique used a precision of from 0·1 mg to 2 g can be repeatably obtained. Maragos (1972, in press) used a similar technique in his studies of Hawaiian corals, and developed a normalized measure of growth, the mean solid radius, R. As derived by Maragos, $R = \sqrt[3]{w/2\pi D}$ (where w is the weight and D the density) and represents the equivalent colony radius of an ideal hemispherical colony of the same mass as the one measured. This permits a comparison of colony calcification independent of geometry; growth either as change in R or as change in mass per unit (equivalent) surface area may be calculated from this geometrical transformation.

Weight measurements have the advantages of sensitivity, repeatability, and the capacity for whole-colony studies. The disadvantages include the necessity for substantial amounts of specimen manipulation, and the need to find a basis for the comparison of weight gains. Both gross weight change and percentage change present interpretational difficulties because of their dependence on colony size or growth form; the mean solid radius provides a measure for normalizing the increase in weight of a wide variety of corallum sizes and forms, and substantially increases the utility of weight measurements.

Calcification flux measurements

Measurement of the rate of flux of a real or surrogate skeletal constituent across the tissue layer must necessarily measure the rate of calcification; a number of approaches to this type of study have been developed.

Change in water chemistry. Probably the earliest attempt at measurements of chemical flux was that of Kawaguti and Sakumoto (1948) who measured the decrease in calcium content in the water in aquaria containing calcifying corals. Unfortunately, the amount of calcium depletion that can be readily measured is also probably adequate to depress the calcification rate of

the corals. Goreau and Bowen (1955) attempted to measure calcification of *Astrangea danae* by monitoring the decrease in ^{45}Ca activity of labelled incubation water, but were not able to detect any measurable uptake.

Another chemical method is that recently developed by Smith and Kinsey (in press) and which is a refinement of the techniques previously applied to studies of community metabolism (Smith, 1973; Kinsey, 1972). This involves the measurement of changes in pH and alkalinity (or some other CO_2-system parameter) in the water in which the coral is incubated. High precision methods are available for measuring changes in these quantities which are well within the range of 'normal' fluctuations (and to which, therefore, the coral is presumably rather insensitive). The pH-alkalinity method is a laboratory technique requiring extensive sample manipulation, and cannot readily provide data on small areas or specific growth dimensions. Its sensitivity does not approach that of the tracer methods discussed below. It has the advantages, however, of permitting repeated measurements (by successively short incubations) on the same specimen, and the data may be partitioned to provide information on both the organic carbon budget and the inorganic calcification rate.

Staining. A variation on the staining method described above was used by Lamberts (1973, 1974). Instead of measuring linear growth by the distance between the stain line and the coral surface, portions of the stained skeleton were dissolved and the total amount of alizarin laid down during a period of time measured spectrophotometrically. If the concentration of stain in the water and duration of exposure are known, this may be calibrated in terms of $CaCO_3$ deposition. Lamberts (1974) has shown a correlation between rates measured by this alizarin method and those from ^{45}Ca uptake; however, his (Lamberts, 1973) incubation procedures make it impossible to conclude that the alizarin itself is completely without effect on the normal calcification of coral. The method requires sample manipulation and is a one-time destructive analysis; its major advantage over isotope studies appears to be the simplicity and safety of the 'tracer' agent and its analytical determination.

Radioisotope uptake. The use of ^{45}Ca as a calcification tracer, as developed by Goreau (1959), can provide an extremely sensitive and precise measure of short-term (minutes to hours) calcification rates. A living coral is transferred to an isolated vessel which may be a laboratory aquarium or a sealable container (e.g., plastic bag, bell jar, etc.) which is returned to the original growth location to duplicate as closely as possible the normal growth environment. The sea water in the container is innoculated with ^{45}Ca solution and, after a known incubation time (normally with aeration and stirring), all or part of the specimen is sacrificed, the calcium carbonate dissolved, and its radioactivity measured. If the initial specific activity of the calcium in the sea water is measured and proper corrections made for non-calcification uptake, the coral activity may be transformed into an absolute calcification rate.

For comparative purposes, the calcium uptake must be normalized on the basis of some value relevant to the coral's growth capability. Most workers have followed the lead of Goreau in reporting Ca deposition per unit weight of protein nitrogen in the tissue overlying the skeleton sampled. Although this may be an appropriate physiological measurement, it is not as relevant

to skeletal accretion as the weight of Ca (or $CaCO_3$) per unit area per unit time. If the skeletal density (see below for discussion) is known or can be estimated, these data may then be converted directly to linear growth rates. Goreau and Goreau (1959) presented data on the variability of tissue nitrogen per unit skeletal area as a function of species and location in the colony, while Clausen and Roth (1975b) made a systematic comparison and interconversion of the units.

For the purposes of comparisons within a given coral colony or set of experiments, absolute rate determinations are not necessary provided that the initial incubation activity is constant. Many physiological studies, therefore, report relative calcification rates; depending on the amount of supporting data some of these may be used to estimate approximate absolute growth rates under the conditions reported.

Coral incubation experiments are also made with ^{14}C (as $NaH^{14}CO_3$ or labelled organic compounds) to study photosynthesis, either alone or along with calcification studies. Table I summarizes the radioisotope tracer studies relevant to coral calcification; only a minority yield growth or absolute calcification rates directly, but all deal at least peripherally with calcification rates or mechanisms.

As mentioned above, the major advantage of the method is its extreme sensitivity, making possible quantitative measurements of calcification in coral fragments weighing fractions of a gram over periods of minutes. In exchange for this advantage, a number of disadvantages must be tolerated. This method requires rather extensive specimen manipulation, and the incubation in a limited body of water is necessarily a departure from normal growth conditions. For this reason, incubation must be limited to periods of a few hours or less (a point not recognized by all investigators) in order to avoid deterioration of the calcification response (Clausen and Roth, 1975b). The analysis is destructive, so comparisons must be made between different, ostensibly equivalent, colonies or pieces of a colony. The choice and measurement of the rate normalizing measurement (surface area, tissue nitrogen, etc.) can be a substantial additional source of uncertainty in determining both absolute and relative growth rates, and the identification of an appropriate method or value for blanks or zero-calcification uptake is a major problem in cases where low absolute calcification values are measured. Finally, the above problems, in combination with various sources of short-term variability in coral growth (see below) necessitate a statistical approach to the interpretation of the results and this complicates extrapolation to longer-term growth rates. On a practical level, the method requires training and instruments not always readily available, and radioactivity measurements need both more care and more money than most of the other methods discussed.

RETROSPECTIVE

Colony size

Because of the obvious advantages inherent in freedom from possible experimenter-induced growth perturbations and access to a longer time period than is convenient for real-time experiments, interest in retrospective growth-rate measurements has been evident from the earliest days of coral studies. A number of the earlier estimates of increase in coral size were made on colonies

TABLE I

Radioisotope studies of calcification: [a]photosynthesis data only; no calcification data. [b]cpm, counts/min; dpm, disintegrations/min.

Reference	Species	Location	Lab. (L) Field (F)	Isotope	Units reported[b]	Experimental details	Comments
Goreau, 1959	*Acropora conferta*	Enewetak	L	^{45}Ca	μg Ca/mgN/h	Light/dark calcification ratios; symbiotic vs. aposymbiotic calcification; rates of apical vs. lateral polyps; effects of location within colony; effects of carbonic anhydrase inhibitor; extent of isotope exchange with dead skeleton	Incubation times >3 h; *Porolithon* sp. also studied
	Montipora verrucosa, *Porites compressa*, *Pocillopora damicornis*	Hawaii					
	Various (6 spp.)	Jamaica					
Goreau and Goreau, 1959	Various (15 spp.)	Jamaica	F	^{45}Ca	μg Ca/mgN/h; μg Ca/h/cm^2	Effects of: location within colony; light intensity; loss of zooxanthellae. Protein N content of tissue as function of surface area, species, location in colony	Depths 1–12 ft; incubation times 4–8 h (mid-day)
Goreau and Goreau, 1960a	*Manicina areolata*	Jamaica	L	^{45}Ca	mg Ca/g (gross wet wt); mg Ca/mgN	Colony wt vs. N content; performance of symbiotic and aposymbiotic coralla; calcification as function of size	50 h incubation; used colonies 0·05–150 g gross wt
Goreau and Goreau, 1960b	Various (7 spp.)	Puerto Rico	L	^{45}Ca	cpm/mg Ca	Loss of ^{45}Ca by labelled corals to unlabelled seawater; effects on skeletal exchange of living and dead coenosarc; comparison of exchange with aposymbiotic and inhibited calcification	Methodological study; growth/calcification rates not derivable

Goreau, 1961							Popular summary of foregoing refs.; useful figure of calcification gradients
Goreau, 1963	*Acropora cervicornis*, *Porites porites*, *Millepora complanata*, +various algae	Jamaica	F	^{45}Ca ^{14}C	μg X/mgN/h; g X deposited/h total g X (X = C or Ca)	Light/dark ratios for calcification and photosynthesis; fixation of skeletal Ca and C, and tissue C; relationship of calcification, photosynthesis, %N and (chlorophyll *a*) to position on branch; comparison of corals and coralline algae	1·5–2·5 h incubation. Considers depth, light effects on growth form and species distributions
Yamazato, 1966, 1970	*Fungia scutaria*, *Porites compressa*	Hawaii	L	^{45}Ca ^{32}P	mg Ca/g/h mg P/g/h	Effects of: light, salinity, Ca^{++} and $PO_4 \equiv$ concen., aposymbiosis; phosphorous metabolism	Small colonies used; variable incubation times
Pearse, 1970							Initial report of data presented by Pearse, 1971
Pearse, 1971	*Fungia scutaria*	Hawaii	L	^{45}Ca ^{14}C	cpm/mg $CaCO_3$	Effect of light on skeletal C and Ca uptake; skeletal deposition of ^{14}C from ingested food	Small specimens; relative data; demonstration of metabolic CO_2 in skeleton
Pearse and Muscatine, 1971	*Acropora cervicornis*	Jamaica	L	^{45}Ca ^{14}C	cpm/μg protein N (C and Ca)	Tissue ^{14}C and skeletal ^{45}Ca uptake as a function of light, zooxanthellae concen; and location on branch; photosynthate composition and translocation	Approx. absolute rate estimable; clear demonstration of translocation effects
Clausen, 1971	*Pocillopora damicornis*	Hawaii	L	^{45}Ca	dpm/mg $CaCO_3$	Effect of temperature on calcification in branch tips; relationship of tip wt to protein N and no. of calices; activation energy of calcification	Approx. absolute rates estimable

