Aspects of Skeletal Growth in the Indo-Pacific Staghorn Coral *Acropora formosa*

Thesis Submitted by

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for the Degree of Doctor of Philosophy in

the Marine Biology Department

James Cook University of North Queensland

July 1987

ABSTRACT

This thesis examines variations in the branch extension of the staghorn coral Acropora formosa at different spatial and temporal scales. The relationship between branch extension and tissue or area specific calcification is first examined. This is followed by investigations of variation in extension within a colony and between colonies at different depths. Seasonal variations in extension are also examined for several colonies at two different sites. Finally the reproductive biology of A. formosa is described and the possibility of competition in energetic investment between gametogenesis and growth is investigated.

If a simplified model of branch shape and structure is adopted, then linear measurements of branch extension can provide a good index of total skeletal deposition and the rate of calcification. The model assumes that all branches consist of a solid cylinder of uniform width and density, and a tapered cap of varying density. Empirical data which support the predictions of this model are presented. In addition it is shown that the weight of newly extended skeleton is less satisfactory as a measure of total skeletal deposition, than linear extension.

Intra-colony growth variations between different tips in a colony are shown to be correlated with tip colour, shape and skeletal structure. White-tipped branches lack zooxanthellae, are lightly calcified, have a well developed axial corallite, and exhibit a range of extension rates. On the other hand, brown- tipped branches possess zooxanthellae, are heavily calcified, have smaller axial corallites, and exhibit no active branch extension. It is suggested that brown tips arise in zones of unfavourable micro-environment, such as are found in the interior of large arborescent colonies. This may provide a mechanism for avoiding anastomosis, and maintaining the overall form of branching coral colonies.

Significant variations in extension rate were found between colonies growing at three different depths at Davies Reef, a midshelf platform reef. There was a trend in which extension increased with increasing depth. This trend, although obvious in

the first year of sampling, became obscured during the second year, possibly due to over-harvesting. A reciprocal transplant experiment between the shallow and deep colonies indicated that the observed growth differences were environmentally induced, rather than being due to genetically based differences between the colonies. Although extension rates were lower at the shallow site, branching was much higher, and resulted in a higher overall rate of calcification at the shallow site. It is proposed that the higher extension rates at the deep site, are made possible by an increase in translocated metabolites from a greater area of tissue than at the shallow site.

Significant seasonal variations in branch extension were found in 7 colonies for 2 different sites (Davies Reef and Nelly Bay, an inshore fringing reef). Extension rates exhibited 2 maxima and 2 minima per year. Minima occurred during mid-winter and mid to late summer. A multiple linear regression analysis between extension and a variety of environmental parameters was able to explain 28% of the variance in the growth rates. An inhibitory effect for high temperature was incorporated into a temperature index, and this index was found to be the most important parameter in the regression model. It is hypothesized that high summer, and low winter temperatures cause the observed growth minima.

Acropora formosa has an annual gametogenic cycle and spawns once a year during mass multispecific spawning events. The period of peak gametogenesis does not appear to be correlated with any period of reduced branch extension. Isolated colony fragments, as small as single branches 35mm in length, still develop gonads of nearly normal size and fecundity. On the other hand juvenile corals up to 143mm in mean diameter were sterile. Branch fragments greater than 40mm in length, isolated from the parent colony half way through the gametogenic cycle, appear to continue normal gonad development.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. M. Pichon for his encouragement and continued assistance with academic and administrative matters during the course of this thesis. I also thank Prof. H. Choat for encouragement and supervision during the last few months of my candidature.

Many of the ideas in this thesis had their origin in discussions with Dr. D.J. Barnes. For this initial stimulation and subsequent permission to use the laboratory and boat facilities at the Australian Institute of Marine Science, I deeply grateful. Dr. B.E. Chalker also provided considerable advice and support during a major phase of the research for this thesis.

The other members of the James Cook University Coral Reproduction Unit: Peter Harrison, Russ Babcock, Carden Wallace, Andrew Heyward and especially Bette Willis are thanked for their assistance in the field and for stimulating discussions and criticism during various stages of this study.

I am also indebted to a host of people, too numerous to mention, who have assisted me in the field and in the laboratory at one time or another. This work could never have been completed without them. In particular, Eric Longmuir and Sandy Tudhope spent many hours with me in the field and to them I owe a special vote of thanks.

Finally, I would like to thank Alastair Birtles for encouragement and constructive criticisms during the final writing up of this dissertation.

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others is acknowledged in the text and a list of references is given.

ACCESS TO THIS THESIS

I the undersigned, the author of this thesis, understand that the following restriction placed on this thesis will not extend beyond three years from the date on which this thesis is submitted to the University.

I wish to place restriction on access to this thesis as follows:

> I do not wish to place any restrictions on access to this thesis. Any one who can think of some use for it should be congratulated. I myself find it of little value; its too small to be a good door stop, and too big to put under the short leg of my unstable computer table.

James Oliver

This day:

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Chapter 1

General Introduction, Materials and Methods

1.1 Significance and Scope of Coral Growth Studies

Growth is one of the most fundamental biological processes in all metazoan organisms. Scleractinian corals, despite their relatively low phylogenetic position, exhibit growth patterns and responses which are surprisingly complex at both the cellular and colony level. Through the coordinated growth of tissue and aragonitic skeleton, corals form colonies of incredible variety in size and shape. The whole growth process is carried out in concert with endosymbiotic unicellular algae, which not only regulate their growth to maintain stable populations within the coral host (Muscatine and Pool, 1978), but also contribute in ways not fully understood, to the growth of the entire colony.

An understanding of the rates of growth of corals under different conditions is important to several different areas of reef science. In ecological research growth is an important factor in determining the outcome of spatial competition (Connell, 1973; Potts, 1976; Rinkevich & Loya, 1985; Stimson, 1985). In population biology studies rates of growth and final size are important population parameters which can be used in modelling the spatial and temporal dynamics of a community (Loya, 1976; Babcock, 1984,1985) and in managing a renewable resource (Grigg, 1984; Ross, 1984; Oliver, 1985). Growth rate is also a valuable indicator of physiological health in environmental monitoring programs since it is an essential physiological process which responds to a number of different environmental parameters (Shinn, 1966, Neudecker, 1976,1977; Coles et al., 1976; Dodge & Vaisnys, 1977; Hudson, 1981a,b; Hudson et al., 1982). Finally coral growth is an important geological process since it is a primary determinant of overall reef growth, and sediment production (Chave et al., 1972; Smith & Kinsey, 1976; Davies, 1983; Dodge et al., 1983).

Coral growth can be studied at a number of different levels. At the lowest level, one can study the biochemistry and cellular physiology of the calcification process (e.g. Goreau & Goreau, 1960; Clausen & Roth, 1975; Chalker, 1976; Barnes, 1982a,b). Such studies are generally short term in vitro experiments using very small isolated colony fragments. They provide accurate information under controlled laboratory conditions. However due to the specific conditions and the short time period, it can be very difficult to extrapolate the results of such studies into long-term responses in the field.

At the highest level, the growth of entire colonies can be studied over long time periods. Such studies are generally in situ field measurements over a period of a year or more (e.g. Mayor, 1924; Stephenson & Stephenson, 1933; Loya, 1976,1985; Dodge & Vaisnys, 1975; Bak & Luckhurst 1980; Hudson, 1981a). Although these studies provide information on actual performance under real conditions, and are thus directly relevant to the interests of the general fields of study described above, the time period involved, and the possibility of heterogeneous growth within a colony mean that several different growth responses are being integrated spatially and temporally. Consequently, it is difficult to create a model which would predict the response of corals to a specific but untested set of environmental conditions.

In many studies, an intermediate approach is taken, in which the growth of small colony portions are studied over a period of one or two months either in the field or in open circuit aquaria (e.g. Shinn, 1966; Jokiel, 1978; Wellington, 1982; Gladfelter, 1984, Yap & Gomez, 1984). This approach has the advantage of producing data on actual growth (as opposed to calcium incorporation) which is directly useful to most of the general areas of interest described above. In addition it restricts the spatial and temporal variability of growth to a single colony portion over a short period, so that some physiological conclusions regarding the response of a coral to different environmental conditions can be postulated. It is important to stress, however that such intermediate level studies would lack credence without complimentary data from low level in vitro studies which can suggest the most

likely controlling factor in instances where field data result in some ambiguity. Similarly high level studies are important in their ability to verify the predictions made by lower level experiments. In the present study, an intermediate approach to growth measurement will be taken.

1.2 Coral Growth: Theoretical Considerations

"Coral growth" is a broad and somewhat imprecise term. For the purposes of this thesis it will be considered to encompass all processes which lead to the increase in size of an individual coral colony. A colony is considered here to be a single physiologically continuous genotype. Isolated fragments of a single genotype will be considered as individual colonies.

Given this broad definition of coral growth it is important to specify the different processes which contribute to growth and to discuss their relative importance. Equal consideration must also be given to the available methods for measuring these processes.

Tissue Growth

Coral growth consists of two primary processes: tissue growth and skeletal growth. There have been very few studies of tissue growth, and these (Barnes, 1972; Cheney, 1973; Meek, 1981; Gladfelter 1983) have concentrated on specific aspects such as the pattern of cell division near zones of high skeletal growth. In most other growth studies, tissue growth has not been measured since it has (presumably) been assumed that skeletal growth is an adequate index of those aspects of growth which are under investigation. This approach is justified in studies where skeletal growth is the only parameter of interest. In other studies the feature of primary interest is the amount of space occupied by a colony. In such studies, tissue is assumed to form a constant and small proportion of the overall colony volume. While this is true for the majority of scleractinian corals, there are some notable exceptions such as Heliofungia actiniformis, Goniopora spp, and Plerogyra spp. In

these cases, the coral tissue extends well beyond the surface of the skeleton and may exhibit variations in size which are poorly reflected in the skeleton.

Although tissue growth may not in itself be the most important aspect of overall colony growth, it can be a significant factor in determining both the growth rate and the growth form of the skeleton. In terms of skeletal growth rate, variations in tissue growth such as changes in gonad volume, may make varying demands on a limited pool of metabolic energy so that skeletal growth may decline during times of high tissue growth.

In terms of growth form, it has been suggested that under certain circumstances a change in the rate of skeletal deposition might, if not accompanied by a simultaneous change in tissue growth, lead to a change in colony shape. In particular it has been hypothesized by Goreau (1963) and Barnes (1973) that the flattening of hemispherical colonies of Montastrea annularis colonies is due to a decrease in the capacity of the coral to calcify in deep water, without any accompanying change in the ability of the coral tissue to grow. Under such circumstances, a plate-like form permits maximum tissue growth for minimum investment in skeleton.

Finally it is important to point out that even if tissue growth is not itself of interest, a knowledge of the total amount of tissue in a sample from which skeletal growth has been measured, is critical to the calculation of a meaningful value for calcification rate. Clearly, a large colony with a large amount of actively calcifying tissue will deposit more skeleton than a smaller colony with less tissue. If the total amount of skeleton is divided by the total amount of tissue, then this "normalized" calcification rate provide an index of the performance of a coral which is independent of its size. A variety of parameters have been use to normalize calcification (see Kendall et al., 1984). Goreau (1959) suggests that the total area of calicoblastic epidermis is the most relevant parameter. Although this provides information of the performance of the calcifying tissue in a coral, measurement of the irregular and highly complex calicoblastic surface has never been successfully carried out. Instead two other normalization parameters are

frequently used. These are "colony surface area" and "total tissue protein". Colony surface area measures the smoothed surface of a colony. The most common method of measurement uses the weight of tin foil cut to cover the colony surface (Marsh, 1970). A shortcoming of this method is that it cannot detect differences in micro-relief on the skeletal surface. Other methods involving dye absorption (McClosky & Muscatine, 1984) or wax and latex peels (Heyward, 1981; Meyer & Schultz, 1985) are more sensitive to micro-relief, but have not yet been rigorously tested. Total tissue protein measurements (e.g. Barnes & Crossland, 1977; Chalker et al., 1983), detects nitrogen content and is a good indicator of structural and enzymatic components, while being insensitive to fluctuations in storage products such as lipids.

These two types of normalized calcification: "area specific calcification" and "tissue specific calcification" can produce different results when comparing apparently similar corals. For instance consider two corals with the same smoothed surface area, both of which deposit the same amount of skeleton. If one of the corals has a higher degree of micro relief which cannot be detected with the method used to measure colony surface area, or if one of the corals has a thicker layer of tissue covering the skeleton, then this coral will be considered to "calcify" more slowly in terms of tissue specific calcification rate, but will be identical to the other coral in terms of area specific calcification rate. Kendall et al. (1984) suggest that fluctuations in tissue volume make tissue specific calcification rates less reliable than area specific rates. However, if this fluctuation can be monitored, tissue specific calcification may still be the most relevant parameter for some studies. In addition the unquantified errors (due to micro-relief) inherent in using smoothed surface area also make it less than ideal as a normalization parameter.