TABLE I—*continued*

Reference	Species	Location	Lab. (L) Field (F)	Isotope	Units reported	Experimental details	Comments
Cooksey and Cooksey, 1972[a]	*Siderasterea siderea*, *Montastrea annularis*	Virgin Is.	F	^{14}C	cpm/cm² (tissue)	Speciation and tissue residence times of photosynthetically fixed carbon	No calcification data presented or derivable
Taylor, 1973[a]	Various (7 spp.)	Jamaica, Florida	F	^{14}C	g C/m²/h	Photosynthetic rates; photosynthate pathways and residence times	No calcification data; primarily review
Barnes and Taylor, 1973	*Montastrea annularis*	Jamaica, Florida	F	^{14}C ^{45}Ca	dpm/cm² dpm/cm²/h	Calcification and photosynthetic rates as function of light, depth and growth form; transplant effects	24-h incubation; absolute calcification rates calculable
Vandermeulen and Muscatine, 1974	*Pocillopora damicornis*	Hawaii	L	^{45}Ca ^{14}C	cpm/mg N	Effects of light and various organic additives on photosynthesis and calcification	Relative data; absolute rates estimable. Review of mechanism proposals
Crossland and Barnes, 1974	*Acropora acuminata*+ others (3)	Great Barrier Reef	L	^{45}Ca ^{14}C	μg Ca; μg C; dpm Ca or C (all $\approx h^{-1}$)	Tests of proposed NH_3/urea cycle calcification mechanism; photosynthate speciation; inhibition effects	Relative data only
Clausen and Roth, 1975a	*Pocillopora damicornis*	Enewetak, Hawaii	L	^{45}Ca	ng $CaCO_3$/mm²/h²	Effects of ambient temperature and specimen history on calcification rates	Comparison of 0·5, 1·0 and 1·5 h incubations
Clausen and Roth, 1975b	*Pocillopora damicornis*, *Porites compressa*	Hawaii	L	^{45}Ca	ng $CaCO_3$/mm²/h²	Comparison of wt, tissue wt, protein N and surface area as normalizing parameters; effects of light, position in colony, diurnal phase, and incubation time; comparison of lab. and field growth rates	Methodological study; comparison with Goreau and Goreau, 1959
Vandermeulen and Muscatine (pers. comm.)	*Pocillopora damicornis*	Hawaii	L	^{45}Ca ^{14}C	dpm/μg prot.-N/30 min	Diurnal cycles, light intensity effects and phase relationships in photosynthesis and calcification	Approx. absolute rates estimable

attached to substrata of known age. Agassiz (1890) gives the sizes of three species of Caribbean corals in heights above a cable that had been submerged for seven years. Gardiner (1901) gives weight increments for five *Stylophora* and *Pocillopora* from Fiji which grew on a chain that had been submerged for 1,030 days. Iams (1969) uses dated substrata around Bermuda to obtain linear growth estimates for *Monastrea annularis* and *Diploria strigosa*. The use of fortuitously recovered colonies will always give minimum estimates of their growth rate and it is difficult to ascribe variation in the results to differences in either the time of settling or other factors. These issues have been considered by Roy and Smith (1970) in an extensive statistical study of the sizes and weights of colonies of *Pocillopora ligulata* retrieved from a boat hull of known history at Fanning Island. Maragos (1972) analysed these same data using the solid mean radius method. Grigg and Maragos (1974) measured the size distribution of colonies on various dated lava flows.

Another retrospective measure of increase in colony size is described by LeConte (1875), who estimates the rate of increase in heights of *Acropora palmata* colonies whose tips are periodically killed by seasonal low tides; the method is conceptually similar to Krempf's (1934) observations on micro-atolls.

A similar time measurement has been described by Gardiner (1903) who estimated the time required to close passes that were periodically dredged through the reef in the Maldives. Sewell (1935 in Yonge, 1940) gives a similar measurement from changes in the charted depth of a channel in the Andaman Islands. These measures, while not useful in determining rate of growth of coral colonies, provide estimates of the possible rates of reef growth. This kind of information is, however, notoriously subjective.

Radiometric dating

Radiometric methods for determining coral growth rates include both the measurement of the decay of naturally-occurring radionuclides incorporated into the skeleton at the time of deposition and the location in the skeleton of artificial radionuclide concentrations resulting from pulses of environmental contamination occurring at known times in the past. The latter is experimentally the simpler and more precise, but is somewhat limited in its applicability. Knutson, Buddemeier and Smith (1972), Knutson and Buddemeier (1973), Buddemeier, Maragos and Knutson (1974), and Noshkin, Wong, Eagle and Gatrousis (1975) have all dated coral growth by the use of known-age fallout inclusions in corals from the former nuclear test sites of Enewetak and Bikini atolls. Global fallout patterns, primarily of ^{90}Sr and excess ^{14}C, have also been used to measure growth rates in corals from places where there have been no local pulsed inputs of radioactivity (Knutson and Buddemeier, 1973; Moore, Krishnaswami and Bhat, 1973; Moore and Krishnaswami, 1974). Naturally occurring radionuclides potentially suitable for measurement of coral growth rates on a time scale of years to decades are ^{228}Ra and ^{210}Pb. These methods have been investigated or applied by Moore and Krishnaswami (1972, 1974), Moore et al. (1973), Dodge and Thomson (1974), and Noshkin et al. (1975).

These methods have the advantages common to all retrospective methods; their disadvantages include limitations of the locations, times or time periods

measurable, size of sample required and the technical sophistication, time and instrumentation necessary for some of the measurements.

All the radiometric studies cited have been made in conjunction with or subsequently compared with X-radiographic growth pattern studies on the same specimens (see below). The results from these two completely independent methods of retrospective growth measurement have in every case agreed to within the uncertainties inherent in the measurements. This has provided mutual confirmation of the annual nature of the skeletal growth patterns and the validity of the necessary assumptions about marine radionuclide concentrations and their reflection in coral skeletons. This rapid intercalibration of independent methods is the exception rather than the rule in coral growth studies, and has provided a data base and a methodological confidence which is largely responsible for the recent and continuing rapid expansion of coral growth studies and the use of corals as environmental samplers and indicators.

Skeletal growth pattern analysis

It has long been recognized that corals contain regular growth patterns in their skeletons. The works of Krempf (1934, 1935), Abe (1940), and of Ma (1933, 1934a,b, 1937, 1957, 1958, 1959, 1960) were based on visual identification of patterns in skeletal structure which were presumed to represent annual increments of growth. In particular, Ma (1957) gives "annual growth values" for more than 500 species of corals from a wide range of tropical and subtropical environments. Although this "annual growth value" is not unequivocally defined, it is apparently the linear radial increase in colony size. (Since some of Ma's works have not achieved wide distribution it is comforting to note that many of the same data appear in more than one publication.) Although subsequent work has confirmed the probable validity of these observations, they received little attention when initially published. Recent interest in the subject arises primarily from the work of Wells (1963), whose observations on growth patterns in fossil corals led him to look for and identify daily and annual pattern groupings on the epitheca of contemporary *Manicina areolata.*

Growth patterns in fossil corals and other organisms have attracted the attention of geophysicists who have attempted to use this apparent record of changes in the day/month/year ratios to deduce the history of the earth–moon system. These studies are not discussed in detail here, since earlier work has been adequately reviewed by Scrutton and Hipkin (1973) and more recent observations are given in the volume edited by Rosenberg and Runcorn (1975).

Epithecal and internal skeletal growth patterns in contemporary corals were studied by Barnes (1970, 1972), who used a sophisticated combination of alizarin staining, in vivo manipulation and scanning electron microscopy to study the accretion of skeletal carbonate and the origin and true periodicity of apparently daily growth patterns. His observations of microstructure are of fundamental importance to current ideas of skeletal development, and his conclusions about the 'daily' epithecal patterns in various corals are that they are basically a daily phenomenon, but are too easily suppressed or duplicated by environmental conditions to provide a highly accurate chronology. The scanning electron microscopy studies of Jell (1974), although not focused on

chronometric or growth rate issues, also provide evidence of internal skeletal patterns, including the possible grouping of daily structures into tidal cycles. Grigg (1974) has reported annual growth lines in gorgonian corals.

One of the most rapidly developing areas of coral research was initiated by the observation (Knutson, Buddemeier and Smith, 1972) that contemporary hermatypic corals exhibit seasonal variations in the bulk density of the deposited skeleton. These density patterns are easily detected by X-radiographic techniques; the methodology is described by Buddemeier (in press). The annual nature of these pairs of high and low density bands normal to the axis of growth has been amply confirmed by comparison with chronologies from radioactively labelled environments (Knutson et al., 1972; Knutson and Buddemeier, 1973; Buddemeier et al., 1974; Moore and Krishnaswami, 1974; Noshkin et al., 1975), by the general agreement between radiographic growth rates and those from conventional radiometric dating (Moore and Krishnaswami, 1974; Dodge and Thomson, 1974), and by general agreement with real-time measurements (see Table II).