Throughout this thesis, the general term "calcification rate" will be used to refer to calcification which has been normalized by one of the two methods described above. Where a distinction between the two methods is important, the terms "tissue specific calcification" or "area specific calcification" will be employed. Total weight increment, or "total skeletal deposition will be used to denote the

total (non-normalized) amount of $CaCO_3$ deposited by a particular coral sample.

Skeletal Growth

The most direct way to measure skeletal deposition is to monitor the weight increment of the skeleton. This method was used by many early researchers (Vaughan, 1915; Mayor, 1924; Edmondson, 1929) and has been refined to correct for tissue weight and minimize aerial exposure (Bak, 1973; Jokiel et al., 1978). However, the weight increment of a colony varies with size, and as discussed above, must be normalized with concurrent measurements of tissue content or surface area. The logistical difficulties involved in obtaining values for either of these parameters reduces the usefulness of weight increment as a measure of calcification. Maragos (1978) has suggested a mathematical transformation which converts weight increment data into the radius of a hypothetical hemisphere of solid aragonite. However, the relationship between the "mean solid aragonite radius" and tissue or area specific calcification rate has not been rigorously tested for irregularly shaped or branching colonies. Some early researchers have used the total weight of a colony as the parameter for normalization. The resultant growth index is a measure of the weight increment per unit colony weight and unfortunately this too varies with colony size, but in the opposite direction. In other words, large colonies add a smaller proportion of their total weight that small colonies. The use of this index led to early suggestions that massive corals are determinate in their growth. This concept has been dispelled by the recent studies on massive corals using density band analysis (Dodge & Thomson, 1974; Hudson, 1981a; Isdale, 1984).

Uptake of ^{45}Ca isotope is another reasonably direct measure of calcification. Although there are potential methodological problems associated with this technique (Barnes & Crossland, 1977; Crossland & Barnes, 1977) it is an effective method for the determination of very short term (1-3h) in vitro calcification rates under carefully controlled conditions. Again, however, concurrent measurements of tissue or area are required for normalization.

A somewhat less direct measure of skeletal deposition is volume increment. This method also requires normalization, but in addition requires the determination fo skeletal density so that volume increment can be converted into weight increment.

Linear extension is a frequently used, but indirect measure of both skeletal deposition and calcification rate. Its major advantages over other methods are firstly, its ease of measurement, and secondly the fact that, in theory, it is independent of colony size, and thus does not require the simultaneous measurement of a normalization parameter. Linear extension measures the extension of skeleton along a single growth axis. This axis can represent the radius of a hemispherical or plate-like colonies, or the growth axis of single branches within arborescent colonies. For linear extension to provide an index of skeletal deposition which does not require normalization, certain assumptions must be made. For instance in the case of a simple hemispherical colony it must be assumed that: 1) skeletal deposition occurs at a uniform rate over the entire skeletal surface under investigation; 2) the amount of skeleton deposited at any point on the colony is solely dependant on the tissue immediately above it (i.e. it is independent of the rest of the colony); and 3) the density of the skeleton is constant, or it oscillates at a much higher frequency than the growth period. If these assumptions are satisfied, and the density of the skeleton is known, then the total weight of new skeleton deposited for any given area can be calculated from the linear extension alone. Furthermore this weight increment will be equal to the area specific calcification rate since it is calculated for a specified area, rather than for the entire colony.

In branching or plate-shaped colonies, where there are localized zones of higher extension, the relationship between extension and calcification rate is not as straightforward. There is evidence (Pearse & Muscatine, 1971; Taylor, 1977) that zones with high extension receive translocated metabolites from other tissues some distance away. If values for calcification rate are to be obtained from extension in these corals, then 1) the skeletal extension at points not directly measured, must be predictable from the measured

value; and 2) the amount of tissue (or the area it covers) which supports calcification at any point must be known. Alternatively, if the preceding items are not measured but are assumed to be constant over time and between samples, then linear extension can be used to obtain an index of calcification rate which is useful for comparative purposes. In this thesis, linear extension is the primary method of growth analysis. Consequently, the relationship between linear extension and calcification in branching corals will be discussed in more detail in Chapter 2.

1.3 Scope and Significance of this Thesis

The principal unifying theme of this thesis centres on the environmental physiology skeletal growth in Acropora formosa. The growth studies which form the core of this thesis were undertaken at in intermediate level in terms of the experimental approaches defined above. This intermediate approach has permitted detailed observations and experiments to be carried out in situ , and has permitted several interesting conclusions to be drawn regarding the relationship between growth and a variety of endogenous and exogenous factors. Some of these conclusions now require further detailed testing at a lower experimental and physiological level.

There are three principal areas in which this thesis makes a significant contribution to our knowledge of coral growth. The first is in the area of methodology (Chapter 2). It is demonstrated that under certain circumstances, the use of linear extension measurements can provide a reasonably accurate measure of total $CaCO_3$ deposition within a branch. This has never before been formally demonstrated. Through the use of a simplified model of branch growth, and through a consideration of all the different modes of growth in a branch, it is shown that: 1) Measurements of the weight of newly extended skeleton (which has been used in some recent publications) are not a valid index of total calcification within a branch. 2) A truly valid study of branching growth, which allows comparisons between different locations and different species, must include measures of radial growth, density and lateral branch growth. These parameters have been largely ignored to date.

In general this study provides the first complete description of all the assumptions and requirements for a rigorous study of branching coral growth, and it is hoped that the concepts and conclusions presented here will provide a useful guide to the planning of future experiments.

The second area in which this thesis makes a significant contribution to our knowledge of coral growth is in the accumulation of long term growth records under a variety of conditions. For instance Chapter 5 presents the longest time series of monthly extension rates ever published for an arborescent coral. This is coupled with a complete set of observations on th local meteorology and in situ water temperatures. The results indicate that growth responses do not follow a simple seasonal pattern, but can exhibit a somewhat variable bimodal pattern of extension, which may be related to retardation of growth during periods of high and low water temperatures. In addition, the analyses carried out in Chapter 6 provide evidence that period oh high energetic investment in reproduction are not correlated with reduced growth. This is a significant finding since it has frequently been assumed (but almost never tested) that reproduction would have a negative effect on growth.

The third area of significance lies in the observations on the relationships between extension rate, branch size, and position within a colony (Chapters 3&4). It is demonstrated in Chapter 4 that extension rates of isolated branch fragments increase with increasing initial branch size. These results strongly corroborate short term studies on translocation in Acropora branches and indicate that both calcification and long-term growth at the tip are dependent on translocated metabolites from tissues located further down the branch. The results in Chapter 3 show that extension rates can vary considerably in different parts of a colony. This finding, together with the conclusions regarding the importance of translocation in determining extension rates within a colony suggest that, by regulating the rate (and perhaps even the direction) of translocation, a colony may be able to coordinate growth in individual branches, and thus control its overall form. This

provides a testable theory for the mechanism by which corals exert a precise endogenous control over their growth form.

The final area in which this thesis makes a significant contribution to our understanding of coral growth lies in the studies (Chapters 3&4) on the relationship between skeletal density and extension rate. It is demonstrated that skeletal density increases with distance from a branch tip, and that the density of new skeletal growth at a branch tip is inversely proportional to extension rate. The simplest explanation for these two phenomena is that there are two distinct mode of calcification within a branch: extension and infilling. This bipartite model of calcification has been previously hypothesised as a result of short term studies on growth and skeletal ultrastructure, but the present study provides strong supportive evidence based on longer term growth studies, and larger scale skeletal measurements (density).

1.4 Organization of this Thesis

This thesis is composed of five separate but related studies. Each study is presented in a different chapter (Chapters 2-6) with its own Introduction, Material & Methods, Results and Discussion. A single unified abstract, however is presented at the beginning of this thesis.

Chapter 2 is devoted entirely to a consideration of the relationship between extension, skeletal deposition and calcification rate. It is demonstrated that extension can, under certain circumstances be a useful indicator of total skeletal deposition, and perhaps even calcification. However, because changes in density and branch width are growth processes which branch extension does not take into account, Chapters 3 & 4 examine these parameters as part of their analysis of intra- and inter-colony growth variations.

Chapters 3-5 examine the *in situ* variation in the extension of *A. formosa* at different spatial and temporal scales. Chapter 6 examines aspects of the reproductive biology of *A. formosa*, with a view to determining whether periods of peak energetic investment in

gametogenesis can be correlated with decreased extension, and whether increased calcification requirements (such as repair growth) result in a disruption of the gametogenic cycle.

The studies in Chapters 3 & 4 have already been published in full (Oliver et al., 1983; Oliver, 1984) and are presented here without modification. However, since these papers were published, several new and pertinent studies or reviews have been published by other authors. Furthermore, in the case of Chapter 4 (bathymetric variations) some additional data has become available which necessitates the reappraisal of some of the original conclusions. Rather than rewrite the original papers, which now form part of the formal literature on coral growth, it has been decided to present the new data and updated discussions in addenda to each of the two chapters.

1.5 General Materials and Methods

In this section, information will be presented on those general aspects of methodology, equipment and study sites which are pertinent to all of the succeeding chapters. However, individual materials and methods sections have also been included for each chapter so that specific information which is relevant only to that chapter can be referred to in a more logical context.

1.5.1 Study Sites

All of the field work for this thesis was carried at two different locations: Magnetic Island and Davies Reef. Magnetic Island is a mainland granitic island located approximately 5 miles offshore form Townsville (Figure 1.1). It has well developed fringing reefs in several bays along its eastern side. Located within a shallow, protected mainland bay, the island and its reefs experience lower wave action, slightly higher temperature and salinity extremes and higher turbidity and sedimentation than the platform reefs in the central Great Barrier Reef Lagoon (Walker (1981a,b). The coral communities of Magnetic Island are dominated by Acropora and

Montipora and are described in detail by Morrissey (1980) and Bull (1982).

At Nelly Bay, four different colonies at approximately 6m depth were used for both growth and reproductive studies. The first colony (Colony 1) was the same as that used by Oliver (1979) and was chosen in order accumulate a continuous series of measurements for as long as possible. The three other colonies (Colonies 2-4) were located within 100m of the first, and were chosen in order to determine the degree of variability in growth between colonies in the same habitat.

Davies Reef lies approximately fifty nautical miles east-north-east of Townsville (Fig. 1.1). The reef is approximately kidney shaped with its consolidated edge facing the predominantly south-east trade winds. Leeward from the reef front are a series of embayments, or "holes", varying in depth from 5m to 20m and in some cases connected to the ocean via a channel through the reef front. The study site was located in a 16m deep hole (Fig. 1.2), with a 9m deep opening to the reef front. Although wave induced turbulence was less within the hole than on the reef front, tidal flow through the opening and over the reef flat during high tides ensured regular water exchange. The south and south-west sides of the hole were dominated by arborescent Acropora species, principally A. formosa, which formed large monospecific stands extending from the unconsolidated rubble side of the hole onto the sandy bottom.