The development of the radiographic technique has rendered almost trivial the previously unsolved problem of measuring long-term growth rates and growth histories retrospectively, and all of the papers cited in this category contain either direct or readily derivable linear growth rate data for corals. In addition, Dodge and Thomson (1974), Buddemeier (1974), Buddemeier et al. (1974), and Baker (1975) report quantitative measurements of skeletal density and density variations; these permit a conversion of linear growth rates to approximate specific mass deposition rates (g $CaCO_3/cm^2/yr$). Other data on the bulk density of coral skeletons may be found in the papers of Sargent and Austin (1949), Odum and Odum (1955), Roy and Smith (1970), Maragos (1972), and Barnes and Taylor (1973). Further discussions of the method and the physical nature of the density variations are given by Macintyre and Smith (1974), Buddemeier (1974) and Buddemeier and Kinzie (1975); the latter two publications also consider the question of sub-annual density fine structure within the bands and suggest that they may represent lunar cycles in coral calcification.

A rapidly expanding sub-discipline in the field of coral growth seeks to use corals as environmental recorders, either by the measurement of the magnitude and pattern of annual growth or through chemical or isotopic analysis of band-dated samples. Questions of colony morphogenesis and the significance and origin of different growth forms have been considered by Macintyre and Smith (1974) and by Glynn (1974). Growth pattern or rate analysis as a function of environment has been undertaken by Dodge, Aller and Thomson (1974), Aller and Dodge (1974), Dodge and Thomson (1974), Buddemeier et al. (1974), Weber and White (1974, in press), Weber, White and Weber (1975a), Baker (1975), Baker and Weber (1975), and has been touched upon in many of the other radiography-oriented papers cited. The chronology of detrital inclusions has been correlated with sedimentation history by Barnard, Macintyre and Pierce (1974), Macintyre and Smith (1974) and Moore and Krishnaswami (1974). Studies of skeletal radioisotope inclusions are cited in the preceding sections; stable isotope analyses combined with radiographic growth band analysis has been performed by Walsh (1975) and Weber, Deines, White and Weber (1975b, in press). Minor element skeletal content as a function of density banding and environment has been studied by

Houck (1975), and mineralogy variations have been reported by Houck, Buddemeier and Chave (1975).

In discussing the relative merits of studies of coral growth based on growth patterns, we will restrict ourselves to the radiographic method, which is the only one to attain widespread application to contemporary corals. It will be readily evident which of our comments are applicable to the other pattern-based methods. The advantages of this approach to growth studies are its complete freedom from experimental artifacts in the growth record (except, of course, where radiographic methods are combined with real-time techniques), its applicability to time scales and environments for which direct observation is impractical, the ability to study growth variations as a function of both time and colony form as well as average rates, and the availability of 'dated' samples for chemical, mineralogical or isotopic analysis. Among its disadvantages must be numbered the fact that time increments of significantly less than a year cannot at present be measured with precision (although there remains hope that lunar and daily skeletal patterns may ultimately be intercalibrated with the seasonal patterns), the fact that the band pattern is annual on the average but does not undergo its density transitions on any conveniently reproducible calendar date, the undeniable personal skill which goes into sample preparation and band identification and measurement, and the fact that the method has so far been successfully applied only to massive and sturdy digitate growth forms.

OTHER METHODS

A large number of coral studies relate to the subject of growth without making or using any observations on growth or growth rates. Most of these lie outside of the scope of this review; however, studies of the calcification mechanism (see above) and environmental controls over calcification rate and skeletal chemistry seem so closely tied to the subject of growth in general as to merit discussion. The intention here is not to provide a complete review of everything related to skeletal accretion, but to provide access to the literature by citing the more recent and relevant papers on important aspects of the relationship between skeletogenesis and growth environment.

Numerous workers have studied the trace and minor element composition of coral skeletons as a function of temperature, depth, species, and, recently, density bands (Houck, 1975). With the exception of the radiometric studies cited above, the growth correlations revealed by these studies remain tantalizing rather than convincing. Weber (1973) presents data on the Sr content of coral skeletons and a review of the literature on trace and minor element compositions in general; he also cites growth rate data on Great Barrier Reef corals derived from a report by Woodhead (1971). Weber (1974b) also gives some analyses of magnesium in coral skeletons. Although many of the authors cited above discuss questions of growth morphology in connection with growth rate, papers devoted exclusively to consideration of growth form and plasticity have been published by Barnes (1973) and Weber (1974c), the latter relating his arguments to stable isotope (carbon and oxygen) variations in the skeleton. Extensive $^{18}O_2/^{16}O_2$ studies of bulk coral samples have been made by Weber and Woodhead (1972); Weber (1974a) has discussed the significance of $^{13}C/^{12}C$ variations in bulk samples to the

calcification process. Land, Lang and Barnes (1975), have related intra-colony variations in both isotopes to the relative extension rates of different skeletal components. The tissue carbon isotope composition has been investigated by Land, Lang and Smith (1975). Finally, stable isotope variations as a function of density band patterns have been investigated for *Porites lobata* by Walsh (1975), for *P. lutea* by Weber et al. (1975), and for *Montastrea annularis* by Weber, White, Deines, Weber and Baker (1975).

RESULTS AND COMPARISONS

The perceptive reader will by now have noticed that the foregoing review nowhere discusses the results of the various measurements. This is, with apologies for any resultant frustration, deliberate; we consider lists of numbers largely meaningless in view of the number of factors which must be considered in assessing the context and validity of a coral growth measurement. The discussion of results which follows is organized around the most obvious feature of coral skeletal accretion—its variability.

VARIABILITY IN CORAL GROWTH

In order to compare different measurements of growth, comparable units are required. By far the largest body of potentially useful growth rate data is in terms of linear dimension increase, even though it is not clear in every case what dimension is being measured or what is its significance in terms of other dimensions. The other unit of utility is specific mass accretion (e.g., $g/cm^2/h$), which is related to linear increase by the skeletal density. The mean solid radius and the use of area-specific mass accretion rates based on it (Maragos, 1972, in press) permit inter-comparison of weight, flux, and linear dimension measurements of coral growth. These categories of growth measurement, and especially those studies whose results are at least semi-quantitatively interconvertible between the different concepts and units, serve as the focus for our discussion of growth rates.

Coral growth is variable on all accessible time scales: hours to days, weeks to months, and seasons to years. Some of the variation is systematic, at least in a qualitative sense. There are definite systematic differences between species and possibly between growth forms or ecotypes of the same species. There may be systematic differences with age or size (determinate growth), and there are clearly differences on diurnal, seasonal and possible lunar cycle bases. Environmental variables (depth, temperature, turbidity, etc.) are known to account for some of the observed differences between coralla, and it has already been pointed out that some apparent variations may be experimental artifacts resulting either from the choice of variables measured or from real perturbations of the normal growth rate. Yet, even when systematic variations are allowed for (as in replicate measurements in a well-designed experiment), a substantial amount of 'noise' remains; this is the present limitation on our ability to identify a single value for the typical or normal growth rate of a single species in a given environment.

The basis for the ensuing discussion is that a normal *range* of growth rates can be associated with a given species in a nearly optimal growth environment, and that this range is probably best represented by the highest cluster

of values of comparable units in the literature. In cases where there are not enough data to evaluate trends or groups (which is the rule rather than the exception) the results of non-manipulative determination on corals in warm water (25–30 °C), well-illuminated, low turbidity, and shallow but protected environments are probably most representative of the optimum value. Since the question of growth determinacy is still unresolved, data on specimens more than 1–3 but less than 10–12 years old are to be preferred as avoiding both juvenile growth spurts and the effects of possible senescence. We first discuss 'optimum' growth rate variations for different species, forms or groups of corals on the different experimental time bases, and then consider the imposition of environmental effects on these 'normal' (here normal is equal to optimal or unperturbed, as with 'normal' 20/20 vision) rates.

Time base considerations

Short-term measurements. Radioisotope uptake studies provide the only major source of data on calcification rates over the time scale of hours. While the experiments inflict substantial trauma on the specimen and incubation times of more than a few hours almost certainly lead to systematically low values, some quantitative data and rather more qualitative comparisons are available.

Random variations show up most clearly as a dispersion in replicate determinations. The papers of Goreau (1959, 1963), Goreau and Goreau (1959, 1960a), Clausen (1971), Clausen and Roth (1975a,b) and Vandermeulen and Muscatine (pers. comm.) all indicate reasonable experimental design and have data in a form permitting assessment of variance. These results indicate that coefficients of variation of pooled results are typically in the range of 20–30%, but with some higher and some lower. The extreme spread within a group of samples is larger, and may range over a factor of two to three. This unpredictable variation is superimposed on the recognized diurnal cycle in calcification, which has been characterized by light/dark calcification ratios (L/D) in a number of studies (all ratios discussed are based on Ca deposition per unit area or per unit weight of tissue nitrogen). Goreau and Goreau (1959) found an average light-to-dark calcification ratio of 9·02 (range, 3·2–22·9) for 11 species, and Goreau (1961) gives an L/D ratio of 5·9 (range, 1·3–13·1) for a different group of corals. Yamazato (1966) found ratios of 2·0–2·5 for *Fungia scutaria.* Pearse and Muscatine (1971) found L/D ratios of about 2 to 3 for intact tips of *Acropora cervicornis* and about 1·5 for isolated tips. Barnes and Taylor (1973) give data showing L/D ratios for *Montastrea annularis* ranging from 2·3 to 9·0 with a typical value near to 3·0. Vandermeulen and Muscatine (1974) report L/D ratios ranging from 1·75 to 3·5 for *Pocillopora damicornis* (branch ends only) under various experimental conditions, and of 7·5 for corals subjected to 23 h of light compared with 23 h in the dark. Clausen and Roth (1975b) report L/D values for *P. damicornis* which are lower than those of Vandermeulen and Muscatine and which suggest that there may be an endogenous rhythm or conditioning effect involved, since corals sampled at true midnight and subjected to an artificial light–dark regimen showed no light enhancement (L/D = 0·77) whereas those sampled at noon did (L/D = 1·4). This dependence of calcification

response on the normal light level and/or solar time receives support, although not rigorous confirmation, from the observation by Vandermeulen and Muscatine (pers. comm.) that peak calcification may precede peak photosynthesis and that corals subjected to constant illumination for 24 h show slight evidence of a residual diurnal cycle. This possibility renders suspect many laboratory results conducted without regard for the coral's own 'time sense'.