Three separate colonies located at approximately 5, 10 and 15m depth were used in all studies at Davies Reef. At this site, there are several different colour forms of A. formosa. Two of these were chosen for analysis because, together, they form an almost continuous cover from 5m to 16m depth. The first colour form occurs between 5m and 8m and is pale brown with a white apical area. The second form is found from 8m to 15m and is dark brown with a bright blue tip, and in some cases, a more distal white zone caused by the absence of zooxanthellae. A shallow station within a pale brown colony (Fig. 1.3a) was chosen at approximately 5m depth, while a middle station at 10m and a deep station (Fig. 1.3b) at 15m were located within colonies of the second colour form. In addition to

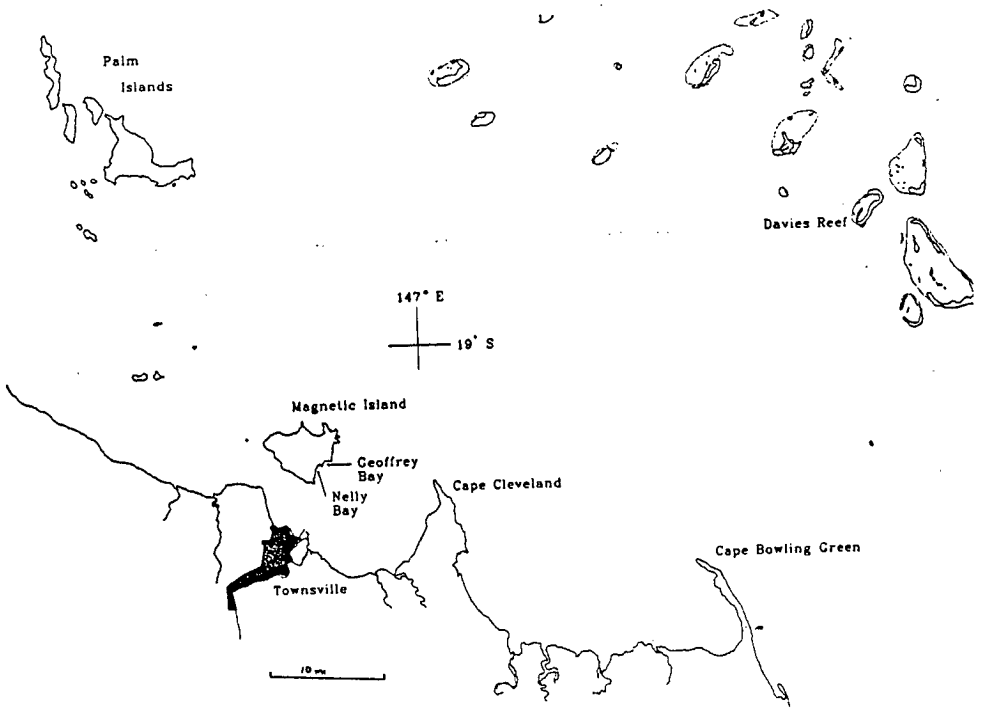


Fig. 1.1 Map of Townsville area, showing the location of Magnetic Island, and Davies Reef. The two study areas on Magnetic Island (Nelly Bay and Geoffrey Bay) are also indicated.

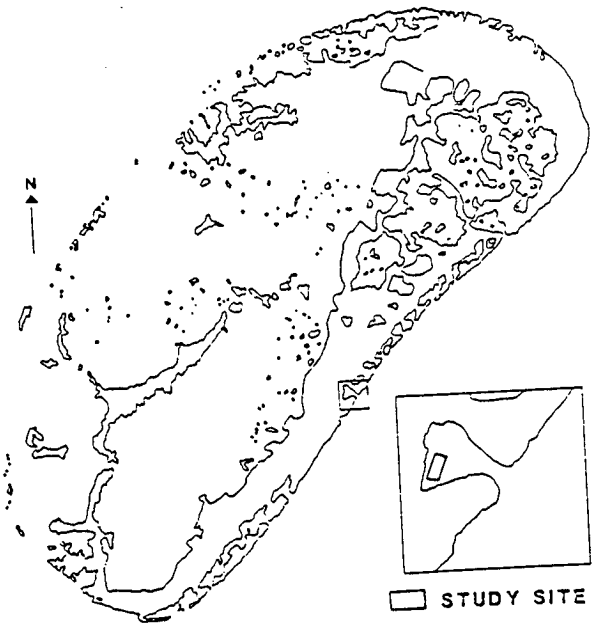


Fig. 1.2 Map of Davies Reef (from aerial photograph) showing location of study site.

changes in colour form between sites, there was a trend towards fewer, more widely spaced branches at the deeper sites. The deepest station approximates the lower limit of distribution for this species (Wallace 1978).

1.5.2 Measurement of Skeletal Extension and Density

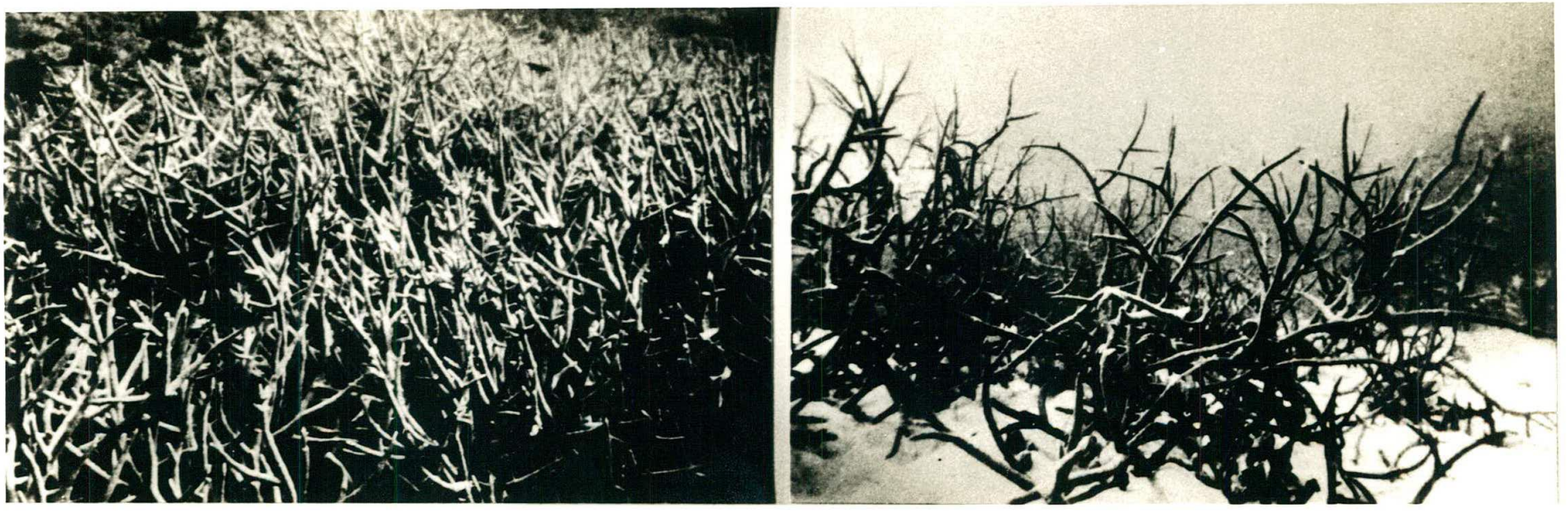
Apical Extension

Linear extension rates of branches were measured using the stain alizarin sulphonate (Barnes 1972, Lamberts 1978). For each sample period, small plastic bags were placed over several branches and secured with elastic bands. Only branches possessing white or blue, zooxanthellae free tips were selected. Brown, zooxanthellae-bearing tips have been shown to be non-growing (Oliver 1979 and Chapter 3). Growth rates measured thus represent mean rates for growing tips but not for the overall colony. Each bag was injected with 5ml of a concentrated alizarin solution to yield a final solution of approximately 12mg per litre. The bags were removed after three hours and each branch marked with plastic coated wire. At the end of each sample period, the branches were brought back to the laboratory and bleached in a saturated calcium hypochlorite solution for 12 to 18 hrs. The extension of the apical corallite on each branch was then measured with vernier calipers or a calibrated microscope graticule. Because each stain bag frequently enclosed several branch tips, the number of measurements varied considerably between samples.

Incorporation of secondary branches into growth indices

Although the growth period for all <u>in situ</u> growth measurements was only 28-60 days, some experimental manipulations were carried out in which the growth period allowed sufficient time for considerable branching to occur. In these instances it was possible for three different measures of apical extension to be made (Fig. 1.4). These were: 1) the total length of all growth, including new and pre-existing secondary branches (Σbr); 2) The extension of the original primary branch tip (1°1); and 3) the mean apical extension

Fig. 1.3 A. formosa colony used for growth studies at the shallow site (a) and the deep site (b).



A

B

of all tips which existed at the time of staining (x1). If the differences in the rate of internal accretion and radial growth between samples or experimental treatments are assumed to be small, then the first growth estimate can be used as a relative measure of overall growth for each transplanted branch. The third measure is equivalent to the extension rates obtained from all in situ samples, where the growth period was not sufficient to measure new branches.

Skeletal Density

Skeletal density was determined on bleached branch portions which were sectioned transversely using a hack saw or a rotary rock saw. Each portion was weighed on an analytical balance, and its volume determined by measuring the rise of water level following immersion in a graduated cylinder. Separate tests showed that the bleaching procedure described above caused negligible skeletal erosion (less than 0.3% weight loss).

To increase the accuracy of volume measurements, cylinders of different diameter were used with correspondingly different sized portions. In order to prevent the water from entering the internal spaces of the skeleton, each portion was first immersed in molten paraffin and then allowed to drain for one or two minutes before volumetric determination. The wax formed an impervious film over the skeletal surface without significantly increasing overall volume. Density values of the branch portions were calculated by dividing the weight by the volume. This yields a measure of the "skeletal bulk density" (ie the density of the skeleton including any internal spaces).

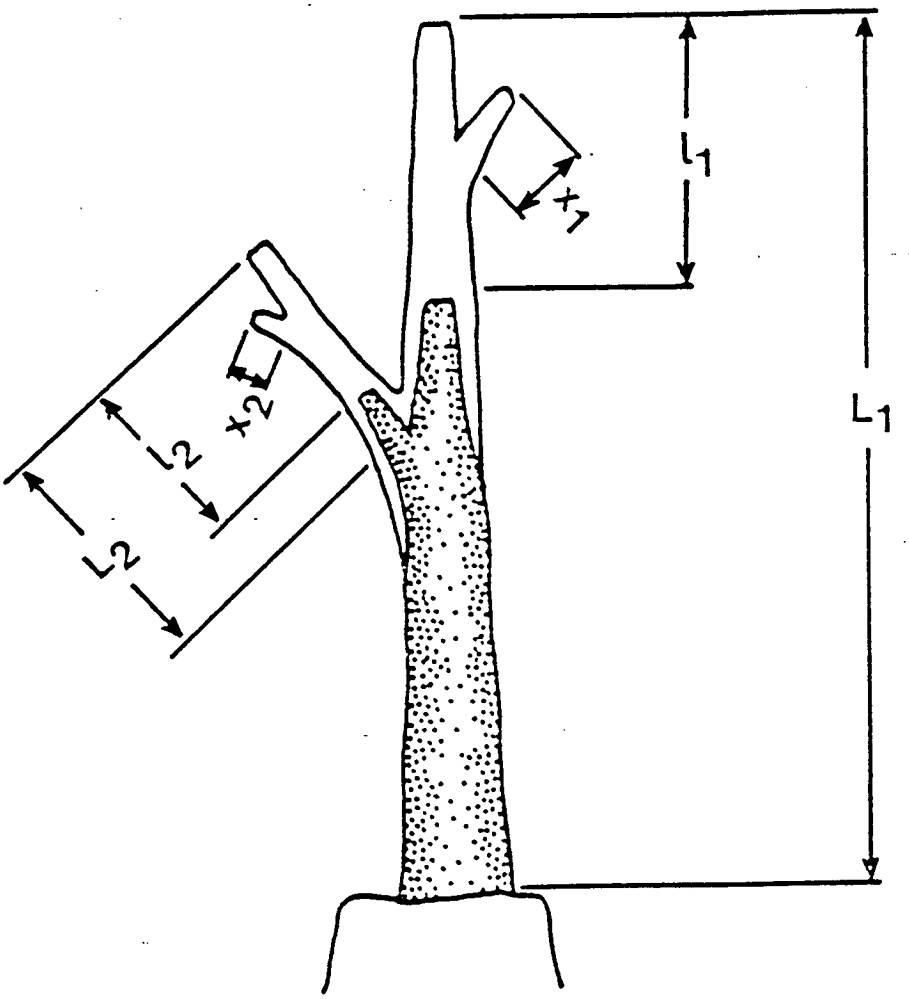


Fig. 1.4 Diagrammatic representation of growth in a transplanted branch, showing derivation of different measures of growth and branching. In the branch figured:

$\Sigma br = x_1+x_2+l_1+l_2$

$l°l = l_1$

$xl = (l_1+l_2)/2$

No. tips = 4

length/tip = $(L_1+L_2+x_1+x_2)/4$

Shaded area represents stained skeleton.

Chapter 2

Inter-relationships Between Apical Extension and Calcification

2.1 Introduction

In this and many previous studies (Shinn, 1966; Gladfelter et al., 1978; Yap & Gomez, 1984,1985; Brown et al., 1985), branch extension is used as an index of "coral growth". Because it can be measured easily and accurately, and with comparatively little manipulation, extension is a useful and convenient index. However, branch extension is not itself a direct measurement of either colony growth, or calcification rate. Since the primary objective of this thesis is to identify some of the parameters controlling the rate and pattern of skeletal deposition and calcification it is important to first examine, both theoretically and empirically, the relationship between extension and these two processes.

Potential inaccuracies in the use of extension as an index of calcification have been highlighted by the extensive work on density banding in massive corals (e.g. Knutson et al., 1972; Buddemeier & Kinzie, 1976; Hudson, 1981; Dodge & Brass, 1984). Obviously, the amount of calcium carbonate deposited per unit extension will be greater within high density compared to low density bands. Dodge & Brass (1984) examined the relationship between extension and total skeletal deposition in the massive coral Montastrea annularis. They found that although extension and calcification were significantly and positively related, variation in skeletal density made extension a rather poor predictor of calcification.