While it is qualitatively evident that, in general, light enhances calcification, the results of all of the cited ^{45}Ca uptake studies indicate very substantial differences in short-term calcification rates between portions of the same colony and between different colonies of the same species, as well as between different species both in the dark and at a variety of light levels. These make it impossible to derive quantitative L/D values with any confidence. While 'typical' values seem to be greater than two and less than ten, it is clear that L/D values ranging from less than unity to more than 50 may be obtained depending on the specimen, experimental design, and random (or at least unpredictable) variations.

A comparison of short-term flux measurements with longer-term linear growth measurements requires a conversion of the calcification rates per hour to rates per (average) day. Since there are essentially no data on the shape of diurnal calcification curves under natural conditions, nor on the relationship between the experimental light regimes and the average light environment of an in situ coral, a daily calcification rate of 12 times the light hourly value plus 12 times the dark hourly value is probably as good an estimate as any other. It would be unduly optimistic to expect that these interconverted measurements of growth would agree better than to within a factor of two, and although tissue nitrogen values can be very approximately converted to surface areas (Goreau and Goreau, 1959; Clausen and Roth, 1975b) the additional approximations make absolute growth rates based on protein-normalized flux measurements not much better than order of magnitude estimates. For this reason we restrict the discussion which follows to those relatively few studies which report data directly convertible to the mass of skeleton deposited per unit area per unit time.

Goreau and Goreau (1959) give values ranging from a few $\mu gCa/h/cm^2$ for lateral polyps in branching species, to several tens of $\mu gCa/h/cm^2$ for branch tips and massive species. Clausen and Roth (1975a,b) report values for *Porites compressa* and *Pocillopora damicornis* which are typically several tens to several hundreds of ng $CaCO_3/mm^2/h$ (1 μg $Ca/cm^2/h$ = 25 ng $CaCO_3/mm^2/h$) and up to a maximum value of about 2,000 ng $CaCO_3/mm^2/h$; the ranges of values agree quite well. Assuming an average daily rate of one half the light value and a skeletal density of 1·5 g/cm^3, these values give a range of linear growth rate of a few tenths of a mm/yr to 6–7 mm/yr, with the typical values in the region of a few mm/yr. (Clausen and Roth, 1975b, use slightly different but completely reasonable assumptions to calculate vertical growth rates of 20 mm/yr for *P. compressa* and 8 mm/yr for *P. damicornis*, illustrating the conversion uncertainties discussed above.) These values are generally of the correct order of magnitude when compared with linear growth data (see below), but appear somewhat low, especially for the extension rate of branch tips. Branch tips, however, present the greatest difficulties in estimating the appropriate surface area, and the inclusion of any

lateral polyps with the rapidly growing apical polyps will result in an apparent reduction of growth rate. In general, it appears that tracer uptake studies, if carefully performed, provide calcification rates comparable with those obtained from longer-term measurements, albeit with some indications of modest reduction from the 'normal' growth rates. This comparison of observed with 'expected' values is an important confirmation in comparative experiments which assume (often implicitly) that normal growth responses are being observed. Both Goreau and Goreau (1959) and Clausen and Roth (1975b) discuss the conversion of tissue nitrogen rates to area-specific rates. The data of Barnes and Taylor (1973), which may be expressed in terms of specific calcification, yield very low growth rates; this will be discussed later.

Short-term experiments provide essentially all the available data on light/dark ratios, and much of the information on calcification gradients (e.g., apical to lateral) within colonies. Even so, there is not yet available a sufficiently large and reliable body of absolute rate data to permit extensive interspecies comparisons, or to do more than support the more extensive field observations of longer-term growth rates.

Intermediate-term variability

Erratic or variable coral growth was reported as early as 1910 (Wood-Jones) and has since been mentioned by virtually every writer on the subject of coral growth. Most observations are on the variation on a time scale of weeks or longer, because periods of days are inconveniently long for isotope measurements and short for most macroscopic observations.

Shinn (1966) studied the incremental growth in branch length of *Acropora cervicornis* on an approximately monthly basis, showing colony average variations in monthly growth in excess of 50%, and individual branch variations in month-to-month growth ranging over factors of 3 or more. The data of Lewis et al. (1968) on five species of corals in Barbados and Jamaica also show average monthly growth increments varying by a factor of 3, with even more dramatic variations in the growth of individual colonies or branches. Both authors found some negative growth increments, which suggests that the limit of accuracy of underwater length measurements is at the level of 1–3 mm; unfortunately, this is comparable to the mean monthly growth of all but the fastest-growing species.

Maragos (1972) reports normalized weekly growth increments (based on weight changes) for five species of Hawaiian corals. Over a period of 15 months, all species showed extreme values of weekly increments differing by a factor of 2 to 3, with a strong seasonal trend (lower growth rates in winter) and with systematic differences between species. Similar studies in Samoa showed much weaker seasonal trends. The laboratory staining experiments of Lamberts (1973) showed qualitatively the patchiness of calcification on a time scale of days. Buddemeier and Kinzie (1975) used field staining experiments on *Porites lobata* in Hawaii and concluded that some colonies were capable of depositing an amount of skeleton in less than 6 months equivalent to their long-term average annual growth, while others of the same species from the same environment exhibited more regular growth. The density band studies of Buddemeier et al. (1974), Dodge and Thomson (1974) and Weber and White (in press), imply seasonal variations in growth rate of up to a

factor of two or more. These growth pattern studies are, however, only loosely related to the calendar chronology and so cannot yield quantitative rates for periods of less than a few years.

Long-term variability: annual growth rates

In dealing with time periods of years or more we are on somewhat firmer ground with respect to skeletal accretion rates, both because of the number and variety of observations and because of the natural damping of the shorter term oscillations in growth rate discussed above.

If we compare colonies of the same species in equivalent macroenvironments, we find that Vaughan's observations (1915a,b), as well as more recent radiographic measurements (Buddemeier et al., 1974; Dodge and Thomson, 1974; Weber and White, 1974, in press) indicate that intracolony rate variations from year to year and intercolony variations on a scale of decades both normally span a factor of about two. Although these observations have primarily related to massive growth forms, the long-term monthly growth studies cited above give the same conclusion, and various earlier observations (Wood-Jones, 1910; Mayor, 1924) in the literature are consistent with this generalization.

Determinate growth and age effects

The question of determinate growth in corals has received substantial discussion, not all of it well-founded. In the first place, it is essential to remember that the conventional growth laws all relate in some way to the volume of the living organism, which is largely irrelevant to coral growth. No matter how intricately it is arranged in three-dimensional space, the living coral tissue is essentially a two-dimensional structure; the observable volume of a colony is composed primarily of skeleton which requires no metabolic support once deposited. Thus corals may exhibit determinate growth, but it is unlikely to be predictable or rationalizable on the basis of conventional growth laws. Secondly, the problems of inherent variability and environmental effects in coral growth greatly complicate observations and interpretations.

Those who have considered corals, in general, to reach determinate growth limits include, among others, Vaughan (1915a,b) and Mayor (1924). On the other hand, Wood-Jones (1910) considered coral growth indeterminate. More recently, attention has been directed to specific growth forms and species. Goreau and Goreau (1960a) have observed determinate growth in *Manicina areolata*, and Bosch (1967) and Maragos (1972) have come to a similar conclusion for *Fungia scutaria*. These free-living poly- or monostomadeal coralla are not typical colonial reef corals; Goreau and Goreau (1960a) showed that tissue mass is proportional to total mass for *Manicina areolata*, so something approximating to a conventional growth law may be valid for this species. These free-living corals survive on loose sediments, so that a genetic limitation on maximum size may also represent an adaptation to avoid sinking (Goreau and Goreau, 1960a).

Another category of corals which appears to exhibit determinate growth is that which includes many of the species with closely spaced branches. In these, the tissue-bearing surface is highly convoluted; interior (or lateral)

polyps are both different in appearance from the apical polyps, and have clearly different degrees of access to light, organic food, freely circulating water, etc. If a growth form alters the ratio of 'producing' (exterior) to 'consuming' (interior) polyps with increasing size, an overall net steady state in tissue metabolism may be reached which is reflected in slow or no calcification. Aspects of this are discussed by Maragos (1972).

Nevertheless, contrary to the suggestions of Barnes (1973), the retrospective growth data now available (Buddemeier et al., 1974; Dodge and Thomson, 1974) indicate, that for massive growth forms the average growth rate shows no systematic decrease over a time scale of decades, and the analysis of cores (Macintyre and Buddemeier, unpubl.) and outside pieces from colonies metres in diameter (R. Pearson, pers. comm.; Buddemeier, unpubl.), indicates that coral heads centuries old may still be growing at 'normal' rates. It appears that this basically indeterminate colony growth is also common to encrusting growth forms and those branching forms (e.g., *Acropora cervicornis*) which can form new points of support or re-attachment, thus permitting rapid branching without any significant change in the ratio of exterior to interior polyps.

A comparison of growth rate behaviour can be facilitated through the mean solid radius of Maragos (1972), who found that for different species and growth forms (albeit for colonies of less than a few kg of gross weight) ". . . there was no longer any size effect on growth rates when expressed as radius increase."

Some corals such as *Fungia*, *Manicina* (see above) and *Pocillopora meandrina* (Grigg and Maragos, 1974) almost certainly have determinate growth. Other reports of determinate growth are based on the ingenuous use of growth measurements based on ratios or percentage increase; this inevitably yields an apparent decrease in growth rate with size, since it implicitly treats the accumulated exoskeleton as a part of the living organism.

All the above relates primarily to maximum size or old age; growth variations in small or young colonies may also be significant. There appears to be a general subjective agreement, although little quantitative data, that many corals calcify more rapidly during the early stages of growth immediately (possibly up to a few years) after planular settling (Connell, 1973).