In arborescent Acropora species such as A. formosa and A. cervicornis, density bands do not occur (Gladfelter, 1984; J.D. Collins pers. comm.), however the potential errors associated with the use of extension as an index of calcification in these corals has been stressed by Barnes & Crossland (1980) and Gladfelter (1982). They present evidence that extension and subsequent infilling (increase in density) are two separate and perhaps

independent processes. Oliver (1984) also found evidence that these two processes are distinct and can vary independently.

Because of the potential inaccuracies in the use of extension as in index of calcification, some recent studies have used the weight of newly extended skeleton (apical weight increment) as a measure of calcification (Gladfelter, 1984; Brown et al., 1985). The primary concern of these authors was that the density of new growth may vary considerably over time. Thus seasonal differences in calcification could be expressed primarily as density variations in a branch tip with a constant rate of extension. Conversely, seasonal variations in extension rate could be the result of constant calcification with variable density (i.e. slow dense growth in the winter vs rapid less dense growth in the summer). Since their studies showed that apical weight increment appeared most responsive to seasonal influences, they suggest it is a more accurate index of calcification rate than branch extension.

During the extension of a branch, several different processes occur: 1. increase in branch length due to addition of new skeletal elements; 2. increase in density due to the gradual infilling of the spaces between the skeletal elements; 3. increase in branch diameter due to addition of skeletal elements and growth of radial corallites; and 4. initiation of new lateral branches involving all the above processes.

Branch extension directly measures only the first of these four processes. However, if some simple assumptions are made concerning the structure of A. formosa branches and their geometry, then it is possible to construct a simplified model of branch growth which allows a clear relationship between extension and calcification to be postulated.

Density and branch width increase from the apical corallite basally in arborescent Acropora species. However, the variation in both width and density are greatest within a few centimeters of the branch tip. These trends are presented in detail in Chapters 3 and 4 (also Oliver et al., 1983; Oliver, 1984).

Since both branch width and density vary only slightly along the non-apical regions of a branch, it is proposed here, for the purposes of growth analysis, that branch shape and density structure can be represented by only two components: 1) a tapered "apical cap" of varying density; and 2) a solid cylinder of uniform width and density which forms the rest of the branch beneath the apical cap (Figure 2.1a).

If the density and shape of this cap are constant over time, and if no new branches are added during the growth period, then extension will be directly proportional to calcium carbonate deposition. In addition the amount deposited (weight increment) will be equal to the weight of a branch section taken from below the tip, and equal in length to the linear extension at the tip (Figure 2.1b). It is important to stress that even if the size and density of the cap are not known, an accurate relative index of skeletal deposition is still obtained and this can be used in comparative experimental studies.

Although it must be assumed that the shape and density of the "apical cap" are constant through time for any one branch, the cap does not have to be the same size or density in different branches. As long as the final basal branch width and density remain constant, the cap may vary between branches without this affecting the relationship between extension and total weight increment.

If it is assumed that the layer of coral tissue covering the non apical regions of a branch is constant in thickness, and that the distance over which tissue behind a growing tip contributes to apical extension is also constant, then both weight increment and linear extension would also be accurate indices of tissue specific calcification over all sizes of branch.

It is clear from Figure 2.2 that if the value for total skeletal deposition was derived from the weight of newly extended skeleton, this would result in an underestimate of total deposition. This underestimate would be not be constant, but would vary according to the length increment. If the length of new growth is much greater

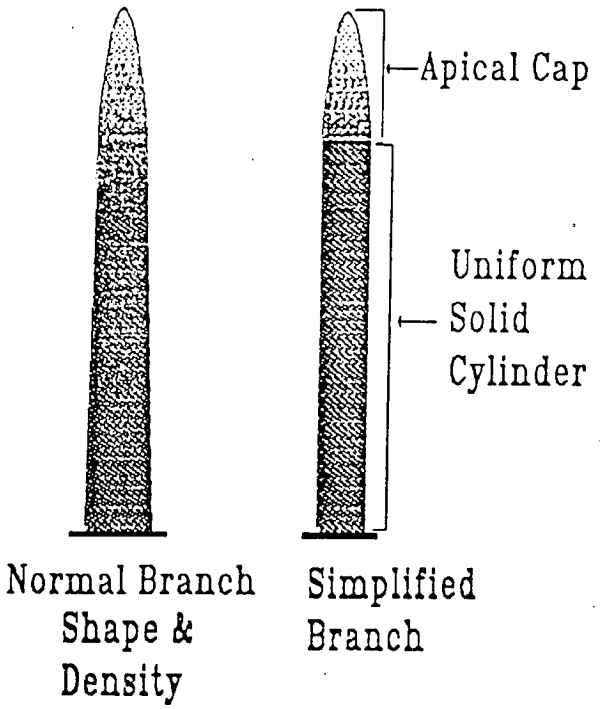


Figure 2.1a Representation of the shape and density structure of a normal single branch of A. formosa, and of the simplified branch used in the model

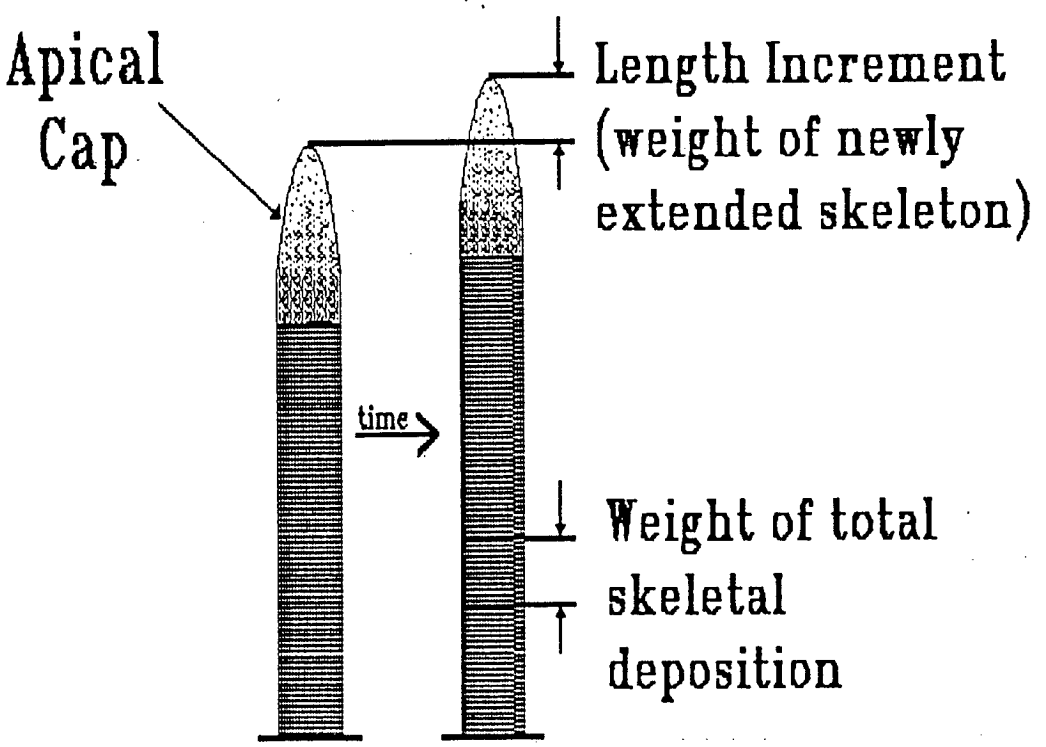


Figure 2.1b Representation of linear increment, and two different measures of weight increment in a simplified branch over time. Since the apical cap remains the same over time, the only change is an increase in the length of the cylinder. Thus the total weight increase of the branch will be equal to a section of the solid cylinder with a length equal to the linear increment. This measure of weight increment is clearly less than the weight of newly extended skeleton.

than the length of the cap then the error will be small. In monthly growth periods, the length of new growth would usually be less than the length of the apical"cap", resulting in significant errors if apical weight increment were used as an index of total skeletal deposition.

Although this "capped cylinder" model of growth is simple and convenient, its assumptions of uniform width, constant density structure, and non-branching are not always valid. For instance branching occurs at regular intervals in most branches, and tip density has been shown to vary with extension rate so that tips which changed their rate of extension would not be expected to maintain an "apical cap" of constant density or dimensions. Consequently in this chapter, empirical data on the relationship between linear extension and weight increment will be presented in order to determine applicability of this model and the usefulness of extension rates as an indicator of calcification rates.

The "capped cylinder" model of growth suggests that apical weight increment used by Gladfelter (1984) and Brown et al., (1985) is not a particularly accurate index of calcification (Figure 2.1b). However, given the fact that some of the assumptions of the model are known to be violated to a certain extent, it was decided to measure apical weight increment as well as linear increment over a series of monthly growth samples. This in effect repeats the experiments of Gladfelter (1984) and Brown et al., (1985), and permits a further comparison of the patterns which are obtained using the two parameters.

It has been stated in Chapter 1 that growth studies using weight increment are handicapped by the fact that this parameter varies with size, even if the tissue specific calcification rate remains constant. In the experiments described here, this problem was minimized by selecting colony portions which consisted of either a single branch, or a large primary branch and a small number of smaller lateral branches. In this way the geometrical assumptions of the capped cylinder model were approximated. In addition the effect of size is accounted for by comparing extension to weight increment in the same corals, thus eliminating size as a factor.

2.2 Materials and Methods

Two different experiments were conducted in order to investigate the relationship between branch extension and skeletal deposition. In the first experiment individual branch tips were grown in aquaria and their total weight increment and branch extension measured over one time period of 177 days (August 1979 to February 1980). In the second experiment, repeated measurements of *in situ* linear extension and linear weight increment were collected over a one year period (February 1979 to February 1980).

Study Site

All corals for the two experiments were obtained from colonies of *A. formosa* at Nelly Bay, Magnetic Island at a depth of 5-6m. The *in situ* seasonal samples were collected from a single colony (Colony 1).

Aquarium Experiment

Several large colony portions were collected at Nelly bay and transported back to the Australian Institute of Marine Science where they were maintained in an open circuit aquarium system. Corals in this system remain healthy for prolonged periods, and extend at rates comparable to those observed in the field (Oliver, 1979). After 24 hours, 45 tips ranging in size from 3 to 15cm were broken from the colony portions and their bases embedded into small short lengths of pvc tubing filled with molten paraffin. The branches were then fixed onto a plastic mesh rack by inserting the PVC holders into alternate openings in the rack. The rack was placed in a 80l plastic bin and an inflow of 20l/min of fresh seawater was maintained throughout the experiment. After a one week acclimatization period the corals were weighed using the buoyant weight technique (Jokiel *et al.*, 1978) and stained with alizarin (Barnes, 1972; Lamberts, 1978) in order to measure linear extension. Staining was accomplished by cutting off the flow to the aquarium for four hours, and adding sufficient alizarin solution to obtain a

concentration of 12mg/l. Although Dodge et al. (1984) have found that alizarin may inhibit coral growth, the shorter incubation periods used in this experiment and in all the other studies in this thesis (3-4h), together with the longer growth periods (≥28d), minimize the effect of this inhibition.

Weighing was carried out by suspending the tips by a cotton thread in a container of water, and measuring their weight in water using either a triple beam balance (for large branches) or an analytical balance (for branches of 5cm or less). Weight was recorded to .01 gram. Temperature and salinity of the water in the container were recorded and used to convert buoyant weight to grams of calcium carbonate using the equations in Jokiel et al., (1978). After 177 days, the corals were weighed again, and then bleached in sodium hypochlorite to expose the alizarin stain line. Apical extension was measured to the nearest .1mm using vernier calipers. Two different measures of apical extension were recorded. In the first, "mean apical extension" was recorded as the mean length increment of all branch tips which existed at the time of staining. In the second, "summed branch extension" recorded the sum of all new branch extensions on both pre-existing tips, and ones which had begun to grow during the experiment (see "Σbr" in Figure 4.4).

Field Experiment

Measurements of in situ growth were obtained using the methods described in Chapter 1. After approximately 30 days, the stained branches were broken from the colony and a new set of 30 branches was stained and marked. This process was repeated for more than two years, but only the samples collected during the first year are analysed in this chapter. A more complete study of seasonal growth over the entire period is presented in Chapter 5.

Each monthly sample of stained branches was bleached to expose the alizarin stain and the new apical growth was measured to the nearest .1 mm using vernier calipers. No record was kept of extension of new apical corallites, since these did not grow to a sufficient size

during the 30 day growth period to be measured. After measuring the linear extension, the new apical growth on each branch was removed by cutting across the branch at the apical point of the alizarin stain line (i.e. the position of the apical corallite at the time of staining). This new growth was then measured to .01g using an analytical balance.

2.3 Results

Aquarium Experiment

Figure 2.2 shows the relationship between mean apical extension of tips which existed at the time of staining, and the total weight increment. It can be seen that the relationship is rather poor, with only 22% of the variation in weight being accounted for by extension. The relationship is poorest among tips with higher extension rates, where the increase in weight is in some cases much higher than would be predicted from a simple linear relationship. In this figure, "mean apical extension" does not take into account the growth of new lateral branches during the growth period. Figure 2.3 indicates that when the extension of all new growth is summed, the relationship with weight is considerably improved and is consistently linear. In this case, extension accounts for almost 85% of the variation in weight increment. Thus when new lateral branches are taken into account, linear extension is a reasonably good predictor of skeletal deposition.

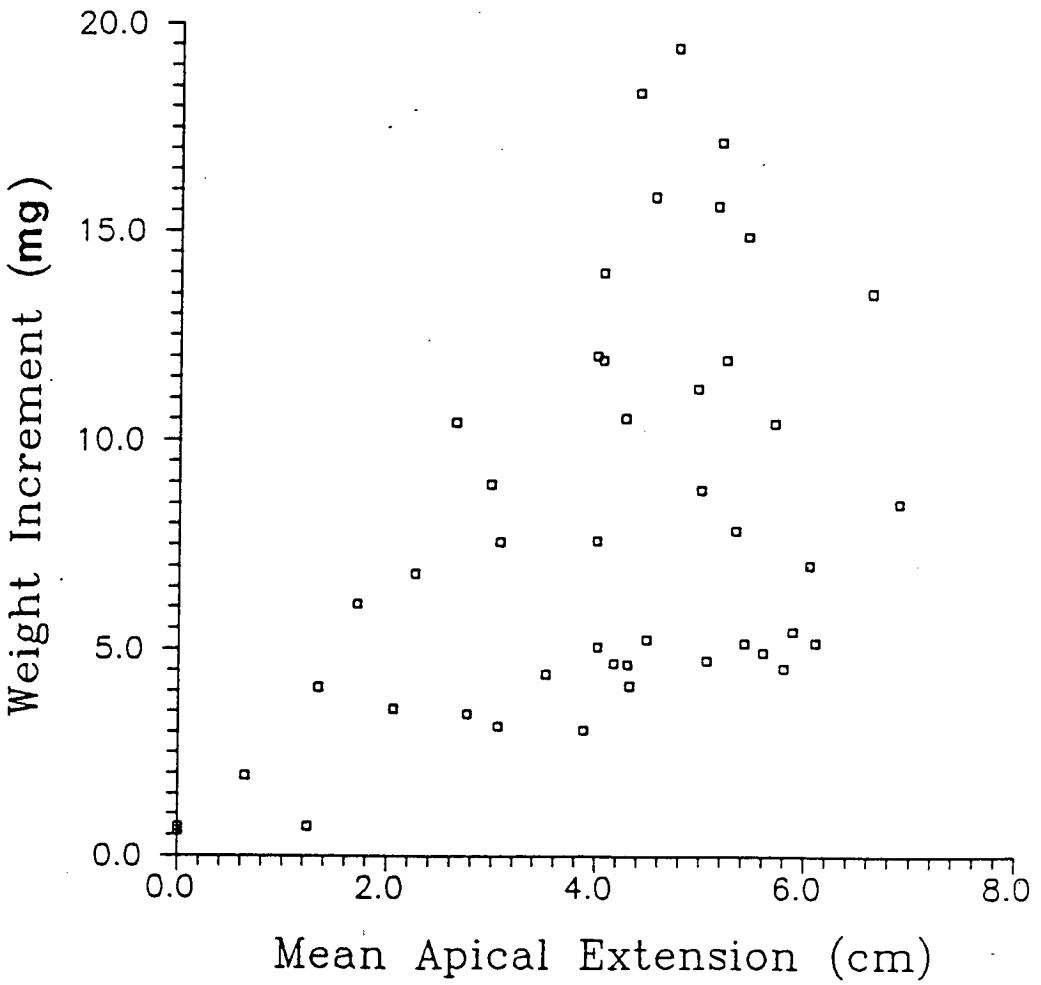


Figure 2.2 Relationship between mean apical extension and weight increment (total skeletal deposition) in branches growing in an aquarium for 177 days.

Field Experiment

Mean monthly values for both linear extension and the weight of newly extended skeleton are compared in Figure 2.4. It is evident that the seasonal pattern is virtually identical for both growth measurements (the seasonal pattern itself is analysed in detail in Chapter 5). Figure 2.5 shows the relationship between weight and length of new growth for every tip measured over the entire period. There is a highly significant relationship between the two parameters, with 76.7% of the variance in the weight data being explained by length measurements. Again there is a slight tendency for the tips with high extension to exhibit disproportionately high weights. The departure from linearity was not due to an increase in skeletal density, since tips with higher extension were invariably less dense (see Chapter 3 for a more detailed description of density variation between rapidly and slowly extending branches). On the other hand, disproportionately high weights among rapidly extending tips would be expected if the maximum apical extension was about the same size as the apical cap. This is due to the increasing width and density of the apical cap between the tip and its base (see Figure 2.1b). Thus if the apical cap is 4cm long, a linear increment of 4cm will result in much more than twice the apical weight increment of an 2cm linear increment.

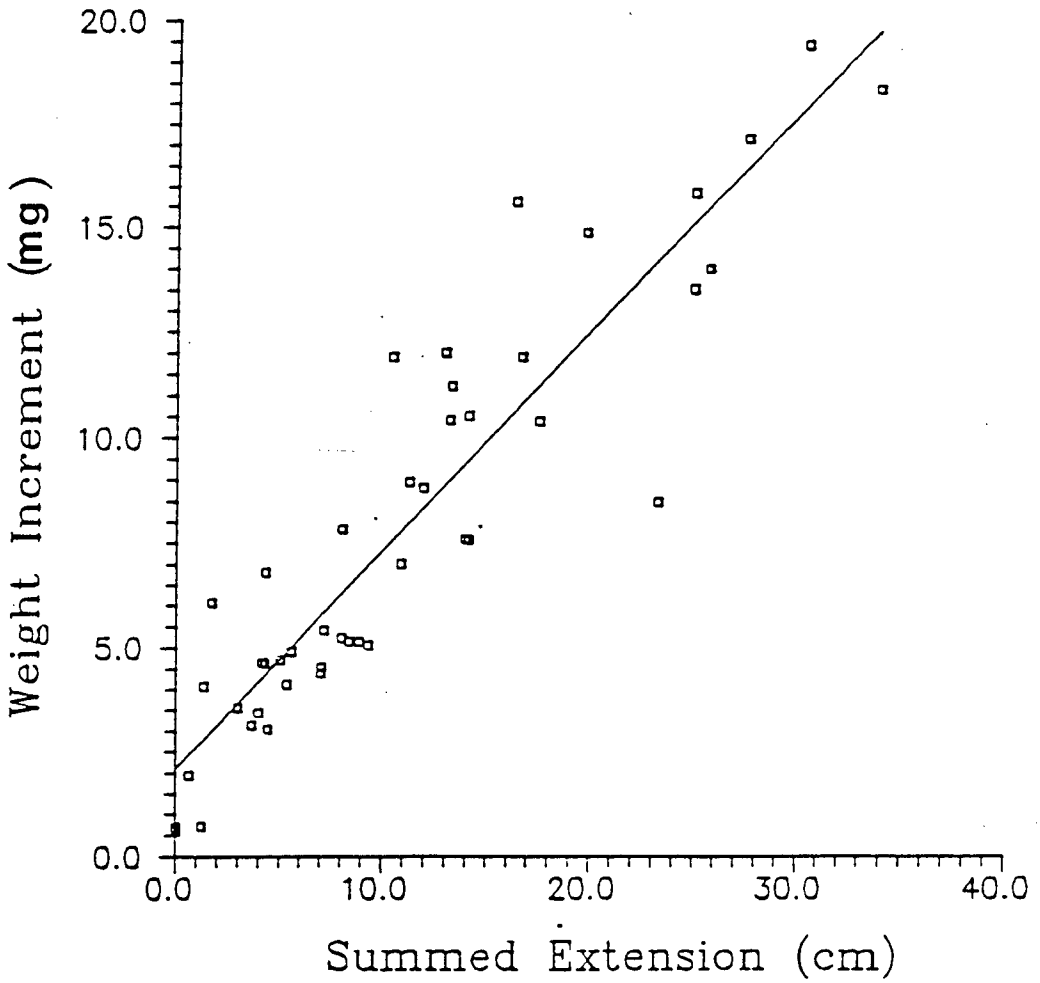


Figure 2.3 Relationship between summed apical extension of all branches, and weight increment (total skeletal deposition) for branches grown in an aquarium for 177 days.

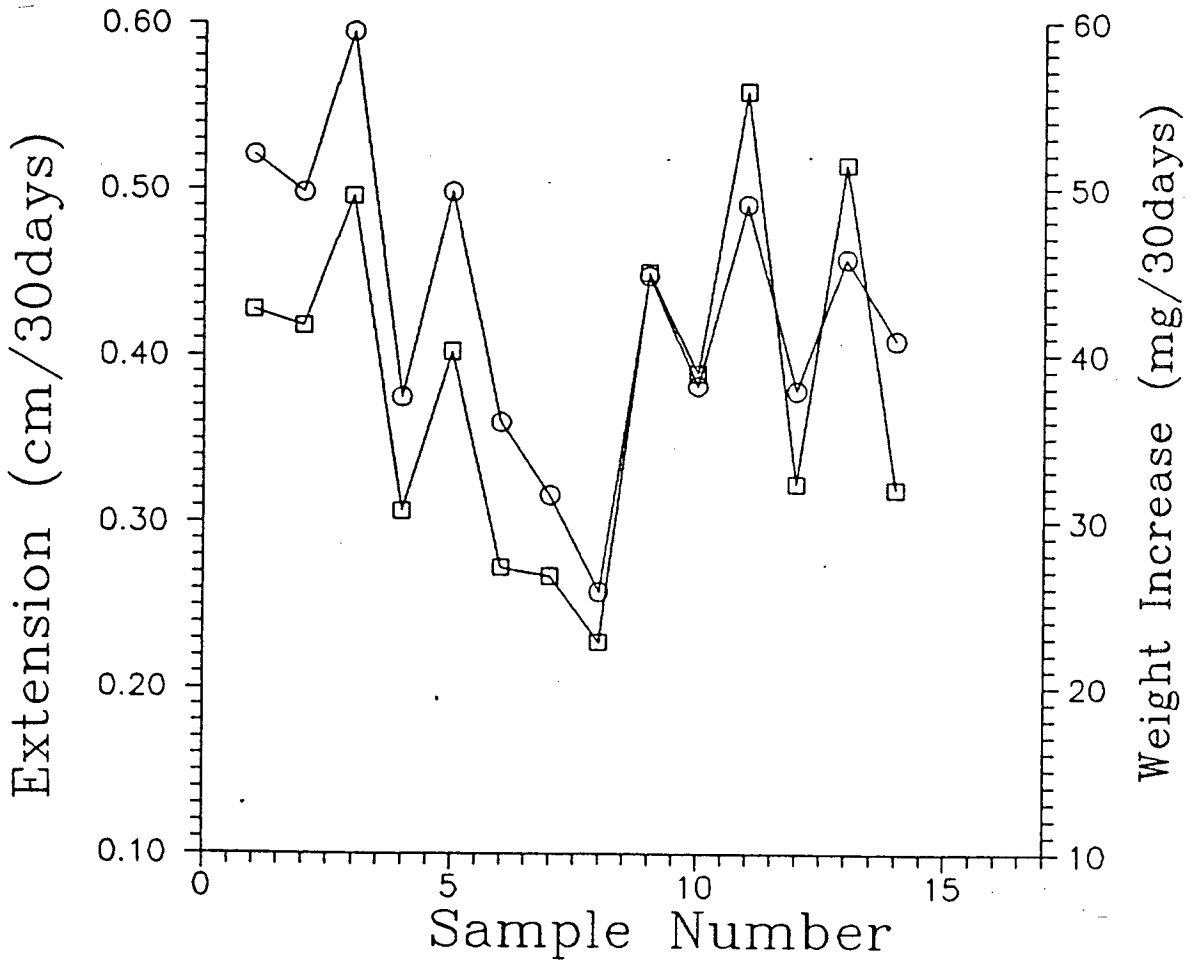


Figure 2.4 Comparison of seasonal skeletal growth pattern using linear branch extension (squares) and weight of newly extended skeleton (circles). Data were obtained from February 1979 to February 1980, at Nelly Bay.