Finally, we wish to point out that a further caveat should be entered in considering coral behaviour as it relates to growth form. Wood-Jones (1910) identified three modes of growth of colonial corals: (1) those in which each polyp is equipotent (e.g., *Porites*); (2) those in which the active site of growth is identified with the most recently produced polyps (e.g., *Montipora*); and (3) those in which the active site of growth is the oldest polyp in the colony or branch (e.g., *Acropora*). He also pointed out that all three types could exhibit grossly similar growth morphologies on quite different mechanistic bases. Radiographic methods tend to confirm these categories and offer new insights into the structure of at least some of the corals in the second category. Some branching species show a rather abrupt, systematic change from axial to lateral growth modes; this is illustrated in Figure 1 (see also Fig. 4 in Buddemeier et al., 1974). The lateral growth shows linear, closely aligned polyp tracks and a substantially higher density than the axial growth. Such transitions are evident in, for example, branching forms of *Pavona* and *Psammacora*, but not in similarly shaped colonies of *Porites*. Corals with a

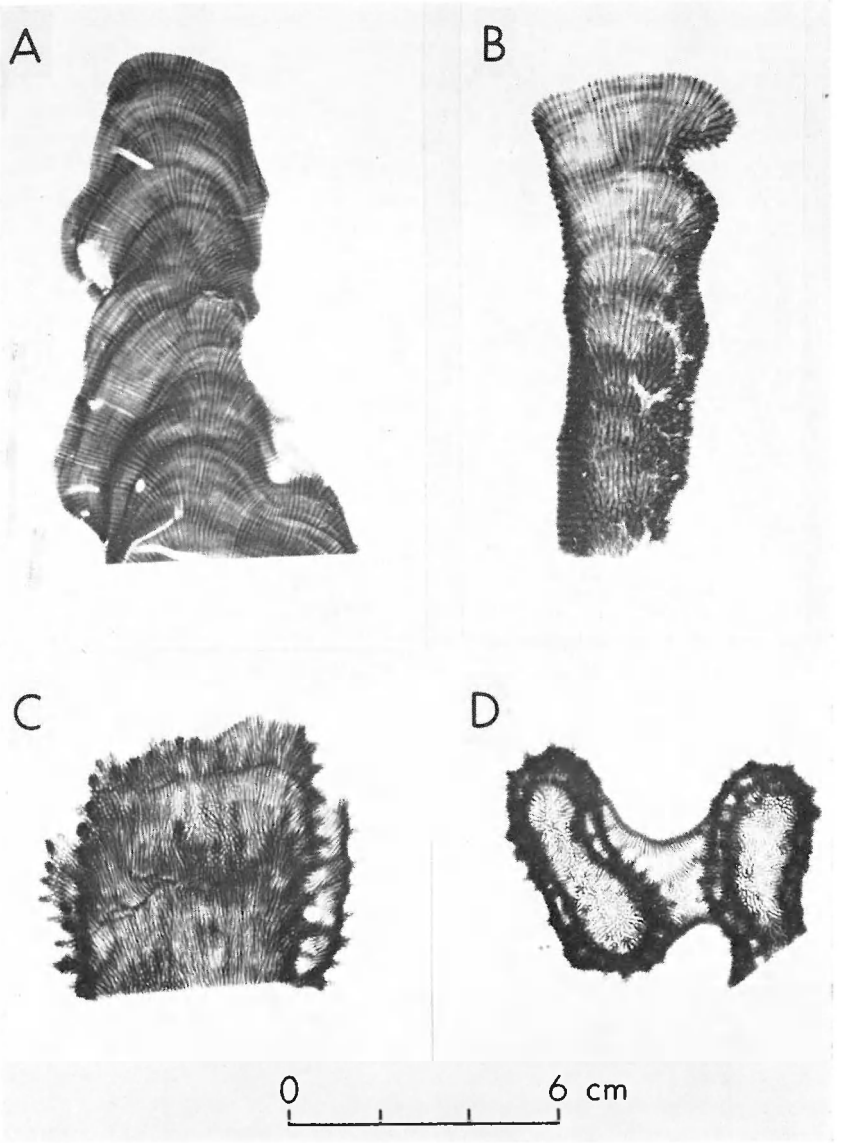

Fig. 1.—Differences in lateral and axial growth in morphologically similar species: all illustrations are X-ray positives of sections through the corallum: A, *Porites* sp. from Christmas Island; seasonal density bands and fine structure are readily apparent, but growth rate and frequency of budding are the only distinctions between apical and lateral-growing polyps: B, *Pavona* sp. from Oahu, Hawaii; lateral growth shows relatively wide polyp spacing and $\approx$1 mm/yr growth rate; axial growth $\approx$13 mm/yr; lateral growth density is $\approx$ twice average vertical growth density, so calcification rates not as sensitive to location in colony as linear growth rates: C, vertical section, and D, horizontal section of *Pocillopora eydouxi* from Enewetak: high-density lateral growth is episodic rather than consistent.

[*To face page 206*]

dense outer layer enhance maintenance of colony form in two ways; namely, by increased structural strength associated with a 'tubular' skeleton and by an increased resistance to boring organisms even without the protection of the living tissue. In the growth mode represented by *P. compressa* the lack of structural integrity is compensated for by its ability to continue and redirect growth after colony detachment and breakup (Dollar, 1975). Thus morphologically similar colonies may represent quite dissimilar strategies and associated metabolic characteristics.

Environmental control over growth

Environmental or ecological factors which could influence coral growth are almost unlimited in number; only slightly less numerous are literature references to qualitative relationships between some aspect of growth and environmental factors. This discussion will concentrate on demonstrated, quantifiable relationships between specific environmental parameters and growth rate, growth form or skeletal composition.

In general, the relationships between coral growth and both community structure and the more biological aspects of water chemistry (productivity, nutrient levels, dissolved organics, oxygen, etc.) have not been explored to a point where skeletal growth correlations can readily be measured. This may well account for some of the unexplained variability in growth, and are certainly worthy of further investigations.

Water chemistry. As noted in the section on radiometric dating (p. 197), coral skeletons seem to be good samplers for ambient trace elements but there is as yet no evidence to suggest that trace elements have any control over coral growth.

Gross water chemistry in the sense of salinity, alkalinity, etc., has been considered to act as a control over coral growth. It has been recognized on the basis of both laboratory and field experiments that, in general, corals can survive only a relatively small variation in salinity, showing substantial mortality below 25‰ and at (Edmondson, 1928), or above (Jokiel, Coles, Guinther, Key, Smith and Townsley, 1974) 40‰. Kinsman (1964), however, reports healthy corals in natural salinities as high as 48‰ in certain restricted areas. Stoddart (1969) reviews many of these observations; unfortunately, there have been no studies of the correlation between survival and growth of the survivors, so that salinity effects on calcification may only be inferred from these studies. Some of the results of field studies of growth rate have systematically included salinity as part of the environmental characterization (e.g., Lewis et al., 1968); Maragos (1972) removed salinity effects on growth and found species-specific response differences with salinity accounting for 36% of the environmental control over the growth of *Montipora verrucosa.*

Smith and Pesret (1974) have suggested that the saturation state of $CaCO_3$ in the water may affect calcification rates. This would represent a complicating factor in that salinity and the ion activity product of $CaCO_3$ will tend to covary, but not necessarily in a linear or consistent fashion. A collection of coral skeletal carbonate deposited in an environment of lower than normal salinity and saturation state of calcium carbonate (Fanning Island lagoon: Smith and Pesret, 1974) was analysed by Houck (1975). Although the records did not

permit an assessment of growth rates, he found that the skeletal contents of Mg and Na were higher and more variable than in corals from chemically 'normal' environments.

Temperature. Stoddart (1969) has reviewed temperature effects on corals; as with salinity, most of the observations are of survival and distribution rather than of growth in any specific sense. Some field correlations of temperature and coral growth have been made on the basis of growth rate differences in different geographic locations. Ma (1957, 1958, etc.) said that "the growth rate of reef corals is directly proportional to the temperature of sea water", but did not derive any constants of proportionality from his extensive collection of data. Weber and White (1974) made radiographic measurements of mean annual growth rates of various *Platygyra* species from 15 Indo-Pacific localities, and by comparison with mean annual water temperatures derived a temperature coefficient of growth of 0·9 mm/yr/°C for the temperature range 23·9° to 29·3 °C. Weber and White (in press) also made a similar study on shallow-water *Montastrea annularis* from various places in the Caribbean, obtaining a temperature-growth coefficient of 0·94 mm/yr/°C over the range 25°–29 °C.

These studies represent the only large-scale latitudinal investigations relating measured growth rates to measured (average) water temperatures. Such observations have the advantage of dealing with locally acclimatized corals in a normal growth situation, but suffer from uncertainty as to whether annual average temperature, as opposed to maximum, minimum or some weighted average, is the most appropriate variable, and uncertainty as to whether average oceanic conditions accurately reflect the corals' micro-environment for growth. The major problem lies, however, with the assumption that temperature is the dominant variable. Decreased seasonality of growth in tropical compared with subtropical situations has often been noted (Ma, 1960, etc.; Lewis et al., 1968; Maragos, 1972; Bak, 1974). While most authors ascribe seasonality to temperature variations, there have been few efforts to remove the effect of other environmental variables (e.g., light) which also exhibit seasonal cycles.

The more common field temperature studies include concurrent monitoring of temperature and growth increments of in situ or transplanted corals. Many such studies, especially the earlier ones reviewed by Glynn (1973b), are primarily qualitative and lack either accurate temperature or accurate growth measurements. Shinn's (1966) study of *Acropora cervicornis* attempted, however, to relate linear growth to ambient water temperature, and Maragos (1972) used statistical techniques to extract the effects of temperature from other environmental variables in his transplant studies of Hawaiian reef corals. Lewis et al. (1968) report water temperatures for the times and sites of their transplant growth studies, but do not attempt any correlation of the data. As with the latitudinal studies, these efforts necessarily suffer from the problems of separating effects of seasonally co-varying environmental variables in order to consider temperature response alone. Yet, more frequent measurements and more reliable local temperature records somewhat compensate for the limited temperature ranges available and the multiplicity of potentially growth-controlling factors.