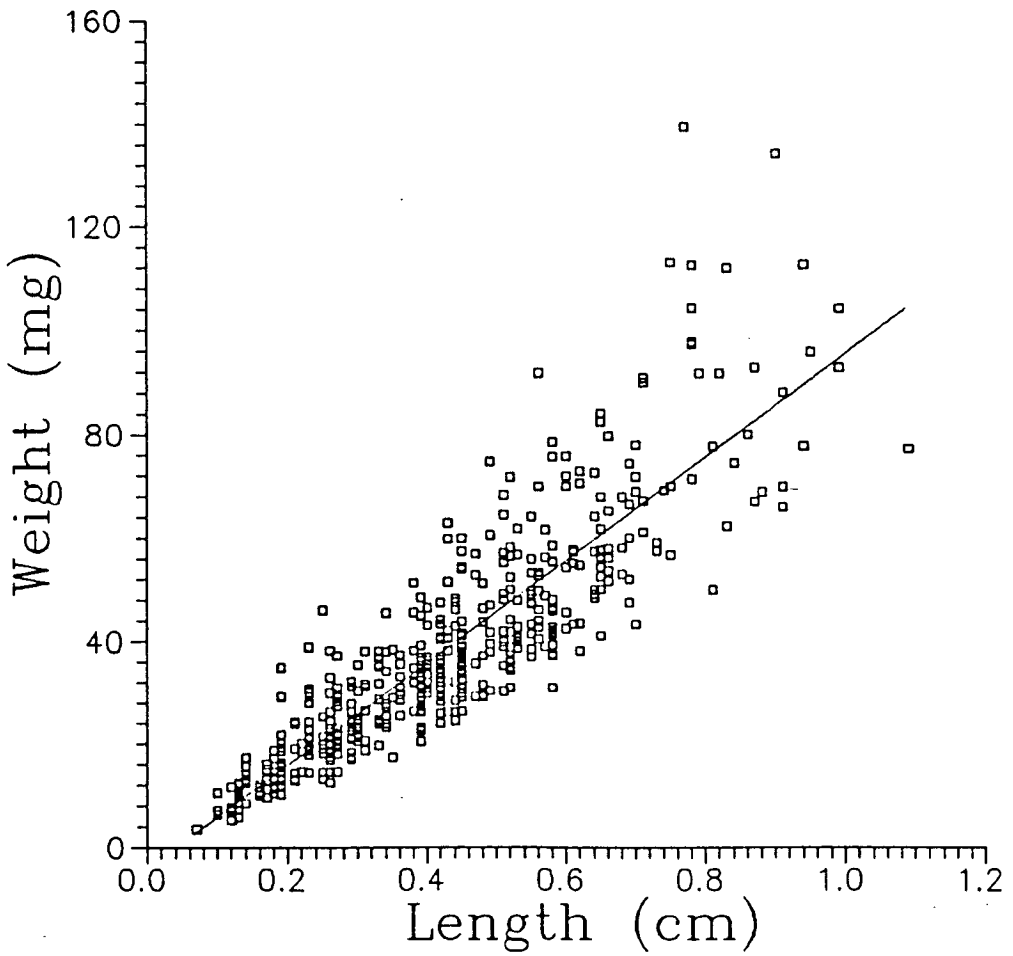


Figure 2.5 Relationship between weight of newly extended skeleton and lenght of nelwy extended skeleton (linear increment) for all tips used for seasonal measurments at Nelly Bay.

2.4 Discussion

The data from the aquarium experiment indicate that the extension of the original apical corallite alone is a poor predictor of skeletal deposition when the growth period is sufficient to permit significant addition of lateral branches. However, if the total amount of new linear growth is summed for each branch then the relation is quite good and can account for nearly 85% of the variance. These results suggest that a simple capped cylinder model of branch growth may be applicable, and that apical extension is a useful measure of skeletal deposition but only if the growth of new lateral branches are taken into account, or if the growth period is so short that minimal lateral branching occurs. The residual variation not accounted for by extension (approximately 15%) may be due to changes in shape and density structure of the apical cap during the growth period and continued thickening of the branch below the apical cap. This residual variation is thus a measure of the error inherent in using linear extension as an index of skeletal deposition.

If the results can be construed as supporting the capped cylinder model of growth, then it would follow that linear extension is a better measure of skeletal deposition than the weight of newly extended skeleton only. Furthermore, because of the geometry and density structure of the apical region, the weight of newly extended skeleton would be expected to increase at a greater rate than the linear dimension. The results of the field experiment suggest that the difference between these two growth parameters is slight, but that there is indeed a tendency for weight to increase faster than length increment. Overall the good agreement between the two variables suggest that both may be reasonable estimates of skeletal deposition. However given the theoretical objections to the use of apical weight increment (see Introduction), and the much greater ease with which extension data may be collected, linear extension would appear to be the more appropriate measurement of the two.

Gladfelter (1984) also measured seasonal variations in weight increment and linear extension in A. cervicornis. Contrary to the

results of the present study, she concluded: 1) that these two parameters did not show the same pattern of variation; 2) that linear extension did not vary significantly during the year (with the possible exception of one sample); and 3) that apical weight increment ($CaCO_3$ accretion in her terminology) did show a significant seasonal variations. Curiously, these conclusions do not appear to be supported by the data she presents. Firstly, a comparison of her Figures 1 and 3 indicate that the seasonal pattern of maxima and minima for linear extension and $CaCO_3$ accretion coincide almost perfectly. Secondly she does not present the results of any statistical test to support the assertion that there were no significant seasonal variation in linear extension. Inspection of the mean and 95% confidence intervals suggests that significant difference might indeed be present, even if the one "exceptional" sample was omitted. Thirdly there is no statistical evidence presented to prove a significant seasonal variation in $CaCo_3$ accretion. Indeed no error bars are presented in the seasonal plot of this parameter. The lack of error bars is presumably due to the fact that the mean monthly values total apical weight increment were not obtained by actually measuring the weight of newly extended skeleton. Rather, it was obtained by multiplying mean monthly linear extension by the mean monthly specific accretion (obtained from a subsample of the monthly data).

In another recent study, Brown et al., (1985) directly measured apical weight increment in an arborescent Acropora species, and compared it with linear extension. They found that variations between certain samples were accentuated when the weight data was compared to the length data. They concluded that: 1. This was evidence for two separate and independent processes (i.e. calcification vs linear extension); and that 2. Calcification was more variable than extension, and was perhaps more sensitive to environmental variation than extension rates. An implicit conclusion was therefore that apical weight increment is a better measure of growth (from a physiological perspective) than length increment.

The theoretical considerations and empirical data presented in this Chapter suggest that such conclusions are perhaps somewhat

premature, since the weight of newly extended skeleton does not adequately measure total skeletal deposition. Apical weight increase would be expected to show a disproportionately high increase in rapidly extending branches. Therefore the accentuated response which Gladfelter (1984), and Brown et al. (1985) found for weight increment may have been due solely to the physical structure of the apical region rather than to a differential response by two distinct physiological processes.

Tunnicliffe (1981) has also used the weight of newly extended skeleton to estimate total calcification. However, in this study the growth period was nearly a year, so that the error due to the presence of the apical cap would have been minimised. In addition her study involved measurements between two colonies with obviously different branch thicknesses. Under such circumstances, her measure of apical weight increment was a better indication of overall calcification than linear increment. Thus linear increment should not be uncritically assumed to be the most approriate measure of calcification. Rather the present study shows that, if certain conditions are met, then linear extension can be a reasonably accurate, and easily measured index of total skeletal deposition.

Although the methodology used by Gladfelter (1984) and Brown et al. (1985) may invalidate their conclusion that extension and calcification are different responses with independant rates, it should be emphasized that these two processes may indeed be discrete, with rates which may (to a degree) vary independently. However the methods required for determining this relationship are not straightforward.

In order to examine the relationship between calcification and extension it is necessary to:

1) Either measure total weight increment directly, or predict it from a detailed model of branch growth which incorporates branch width and density structure variations over time and along a branch at different rates of extension, and rates of lateral branching.

2) Determine the amount of tissue which contributes to apical calcification for each branch

Even the data presented here are only able to compare total weight increment to different growth measures. Although total weight increment is a direct measure of total skeletal deposition, it may not be tightly related to actual tissue specific calcification rates since it is not known how much tissue contributes to skeletal deposition. Translocation allows tissue some distance from the tip to be involved in apical calcification and the distance over which tissue contributes, and the quantity which it contributes is not known and may not be constant over time or along a branch.

Conclusions:

1. Since calcification in arborescent Acropora species such as A. formosa occurs both at the tip, and for some distance beyond the tip, simple weight measurement on newly extended skeleton are not adequate to measure skeletal deposition.

2. A significant proportion of the variation in total skeletal deposition can be explained by linear extension rates. The strength of the relationship is best if new lateral branches are measured, or growth period is so short that new laterals don't occur; tips of uniform appearance are selected (i.e. white-tipped growing branches on the periphery of a colony).

3. Variations in both the density of new growth and the shape of newly extending tips can occur, and are a source of error when using linear extension as an index of skeletal deposition. Actual density and tip width measurements may improve the accuracy of such measurements, however it is possible that variations in calcification some distance from the growing tip could also cause significant error, and this is much more difficult to measure.

4. At best extension, or even total weight increment can only measure skeletal deposition, not tissue specific calcification rates. Actual calcification rates would require information on the amount of tissue contributing, through translocation, to apical

calcification. This is a poorly researched, but extremely important aspect of calcification.

5. In the absence of more detailed data on translocation, and variations in branch width and density, linear extension may be regarded as a useful indicator of calcification which could provide valuable information on the physiological responses of a coral colony under different environmental conditions.

Chapter 3
In Situ Growth: Intra-colony Variations

3.1 Introduction

One of the most conspicuous and universal aspects of coral growth is its variability (Wood-Jones 1910; Vaughan 1915; Buddemeier and Kinzie 1976). This has been variously attributed to differences in physical factors such as temperature, light and sedimentation (Houck et al. 1977; Jokiel and Coles 1977; Dodge et al. 1974); biological factors such as competition and food availability (Sammarco *et al.* 1983; Glynn 1977); seasonal variations in temperature, light or food (Shinn 1966; Bak 1976; Glynn 1977); endogenous zooxanthellar rhythms (Chalker and Taylor 1978); differences in age or size (Barnes 1973; Isdale 1977); or differences in experimental methodology (Barnes and Crossland 1977; Buddemeier and Kinzie 1976).

Although all of these factors undoubtably affect coral growth and calcification, there is often considerable residual variability which cannot be explained in terms of the above factors. Intra-colony growth variations could account for much of the variation in experimental results where only small portion of individual colonies are compared. This phenomenon has received little attention from coral researchers. Although Goreau (1959,1961) has shown that, in branching corals, the branch tips calcify more rapidly than the basal regions, considerable variation may still occur between individual tips within a colony.

There are two potential sources of intra-colony growth variations: fine scale differences in exogenous environmental parameters; and endogenous control of growth rates within different parts of a colony. A combination of both these alternatives is also possible.

A knowledge of the nature and extent of intra-colony variation is therfore of interest, not only because it would permit more accurate predictions of colony growth, but also because it may provide insight into the mechanism behind the coordination of growth within a coral colony.

This chapter deals with certain aspects of a particularly conspicuous form of intra-colony variation: the presence, in arborescent corals such as Acropora formosa, of two different kinds of branch tip. "White tips" are characterized by the absence of zooxanthellae from the apical region of branches, while "brown tips" posess zooxanthellae and are uniformly brown over their entire length. Occasionally the presence of animal pigments within the coral tissue renders white tips a pale blue, but these tips are readily distinguished from zooxanthellate brown tips, and the term "white tip" is still considered to apply. The existence of brown and white tips has been known to coral researchers in the Caribbean and the Pacific for some time, and it is commonly assumed that brown tipped branches exhibit reduced growth (Barnes and Crossland 1980; D.J. Barnes and B.E. Chalker pers. comm.). Only one published report, however, has been found which deals with the relative growth of brown and white tipped branches. Bak (1976) reported that the white, growing edges of some A. palmata branches turned brown and showed a simultaneous cessation in weight increment. Recent, unpublished work by Meek (1982) has extended the preliminary findings of Oliver (1979) to describe the histology and skeletal fine structure of brown and white tips in A. formosa.

This study assembles observational and experimental data on the growth, morphology, abundance and distribution of brown and white tips in A. formosa colonies, and discusses possible proximate and ultimate factors which may cause changes from one form to the other.

3.2 Materials and Methods

Experiments and observations were carried out at Nelly Bay, Magnetic Island and Davies Reef between March 1979 and December 1982 (see Chapter 1 for descriptions of study sites and experimental colonies).

Morphology and Skeletal Structure

Observations on the skeletal structure of stained branches were made using a stereo dissecting microscope. In addition, low magnification observations on a small number of brown and white tips were made using an Etec scanning electron microscope.

Growth Experiments

Linear extension rates of brown and white tipped branches were measured using the alizarin method (see Chapter 1) or by direct measurement of branch length in situ using a plasitci ruler (Shinn 1966). Three separate growth experiments were conducted. In the first experiment, an entire colony of A. formosa at Nelly Bay was enclosed in a plastic tent similar to that used by Dustan (1975). Alizarin was added to yield a final concentration of approximately 12 mg per litre, and the tent was left in place for three hours. The colony was left for 36 days and then 104 branches were broken off and brought back to the laboratory for analysis. The colour of each tip was recorded during collection.

In order to minimize the possibility of branch tips changing colour during an experiment, a second short term experiment was conducted at Davies Reef. Several white and brown tipped branches were stained within colonies at 5 m and 15 m sites. The branches were collected 13 days after staining. This is slightly greater than the minimum period over which growth can be reliably measured using the alizarin method. The colour of each tip was recorded at the beginning and end of the experiment. None showed any noticeable changes in appearance.

In a third, long term experiment at Nelly Bay, several white and brown tipped branches were marked with plastic coated wire and numbered tags. Only brown tipped branches which had not undergone changes in skeletal structure (see below) were selected. The length of each branch from the wire to the tip of the axial corallite was measured with a plastic ruler graduated in millimeters. Branches were remeasured at intervals of 30 to 40 days for up to 250 days

from the beginning of the experiment. The colour of each branch was recorded during measurements.

Reciprocal Transplants

Field observations indicated that brown tips predominate in the interior of a colony, while white tips were most common on the periphery. A transplant experiment was conducted to determine if a change in position within a colony could induce a change in the colour and/or growth rate of branch tips. Five white tipped and five brown tipped branches at both the shallow and the deep sites were broken off approximately 10 cm from the tip. The branches were then exchanged such that the brown tips were tied to the broken bases of white tipped branches and the white tips were attached to the bases which had borne brown tips. At each site, five white tipped and five brown tipped branches were broken off and then retied to their original broken bases to serve as controls. Only brown tips showing some degree of modification of the axial corallite (see below) were selected. Each branch was positioned along the broken basal portion with an overlap of approximately 3 cm and tied in this position with plastic coated wire.

Each branch was photographed at the beginning of the experiment and again at 12 months time. The photographs were used to determine the colour and shape of each tip, the number of new lateral branches and the amount of growth. Growth status was scored as "inactive" if a branch (including new laterals) increased by less than 30% of its original length, and "active" if growth was greater than 50%. No tips fell between these two categories. One white tipped branch died during the first 8 months and was not included in the analysis.

Density Analyses

Differences in skeletal structure between brown and white tips involved considerable changes in the degree of infilling of internal spaces within the skeleton. In order to study this phenomenon in more detail, density measurements were performed on branches from the 5m and 15m deep colonies at Davies Reef. Branches 9 cm to 18 cm

in length were sawn into successive 3 cm lengths. Density values were obtained usign the method described in Chapter 1. Densities were then examined as a function of distance from the tip in brown and white tipped branches.

Density variations within white tipped branches were also studied, since preliminary observations indicated that increased infilling (a feature of brown tips) occurred to some extent in slowly extending white tips. To determine to what extent infilling was corellated to extension rate, branch tips from the stained colony at Nelly Bay were cut off exactly at the alizarin stain line, which demarcates new apical growth. Weight and volume measurements were obtained as above and density was then plotted as function of extension rate.

The increased density of slowly extending tips raised the possibility that increased infilling compensates for the reduction in extension, and that calcification is therefore constant, and independant of extension rate. To test for this, the weight of newly deposited skeleton from the preceding sample was plotted against extension rate.

Proportions of Brown and White Tips

In order to determine the proportion of brown and white tips in a colony, all the coral from within a 1 m^2 quadrat, placed within the deep and shallow colonies, was collected and brought back to the laboratory. The total number of tips from each colony was counted and each tip was identified as brown or white on the basis of previously determined differences in skeletal morphology.

3.3 Results

Morphology and Skeletal Structure

Figure 3.1 shows the appearance of typical living white and brown tips. In white tips (Fig. 3.1a) the tissue covering the axial

corallite is free of zooxanthellae, and the white skeleton can be seen through the translucent tissue. A variable number of radial corallites near the tip are also free of zooxanthellae. The length of this white zone can vary from 0.5 cm to 6 cm or more. Zooxanthellae first begin to appear on the radial corallites, in the grooves between the parallel costae. The coenosarc between the corallites remains white in this zone, but gradually turns brown further from the tip. In brown tips (Fig. 3.1b) zooxanthellae are present throughout the apical region.

Observations of skeletal morphology indicate that there are consistent differences between brown and white tips. Figures 3.2 and 3.3 show that white tips are characterized by axial corallites which are constructed of relatively thin, widely space skeletal elements. Lateral corallites are sparse or only poorly developed in this region. Brown tips, on the other hand, are more heavily calcified, with much thicker skeletal elements. In some cases, additional growth of the coenosteal areas has altered the profile of the apical region, rendering it more rounded in profile. The axial corallite of many brown tips also has a smaller aperture, which reflects a diminution in the size of the axial polyp. The range in morphology of brown tips is quite large. In some instances lateral corallites have developed around the axial corallite, and in extreme cases the axial corallite has degenerated so far that it can no longer be distinguished from the radials surrounding it (Fig. 3.2c, 3.3c).

It is possible to arrange the morphological variations of brown tips into a series (Figs 3.2, 3.3, a-c) in which the following simultaneous trends, leading to increased modification away from the condition in white tips, can be seen:

1. Increased density of the skeleton caused by thickening of the skeletal elements;

2. A progressive "rounding off" of the profile of the apical region caused by coenosteal growth;

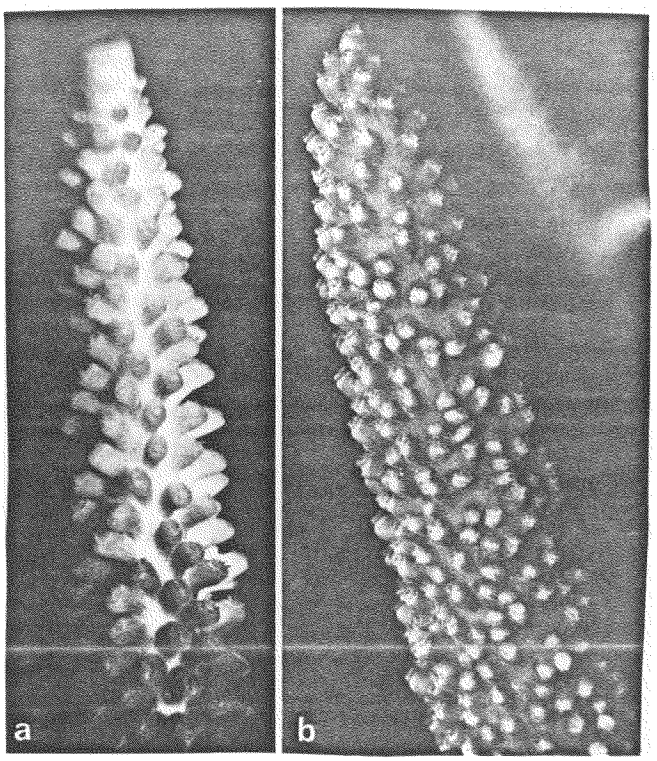


Figure 3.1 Typical living white tip (a) and brown tip (b).

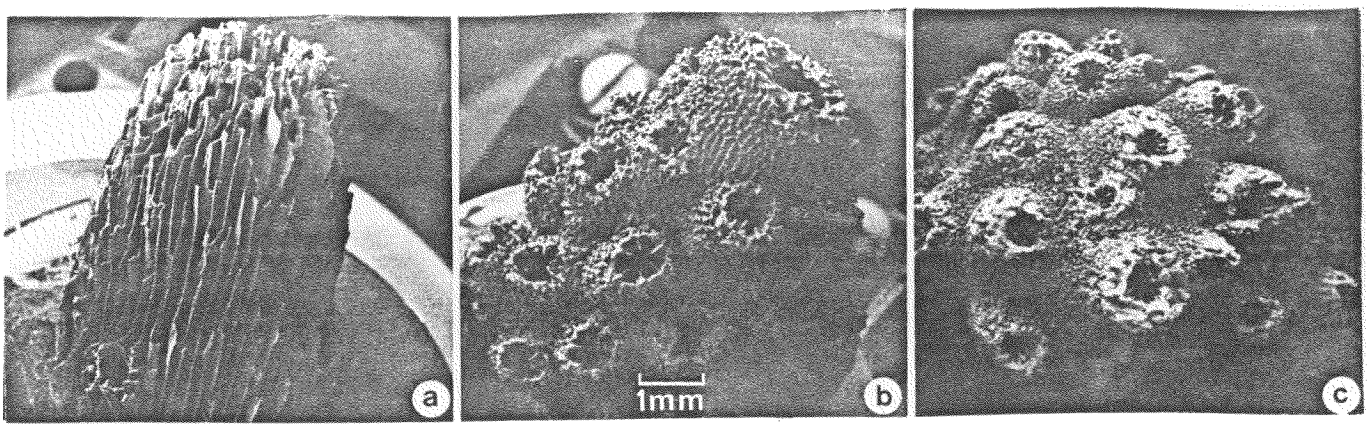


Figure 3.2 Low power S.E.M. showing skeletal morphology of a white tip (a), a brown tip (b) and a brown tip in which the axial corallite has become indistinguishable from adjacent radials (c).

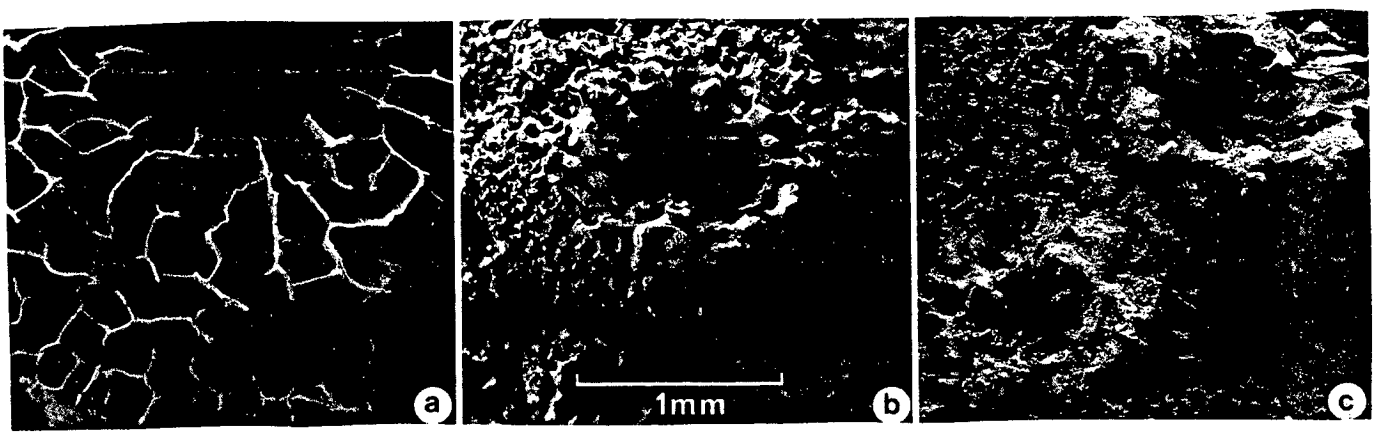


Figure 3.3 As for Figure 3.2, showing axial corallite from above.

3. Encroachment of well developed corallites around the apical corallite, together with the diminution in size of the apical aperture. In some cases, new corallite walls are erected around the diminished apical appeture, giving the axial corallite similar dimensions and appearance to adjacent radial corallites.

Brown tips which exhibit the greatest degree of modification are invariably found on branches with the largest branch diameter. If it is assumed that branch diameter increases with time, then the above trends represent a progressive alteration of brown tips through time.