Laboratory studies of coral temperature responses have the advantages of

the control over variables other than temperature, but they assess growth response under artificial conditions, and the effects of temperature on corals from a single environment may not accurately reflect the effects of adaptation or ecotypes present elsewhere in the natural range of the species. This is exemplified by the finding of Clausen and Roth (1975a) that *Pocillopora damicornis* in Hawaii showed a maximum rate of growth at 27 °C, while the same species from the warmer waters of Enewetak showed two optima at 27° and 31 °C. Coles (1973) studied temperature effects on *Montipora verrucosa* in Hawaii and found 27–28 °C to be optimum for growth. Jokiel et al. (1974) conducted extensive experiments with *M. verrucosa*, *Pocillopora damicornis* and *Fungia scutaria* in Hawaii, and found optima at 26–27 °C for all species. All of these studies found significant adaptation—the coral responses changing over a period of a week or more after the establishment of a new temperature regime.

The laboratory studies all agree on a curvilinear relationship between growth and temperature with an optimum ≈27 °C (26–28 °C); the one experiment with corals from a higher temperature environment (Enewetak) showed a second optimum at 31 °C. Weber and White (1974, in press) and Baker and Weber (1975) indicate that the growth optima for both *Platygyra* spp. and *Montastrea annularis* are in the 28–29 °C range of average annual temperature or higher, that growth-temperature coefficients are 0·9 mm/yr/°C, and that the linear growth rates associated with these optima are 10–11 mm/yr. The temperature coefficients of growth, expressed in terms of the normal optimum rate, are thus about 8–9%/°C. If we consider the plots of growth rate against temperature for the laboratory studies we find that a straight line connecting the lowest measured growth rate with the optimum growth rate has a slope of 10%/°C for *M. verrucosa* and 17% for *Pocillopora damicornis* in the study of Jokiel et al. (1974); the data of Clausen and Roth (1975a) give slopes ranging from 10 to 20% when referred to the 27 °C optimum, and 8–9% when referred to the 31 °C optimum. If we assume that the higher optimum temperatures result from adaptation or an alternative calcification pathway (Clausen and Roth, 1975a) not developed in the Hawaiian corals used in most of the laboratory studies, then the field and laboratory studies agree tolerably well, since the scatter of the data is such that the exact forms of the curves cannot be determined. These temperature coefficients agree well with the lower temperature limits for reef coral abundance (18–20 °C) as deduced from zoogeographic distribution (Wells, 1957), and suggest a striking degree of interspecific and intergeneric similarity of behaviour in terms of temperature-growth responses. As usual, exceptions must be noted; Macintyre and Pilkey (1969) have observed symbiotic corals in water with temperatures reaching as low as 9 °C.

An aspect of temperature-growth relationship which is of particular interest from the standpoint of the use of corals as environmental indicators is that of temperature effects on skeletal composition. Weber has analysed the magnesium content (1974) and strontium content (1973) of large numbers of corals from diverse locations. He concludes that there is no large-scale environmental control over magnesium content, and that systematic variations in strontium content represent species and growth rate effects rather than temperature effects in coral. Houck (1975) studied the magnesium, strontium, sodium and potassium content as functions of seasonal density

bands in corals from several sites, and concluded that there was little evidence for direct environmental control over any of the element concentrations. Stable isotope studies of the $^{18}O_2/^{16}O_2$ ratio have been conducted by Weber and Woodhead (1970, 1972) and Weber et al. (1975) who propose a species-specific temperature-$^{18}O_2$ relationship. This has been contested by Land et al. (1975) who cite large-scale intracolony variations in $^{18}O_2$ content, and Walsh (1975) who finds no consistent seasonal variation between the density bands of massive *Porites* from different locations. The subject of $^{13}C/^{12}C$ variations is discussed under light effects, to which it seems most closely related (p. 211).

Depth. Depth is a mixed environmental variable, including the effects of light, water movement, and in some places temperature and /or salinity; however, it is frequently directly measured, the others being secondarily inferred. Prior to the development of SCUBA, only a few observations of coral growth in other than shallow water environments had been made. Most of the published assertions even after this are essentially qualitative discussions of the effect of depth on growth rate and form. In vivo studies of the relationship between depth and growth rate include those of Maragos (1972) and Dollar (1975), who both made transplant studies of Hawaiian corals, and Barnes and Taylor (1973), who investigated depth dependent calcification and photosynthesis on *Montrastrea annularis* in Jamaica and Florida. Weber (1973) cites depth studies on Great Barrier Reef corals made by Woodhead (1971), while Buddemeier et al. (1974) report radiographic growth data for a number of Enewetak corals at various depths, including a profile of growth rates as a function of depth for *Porites lutea.* Baker (1975) and Baker and Weber (1975) give similar measurements, including density variations with depth, for *Montastrea annularis* at St Croix.

The general results of these studies may be summarized as follows. Within the upper 10–15 m of the water column the response of coral growth to increasing depth is dependent on species and other local environmental factors; general depth trends are not apparent. Below that, growth rate drops precipitously with depth; for *M. annularis* at 30 m it is only 10% of its optimum growth rate (Baker and Weber, 1975) and *Porites lutea* is reduced to less than 40% of its optimum value (Buddemeier et al., 1974). A number of corals show optimum growth at depths appreciably below the surface; this is presumably a light response, and is discussed under that category.

A more common point as regards the effect of depth is the effect on changes in growth form. It has long been known that species with a wide depth range tend toward more flattened (plate-like or encrusting) growth forms with increasing depth. This has customarily been interpreted as a response to changing light levels (Goreau, 1959; Roos, 1967), but other factors such as sedimentation or substratum stability (Glynn, 1973b) may also play a rôle. Barnes (1973) has attempted a somewhat controversial theoretical discussion of growth forms; Baker (1975), Macintyre and Smith (1974) and Barnes and Taylor (1973) all discuss alterations of growth form with depth in *Montastrea annularis.* Other observations are numerous, but essentially qualitative in nature.

Variations in skeletal carbon and oxygen stable isotope ratios as functions of depth have been studied by Land et al. (1975) and Weber et al. (pers.

comm.); Land, Lang and Smith (1975) have also investigated carbon isotope ratios of coral tissue and zooxanthellae at various depths.

Sedimentation. As with many other environmental factors, it has long been qualitatively known that sedimentation is a hazard to corals, that species vary in their ability to recover from siltation, and that burial can be a major cause of coral mortality in many areas. The only rigorously quantitative study is that of Dodge et al. (1974) and Aller and Dodge (1974), where radiographic growth rates for *M. annularis* were correlated with sediment re-suspension at three stations in Jamaica with equivalent depth ($\approx$4 m), temperature, and salinity. Both maximum (range, 0·65–1·00 cm/yr) and average (range, 0·62–0·88 cm/yr) colony growth rates were found to be inversely correlated with the amount of sediment re-suspension. Although the mechanism of the effect is not clear, its existence may explain a substantial amount of micro-environmental variation in coral growth rates.

Light. Although light as a factor in coral calcification has probably been studied more extensively than any other environmental variable, it remains one of the most poorly understood. There are a number of reasons for this such as, the paucity of studies involving the measurement of absolute light intensities at the surface or (particularly) at the coral growth site, the lack of knowledge of the action spectrum for calcification and differential attenuation of various wavelengths with depth and water conditions, the apparent complexity and lack of understanding of the mechanisms of calcification enhancement by zooxanthellar photosynthesis, and the possible existence of endogenous rhythms or non-linear threshold effects which would modify any potentially monotonic relationship between light and growth.

Virtually all of ^{45}Ca and ^{14}C studies cited above relate calcification or photosynthesis to light. The results, however, are generally relative rather than absolute and serve primarily to confirm that light does indeed enhance calcification and photosynthesis, and that corals exhibit a very wide range of L/D values. Three exceptions should be noted. Barnes and Taylor (1973) attempted an ambitious series of depth and controlled light studies, but their data (see below) suggest that their animals were not calcifying normally. Clausen and Roth (1975b) showed that light enhancement is strongly dependent on the time of day, and the data of Vandermeulen and Muscatine (pers. comm.) suggest an inherent rhythm in calcification and a possible decoupling of photosynthesis from calcification.

Field studies which have produced both light and growth data include those of Maragos (1972) and Dollar (1975). Bak (1974) showed that the growth of *M. annularis* and *Madracis mirabilis* in Curaçao was positively correlated with the number of sun hours. Roos (1967) investigated growth form and various metabolic factors as a function of in situ light. Buddemeier et al. (1974) suggested a possible negative correlation between skeletal density and available light, and Buddemeier (1974) attempted to correlate rainfall records with measured skeletal density. Jokiel et al. (1974) report on the only major laboratory controlled-light study using direct rather than radiotracer growth measurements. Walsh (1975) studied growth rates and stable isotope contents of *Porites lobata* and found that skeletal ^{13}C content, but not growth rate, was strongly correlated with sunlight hours.

In addition to the findings already cited, it seems reasonably clear that different species have significantly different light responses—e.g., enough measurements have been made to be sure that *Pocillopora damicornis* has an L/D ratio of less than two, substantially lower than typical values. Surface light intensities are in excess of coral needs and may cause photo-inhibition of calcification in shallow corals. *Monastrea annularis* appears to have a depth optimum of about 10 m (Barnes and Taylor, 1973; Baker and Weber, 1975) while *Montipora verrucosa* seems best adapted to a depth of 2 m (Maragos, 1972; Jokiel et al., 1974). Growth rates are not directly proportional to light intensity, and adaptation apparently exists. If any feature of coral skeletogenesis is related directly to light it appears to be the $^{13}C/^{12}C$ ratio of the skeletal carbonate (Weber, 1974, pers. comm.; Walsh, 1975) but even this apparently direct relationship is conditioned by some other aspect of the coral's metabolism.

GROWTH RATES AND THEIR MEASUREMENT

From the discussion in the preceding section it is evident that sources of variability in coral growth rate are numerous, quantitatively important, and only partly understood. For this reason measurements made without careful consideration of methodology, experimental design and purpose, and environmental factors will yield only another set of ill-characterized and possibly misleading values to add to the already wide range of growth rate values in the literature. This does not mean, however, that true rates of coral growth are either unmeasurable or uninterpretable. With proper precautions as to experimental design and interpretation, consistent and useful results may be obtained by a variety of methods and for various purposes.

We consider it appropriate to pursue the idea that a coral species will exhibit an optimum (maximum average) growth under some particular set of environmental conditions. It appears that for most hermatypic species an optimum growth environment has extreme temperatures within the 25–31 °C range, normal oceanic salinities, a few metres depth, a low sedimentation rate, and protected but not still water. In attempting to identify optimum growth rates from the literature, where environmental conditions are seldom fully specified, we feel that the best approximation is the highest cluster of average rates, with preference for those results which are supported by more than one method or study, and for measurements recognized to be the least likely to perturb or distort growth in the process of measurement.

Only for a few species (or groups of closely related species within a genus) are there enough data to establish a 'species' value for these 'normal' growth rates. Table II gives a selection of representative growth rate values for three such corals. There are, however, marked consistencies in growth behaviour at the growth form level independent of species, and some generalizations about the growth behaviour of classes of corals seem reasonable.

For massive colonial corals in general, recent radiographic studies have dramatically expanded the data with, in general, good agreement with results derived by other methods. If we exclude deep-living or clearly stressed corals, the range of linear growth rates exhibited by the massive corals is from about 4 to 20 mm/yr; however, there is a strong indication that the 'normal' growth rate under optimum conditions is 10–15 mm/yr for maximum growth/

dimension, and 10–12 mm/yr for average growth for most of the massive corals. These values are best established for *Platygyra* and *Montastrea annularis*; although there are indications that faviid corals may grow slightly slower and massive *Porites* slightly faster, the use of these values for typical unstressed growth rates is unlikely to lead to errors of more than a few tens of percentages.

The other extreme of growth rates is probably best represented by *Acropora cervicornis* and similar branching species of *Acropora*. Linear (branch extension) rates of growth are an order of magnitude more rapid than for massive corals (Table II); well documented growth rates of ≈ 100 mm/yr have been reported from clearly suboptimal environments, and several growth rates in excess of 200 mm/yr have been measured. Because of measurement problems and the fewer data available compared to the massive corals, a maximum growth rate of ≈ 200 mm/yr is all that can reasonably be assigned.

Species representing other growth forms (digitate, very finely branching, etc.) exhibit linear growth rates in between these extremes—typically, a few cm/yr. Optimum values on a species or growth form basis are not precisely identifiable, since for only a few species are there adequate statistical data (e.g., *Pocillopora damicornis*). It is interesting to note that Maragos (1972) found mean solid radius increases for *P. damicornis* in Hawaii in the range 0·8–1·3 cm/yr. This is surprisingly close to the vertical growth rates measured by others in Hawaii (see Table II) in spite of the branching form of this species.

If enough measurements from a given locale are made to average the substantial inherent variability, then average growth rates lower than the optimum values must represent the effects of sub-optimal growth environments, determinate growth, or experimental disturbance. Higher growth rates may result from damage repair responses, the use of juvenile animals, or possible inaccurate assessment of the true optimum rate.

An important point to remember is that order of magnitude differences in linear growth rates for different growth forms represent far smaller differences in specific calcification rates on a per colony basis. In Maragos' (1972) study of five colonial Hawaiian corals of substantially different growth forms (*Porites compressa*, *P. lobata*, *Pocillopora damicornis*, *P. meandrina*, and *Montipora verrucosa*) he expressed his weekly weight increment results as changes in mean solid radius. Over the course of 14 months the average weekly values for all species fell in the range of 1×10^{-2} to 3×10^{-2} cm/week, equivalent to 5 to 15 mm/yr of mean solid radius increase. This is strikingly close to that of observed radial increase values for hemispherical massive colonies, suggesting that there may be much more consistency in inherent calcification capability than linear growth rates and growth form comparisons would suggest.

We consider it instructive to conclude this section with a discussion of one of the few corals for which adequate data are available for comparison of both results and methods. *Montastrea annularis* (see Table II) has been studied by a number of workers and techniques. Both real-time dimensional measurements and a number of retrospective radiographic studies in Florida, Jamaica, Barbados and St Croix have yielded linear growth rates of 7 to 11 mm/yr, with 9–11 mm/yr representing the near optimum environments. Goreau and Goreau (1959), working in Jamaica, reported a calcification

TABLE II

*Growth rate measurements for three species of coral using a wide variety of techniques: it is not meant to include all studies on these species but rather to give data so that comparisons can be made between the different methods: three very different growth forms were chosen and species that had been extensively studied were used. *Where a range of growth rates for the same species and environment is given, data are pooled and converted to average rate ± S.D.*

Reference	Method	Location	Growth rate	Converts to (cm/yr)*	Comments
Montastrea annularis					
Vaughan, 1915	Real time-field	Florida	0·5–0·68 cm/yr	0·5–0·68	Upward growth of 47 specimens
Hoffmeister and Multer, 1964	Real time-field	Florida	1·07 cm/yr	1·07	Three year study
Lewis et al., 1968	Real time-field	Barbados Jamaica	1·2–3·6 cm/yr 1·2–6·0 cm/yr	1·93 ± 0·84 2·50 ± 1·08	Upward growth of transplanted fragments
Macintyre and Smith, 1974	Retrospective X-radiographic	Florida Br. Honduras	0·66–0·87 cm/yr	0·66–0·87	Three specimens
Weber and White, 1974	Retrospective X-radiographic	Various	0·41–0·71 cm/yr	0·41–0·71	Various depths; average colony growth
Baker and Weber, 1975	Retrospective X-radiographic	St Croix	0·92–1·04 cm/yr	0·92–1·04	0–15 m deep; average
Aller and Dodge, 1974	Retrospective X-radiographic	Jamaica	0·62–0·88 cm/yr	0·62–0·88	Average colony growth

Goreau, 1959	Isotope uptake	Jamaica	7·3–11·7 μg Ca/mg N/h	0·4	See text (p. 216) for conversion
Pocillopora damicornis					
Stephenson and Stephenson, 1933	Real time-field	Gibraltar	6·2–7·1 cm diameter	3·15–3·59 radius	14 specimens of "*P. bulbosa*"
Manton, 1932	Real time-lab.	Gibraltar	6 mm/0·244 yr	2·45	A single tip of "*P. bulbosa*"
Mayor, 1924	Real time-field	Samoa	0·7–4·0 cm/yr	2·78±1·53	10 specimens; various conditions and forms
Edmondson, 1929	Real time-field	Hawaii	0·13–3·3 cm/yr	1·39±1·17	6 specimens of "*P. caespitosa*"
Glynn and Stewart, 1973	Real time photo. Real time staining	Panama	0·6–7·2 cm/yr	2·37 2·20	The range is for all their studies; the avgs are for one test
Clausen and Roth, 1975b	Isotope uptake	Hawaii	400 ng $CaCO_3$/mm²	0·82	Converted in Clausen and Roth, 1975b
Goreau, 1959	Isotope uptake	Hawaii and Enewetak	7·8 μg Ca/mg N/h	0·16	Converted in Clausen and Roth, 1975b
Acropora spp.					
Tamura and Hada, 1932	Real time-field	Yap	10·17–12·53 cm/yr 22·58 cm/yr	10·17–12·53 22·58	*Acropora abrotanoides* *A. pulchra*
Mayor, 1924	Real time-field	Samoa	13·3 cm/yr 8·5 cm/yr 18·5 cm/yr	13·3 8·5 18·5	*A. teres* *A. vanderhorsti* *A. formosa*
Shinn, 1966	Real time-field	Florida (station "A")	7·0–13·2 cm/yr	10·92±1·64	*A. cervicornis*
Lewis et al., 1968	Real time-field	Barbados Jamaica	3·6–28·8 cm/yr 10·8–43·2 cm/yr	14·5±55·91 26·6±12·88	*A. cervicornis* averaged over 12 months

rate, based on 4–8 h ^{45}Ca incubations on the reef, of $54 \pm 11{\cdot}9$ μg Ca/h/cm, and an L/D ratio of 22·9. If we assume that the coral calcifies at its light value (54) 12 h per day and at its dark value (54/22·9 = 2·4) for the other 12, then this would result in the addition of 0·25 g Ca or 0·62 g $CaCO_3/cm^2$/year. At an average density of 1·6 g/cm^3 (Baker and Weber, 1975), this yields a linear growth rate of 0·39 cm/yr, which although slightly low is not outside the range of values covered by the scatter in the data together with the known uncertainties in some of the assumptions used in the conversion. Barnes and Taylor (1973), also working in Jamaica, incubated samples on the reef for 24 h. Although they report their results as dpm $^{45}Ca/cm^2$/h, they give the initial sea-water activity as 0·07–0·08 μCi ^{45}Ca/ml, and measured a skeletal density of 2·0 g/cm^3 for their shallow animals. On this basis, their *highest* observed 24-h rate (851 dpm/cm^2/h) gives $4{\cdot}5 \times 10^{-2}$ g $CaCO_3/cm^2$/yr or $2{\cdot}2 \times 10^{-2}$ cm. An equivalent growth rate of 0·2 mm/yr is 20–50 times below the observed field values, and is approximately what might be expected had the coral calcified normal for only the first hour of the 24-h incubation period. Whatever the origin of the depressed growth rate, it is doubtful whether conclusions based on differences between abnormal growth behaviours may be reliably interpreted as indicative of normal coral responses. This serves to demonstrate the importance of examining experimental measurements in terms of known coral behaviour, and of making the observations necessary for the production of absolute growth data. On the other hand, the transplant experiments of Lewis et al. (1968) gave linear growth rates of nearly 2 cm/yr in Barbados and 2·5 cm/yr in Jamaica for *M. annularis*. These results are consistent with their measurements on other species—all were significantly higher than any others reported. Since this study was a transplant experiment which utilized rather small colonies and involved extensive relocation, it is possible that the results reflect either rapid juvenile growth or the so-called 'damage repair' response; however, the results are not so completely outside the realm of possibility as to be necessarily invalid, but the reasons for the differences from the field observations are more intriguing (although less accessible) than the data themselves.

SUMMARY AND PROJECTION

CURRENT STATUS OF QUESTIONS

In this section we summarize our assessment of the current state of coral growth studies with respect to the categories of motivating questions given in the Introduction (pp. 183–186) and indicate where we see major unanswered questions related to coral growth.

The growth of reefs

While interest in the rate of reef growth was the impetus for the initiation of growth rate studies, the increase of knowledge on two fronts has weakened the presumption of any causal connection between coral growth and reef growth. First, with increasing knowledge about the processes and structure of reefs, both atoll and otherwise, the complexity of the factors governing

their dynamics has become increasingly obvious. The recognition of the importance of organisms other than corals as both constructional and destructive agents on reefs has reduced the apparent primacy of coral growth rates as major determinants of reef growth. In addition, the great importance of physical factors controlling reef construction and erosion has been shown by the facts that many hundreds of years of structured coral growth can be redistributed overnight by storms (Maragos, Baines and Beveridge, 1973) and that in many cases the potential of coral growth is never realized due to physical or biological factors such as sea level fluctuations (Buddemeier, Smith and Kinzie, 1975), crowding, coral mortality caused by boring organisms (Goreau and Hartman, 1963), killing by *Acanthaster* (Glynn, 1973a), etc. Secondly, the precision of the data on coral growth rates, although poor, still surpasses that of the data available for most other reef-constructing organisms. Furthermore, the detail in which coral growth, especially of the framework builders, is known is much greater than that for reef growth rate measurements. Thus, as a tool for studying reef processes, knowledge concerning coral growth rate is now excessively refined. While studies of reef development remain interesting in their own right, they require little if any further information from the field of coral growth studies.

Biology

As discussed above, the attention of a number of earlier workers turned to the question of coral growth per se. It is easy to understand that the curiosity elicited by corals and the widely varying ideas about their growth would lead to studies aimed at finding out just how fast they grow; however, as with reef growth, the increase in information has largely caused the original goal to become a 'non-question'. There is no single answer to the question of how fast corals grow. Corals are particularly unsuited for the derivation or application of simple growth models because of their extreme variability in growth rates and forms. This variability is due to combinations of species differences, environmental effects, geometry, 'noise' due to temporal variability in the preceding two effects, and methodological differences. The question "how fast do corals grow" is unanswerable simply because corals, although colonial, are not collective. It is, however, precisely this variability which has made the study of coral growth of interest to scientists asking specific questions.

Ecology

The great plasticity of coral growth form, frequently an apparent response to environmental factors, has led to studies of the strategies of corallum evolution and the ontogeny of corals in particular situations. In general, the more corals are studied, the greater the range of their structural and behavioural variability appears to be. In addition, the studies of reefs as ecosystems with physiological and mineralogical components is analogous to the study of the corals themselves. Questions of coral growth rates assume new dimensions when viewed in the light of the flux and re-cycling of both organic and inorganic materials in the system. Finally, corals are significant sources of food and shelter for other members of the reef community. The rate of

increase, both potential and actual, of such a basic component of the ecosystem is clearly important in understanding reefs as entities.

Corals as environmental indicators

This area of research has passed from innocence through optimism into a period of steady but not spectacular progress. The initial hope that the skeletal chemistry or isotope ratios would prove simply and directly interpretable in terms of the physical environments prevailing during growth has largely faded; it is clear that inorganic chemical models alone cannot link coral skeletal chemistry to the environment of deposition, and the physiology and biochemistry of calcification is too poorly understood to allow description of environmental controls on either a theoretical or empirical basis. Nonetheless, correlations do exist, holding out hope of eventual calibration.

It seems likely that historical correlation of coral density band patterns will yield information on marine climate analogous to that obtained from tree rings in the terrestrial case. Such studies are only in their initial stages and much environmental and coral data will have to be processed before statistical validity can be demonstrated.

The tendency of coral skeletons to reflect the ambient concentrations of at least some trace elements in the surrounding waters also appears well demonstrated, but whether these elements are co-precipitated in the skeleton, actively associated with organic matrices or present as particulate inclusions remains to be determined.

The use of coral skeletal characteristics for environmental hindcasting and ecological analysis is a challenging field with substantial promise but elusive answers, many of which may have to wait for an improved understanding of calcification mechanisms and their external control.

Calcification mechanisms

The exact cellular and molecular natures of the calcification process, its enhancement by symbiotic algae, its 'selectivity' in terms of growth form or rates, and the influence of physical factors are the keys to most of the coral growth problems relating to skeletal accretion. Although a number of competent people have devoted considerable attention to the subject for nearly two decades, we have still neither a theoretical, mechanistic understanding nor any very significant predictive ability. This appears to be due, in substantial measure, to the use of sophisticated tracer and biochemical studies in combination with experimental designs producing correlative rather than causal results and rather simplistic approaches to the control or measurement of the factors of the physical environment. Calcification mechanisms merit continued attention, but would seem likely to profit from the increased emphasis on development and from integration of different experimental approaches to skeletal deposition.

RECOMMENDATIONS

In conclusion, we wish to summarize our observations and suggestions. These fall into three basic categories: procedural suggestions which are basically independent of the problem or methodology; identification of some problems

or questions which are almost certainly answerable on the basis of existing concepts and techniques; and identification of more general goals and areas of fruitful research, regardless of their immediate feasibility.

Procedural suggestions

We urge writers to pay particular attention to definitions, both descriptive and operational. Words such as "growth" and environmental terms (e.g., names of seasons) carry intuitive and colloquial connotations, as well as a variety of possible technical definitions; ambiguity yields wasted effort at best, outright misunderstanding at worst.

Growth and calcification measurements should, if at all possible, be placed on an absolute rather than a relative basis, particularly in tracer studies, and the data necessary for conversions to other units should be made available if at all possible. As examples, it requires only a modest additional effort to estimate surface areas in addition to measuring protein nitrogen or to measure density to allow interconversion between linear and mass accretion growth. The ability to compare and evaluate quantitative results is a prerequisite for the development of any coherent concept of coral growth.

In recognition of the variability between species and growth forms, and the variety of coral responses to the environment, it is critical that animals be carefully identified and the environmental characteristics (whether laboratory or field) be fully described. A possible corollary of this is that some types of research may yield better results if concentrated on species and locations for which good data already exist.

Answerable but unanswered questions

The relationship of tissue growth, metabolism, and coral reproduction to variations in the rate or nature of calcification is ripe for investigation. The quantity, chemical composition, and structure of the coral tissue are all experimentally accessible, yet the question of how these and their variations relate to the characteristics of calcification is virtually uninvestigated.

The related questions of determinant as opposed to indeterminant growth, senescence, rates of juvenile calcification, etc., occupy a great deal of space in the literature and still remain topics for lively and frequently ingenuous discussion. The techniques of growth measurement developed within the past few years (sensitive in situ weighing, radiography, staining) should be more than adequate for resolution of these questions for selected species or growth forms.

The use of radiographic growth measurements, especially in correlation with environmental variables, has been empirically expanded well beyond our comprehension of the phenomenon with which we are dealing. It is time for some thoughtful laboratory and field studies of the nature and origins of density variations in coral skeletons and the reliability and significance of their observed periodicities.

Long-term questions

Symbiotic corals are frequently objects of study precisely because of the complexity of their interacting plant–animal system and its response to the

marine environment. In spite of this, focus has been almost exclusively on one aspect of the coral system (photosynthesis, feeding, or environmental response), assuming that the other aspects are either negligible or held constant. What is needed is either greater experimental sophistication in trying to decouple the different response systems (in fact as well as in mind) or a greater conceptual breadth in analysing the results of concurrent variations in a multi-parameter control system.

Related to the above, and with recognition that much thoughtful work has been done, there is a continuing need for testable and clearly differentiable calcification mechanism hypotheses which take into account advances in knowledge of the skeletal structure and chemistry as well as studies of tissue responses.

It is inappropriate to assume that corals are simple analog recorders of environmental stimulus, either individually or statistically, yet this remains the implicit basis for much experimental design. An important first step in breaking this thought pattern would be the investigation of endogenous rhythms in coral metabolism. There is now evidence suggesting they exist on all time scales—daily, monthly, and annual. Their nature, their separability into plant or animal based mechanisms, and their response to entraining external signals should provide substantial insight into the nature of the living coral, and will certainly permit much more intelligent design and interpretation of other experiments.

In spite of a non-linearity of response, the quantification of relationships between coral growth environment and skeletal characteristics remains an important goal at both practical and theoretical levels. Even though the response characteristics of the 'transducer' are not known, the connection between environment and skeleton is physically obvious: it is the living tissue. Yet, the three-way connection of environment-tissue-skeleton is seldom considered as such; geologists and chemists attempt to relate environment directly to skeleton, while biologists consider tissue alone or in relation to one, but not both, of the other elements.

In conclusion, we wish to summarize the theme running throughout our discussion and recommendations by making a plea for a far broader and deeper integration of concepts, knowledge, and disciplinary approaches to what is necessarily a field of study which transcends any single approach.

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Finally, we recognize that all coral growth studies owe much to the guiding spirit of Rafael Pompelley's mouflon (Wells, 1963).

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Note: After considerable soul-searching we have opted for making this bibliography as complete as possible. We have, therefore, included references which were not

available to us at the time of writing but which reliable secondary sources identified as being relevant. These are marked with an asterisk; in view of the well-known dangers of secondary citation we have refrained from basing any substantial discussion or critical interpretation on this material. We have also included a number of items of limited availability (e.g., Master's theses, technical reports, etc.) since photocopy technology and the system of interlibrary loans mean that very few are completely out of reach. Where we were aware of significant works in press we have cited them, but our coverage of the literature after 1974 is of necessity only partial.

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