Growth Experiments

The frequency distribution of extension rates from the first experiment (entire colony stained at Nelly Bay, Magnetic Island) is shown in Fig. 3.4. If all tips are considered together, the distribution appears bimodal. The majority of brown tips did not grow during the experiment, and if these tips are excluded from the distribution, it can be seen that the remaining white tips show a range of extension rates which is not significantly different from a normal distribution (X^2, $P>.1$). Although a few brown tips exhibited substantial extension, these tips may initially have been white, and have turned brown during the course of the experiment.

The second experiment, at Davies Reef, was conducted over a shorter time period and none of the tips appeared to change colour. The results in Table 3.1 indicate that the difference between extension rates in brown and white tips is clear cut. None of the brown tips showed any extension, while the white tipped branches exhibited a range of extension rates.

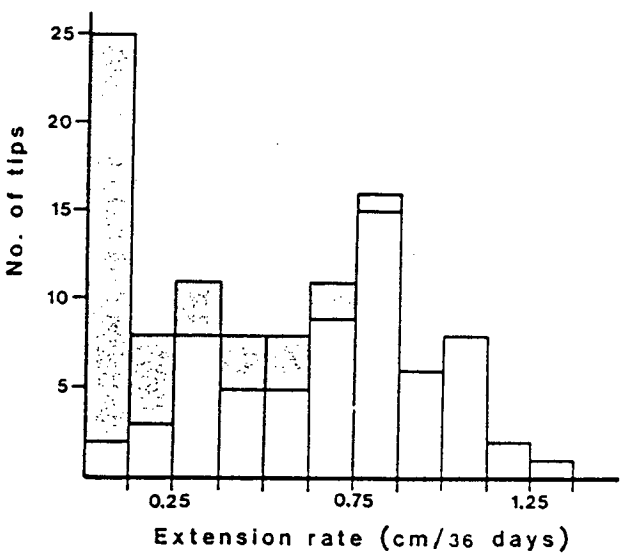


Figure 3.4 Frequency distribution of extension rates from an Acropora formosa colony at Nelly Bay. Shaded area: brown tips. Unshaded area: white tips.

Table 3.1
Growth of brown and white tips at Davies Reef

	Depth	N	Mean Extension Rate (cm/13days)	95% Confidence Interval
White tipped	5	7	0.24	±0.11
Brown tipped	5	10	0	-
White tipped	15	10	0.38	±0.10
Brown tipped	15	7	0	-

The extension rates of individually marked tips from the third experiment are shown in Table 3.2. Since some branches were broken or damaged during the observation period, the growth period in Table 3.2 varies between branches. Thirteen out of nineteen branches did not change colour during the experiment. Consistently brown tips showed no extension at all over periods up to seven months, while consistently white tips grew steadily with little variation between tips. Five tips changed from brown to white during the course of the experiment, and in each case this was associated with an increase in extension rate, from almost nil, to rates comparable to white tips. One tip changed from white to brown and showed a corresponding cessation in growth. No tips changed colour more than once. These results indicate that tip colour can be used as an indicator of growth status, and that tips which have not undergone morphological alteration may change from one form to the other in either direction.

Table 3.2
Extension of marked branches

(a) No change in tip colour

Tip Colour	Extension Rate (cm/30 days)	Period (days)
White	0.44	217
White	0.33	217
White	0.46	250
White	0.40	217
White	0.51	184
White	0.47	217
White	0.43	217
White	0.52	121
White	0.40	217
Brown	0	250
Brown	0	217
Brown	0	217
Brown	0	217

(b) Change in tip colour

Initial Status			Final Status		
Tip Colour	Extension Rate (cm/30 days)	Growth Period (days)	Tip Colour	Extension Rate (cm/30 days)	Growth Period (days)
Brown	0.05	63	White	0.53	187
Brown	0.05	63	White	0.35	154
Brown	0.07	92	White	0.46	125
Brown	0.04	92	White	0.67	125
White	0.19	63	Brown	0	154

Reciprocal Transplants

The results of the reciprocal transplant experiment are expressed in terms of whether a tip changed colour or growth status during the experiment (Table 3.3). It was assumed that white tips were growing prior to the experiment and that brown tips were not. For example, a brown tip showing nil or slight growth during the experiment was considered not to have changed.

Table 3.3
Reciprocal Transplant Results

Branch Type*	Depth	Growth		Tip Colour	
		Change	No Change	Change	No Change
W - W	5	0	4	1	3
	15	2	3	1	4
W - B	5	3	2	2	3
	15	4	1	4	1
B - B	5	2	3	1	4
	15	1	4	1	4
B - W	5	4	1	1	4
	15	0	5	0	5

*W - W: White tip broken off and replaced on the same branch
W - B: White tip transplanted to broken base of a brown tipped branch
B - B: Brown tip broken of and replaced on the same branch
B - W: Brown tip transplanted to broken base of a white tipped branch

The results were analysed by means of a series of 2 x 2 contigency tables, in which the proportion of branches which changed their tip colour or growth status was compared between the transplanted branches and the controls. Due to the small sample sizes, exact probabilities were calculated (Fisher 1950) rather than X^2 values. In instances where there were no significant differences between individual groups, brown and white tips were pooled into "controls" and "transplants". Similarly, deep and shallow sites were pooled if none of the component subsets were significantly heterogeneous.

If brown tips arise within a colony due to unfavourable growing conditions at the tip, then it would be expected that a greater proportion of the transplanted branches would change colour or growth status than the controls. Although this trend was in fact evident in most of the contingency tables, none were significant beyond the P=.05 level. Some tables, however, showed a significance beyond the P=.12 level, and are thus considered here as pointers to future, more detailed experiments. Pooled results for both sites indicate that white tips tended to stop growing (P=.051) and turn brown (P=.115) more frequently if transplanted onto branches which had borne a brown tip, than if left at their original location. In

addition, "transplants" (pooled brown and white transplanted tips) at the shallow site changed their growth status more frequently than the "controls" (P=.051).

In addition to the above results, two interesting trends were noticed, which reinforce field observations on brown tips. Firstly, very few transplanted brown tips turned white. In fact, brown tips as a whole, (transplants and controls) changed colour less frequently (10%) than white tips (60%). Secondly, despite the failure of transplanted brown tips to turn white, several of these branches at the shallow site exhibited substantial growth through the extension of new lateral branches. Since the brown tips selected for this experiment all had some degree of skeletal modification and degeneration of the axial corallite, these results suggest that at some stage during the progressive change in brown tips, the ability of the axial corallite to reinitiate extension is lost. In such cases reinitiation of growth after the onset of favourable conditions appears to be achieved through the development of a new axial corallite.

Density Analyses

Figure 3.5 shows the changes in skeletal bulk density from the tip towards the base in white and brown tips from the deep site at Davies Reef. Similar results were obtained at the shallow site. In white tips, density increases with distance down a branch. A similar pattern of density changes has been found by Oliver et al. (1983) and Gladfelter (1982). In brown tips the density is approximitely uniform along its length, indicating that infilling continues along the entire branch after extension ceased. These results are from brown tips with small axial corallites and a rounded profile, and probably represent tips that have been brown for an extended period. Less developed brown tips would probably show density changes intermediate to those in Fig. 3.5.

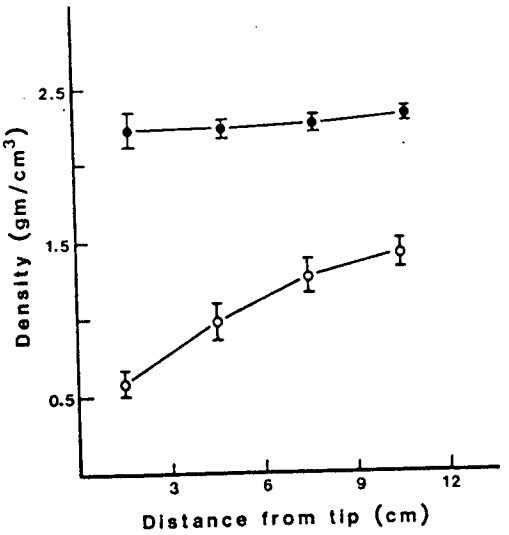


Figure 3.5 Skeletal bulk density as a function of distance from the axial corallite. Open circles: white tips. Closed circles: brown tips.

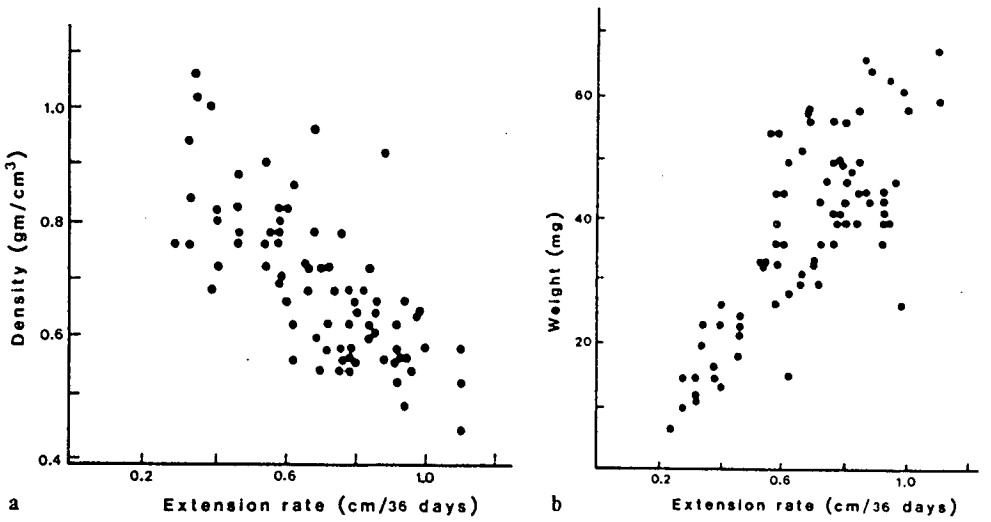


Figure 3.6 Skeletal bulk density (a) and weight of newly deposited skeleton (b) as functions of extension rate.

Analysis of white tipped branches from Nelly Bay (Figure 3.6a) indicates that the density of white tipped branches is inversely proportional to their extension rate. Thus, in rapidly extending tips, the rate of infilling does not increase sufficiently to maintain the density levels found in slowly extending tips. This relationship between extension rate and infilling tends to produce a continuous range of variation in white tips, such that the more slowly extending tips have skeletal characterisitics similar (highly infilled) to brown tips.

Figure 3.6b shows that while rapidly extending tips are less heavily calcified, they still deposit significantly more skeleton than slowly extending tips. This demonstrates that the relationship between infilling and extension is not simply one in which a constant amount of energy available for calcification is differentially allocated between these two processes. Rather, increased extension rates reflect a real increase in overall calcification.

Proportions of Brown and White Tips

The number of brown and white tips in 1 m^2 quadrats is shown in Table 3.4. Approximately 70% and 65% of all tips at the shallow and deep sites respectively were "brown" in terms of their shape and skeletal morphology. The ratio of brown to white

Table 3.4
Number of white and brown tipped branches per 1m^2

	White Tips			Brown Tips		
Site	Length of branch >1cm	Length of branch ≤1cm	Total	Length of branch >1cm	Length of branch ≤1cm	Total
Shallow	394	74	468	660	418	1078
Deep	200	62	262	268	221	489

tips was not significantly different between sites (X^2=4.97, P>.05). Thirty-nine and forty-five percent of brown tips were 1 cm or less in length at the shallow and deep site respectively. Since branches must start as white tips, these figures indicate that a large proportion of white tips stop growing very soon after initiation. This is supported by observations that branches arizing from the middle of a colony tend to have only one or a few white tips growing vertically to the upper surface of the colony, but possess many small brown lateral branches along their length. These laterals were probably aborted due to the close proximity of other branches and the associated limiting growth conditions.

Field Observations

During the course of a related study on long term growth rates, a large branched portion from the 15 m colony at Davies Reef broke near the base and fell so that several white tips which had been at the edge of the colony ended up in the interior of the colony. Some of these tips had been stained prior to this event. The breakage was first noticed some two months after staining, and at this time all the stained branches had turned brown. Subsequent analysis showed that extension in these tips was nearly nil. Since manipulation does not decrease growth rates (Oliver et al. 1983) this observation supports the notion that conditions within the interior of a colony are less suitable for growth and tend to induce tips to turn brown. This view is further supported by numerous observations that brown tips occur most frequently in the interior of a colony.

In another experiment (Oliver, unpublished) it was observed that white lateral branches growing towards other branches turned brown and stopped growing before coming into contact. This response suggests that the ability to turn brown and stop growing may enable large colonies to prevent their branches from growing into each other. Field observations on numerous A. formosa colonies indicate that branch anastamosis is a rare event.

Extensive field observations indicate that although white and brown tips are most conspicuous in arborescent Acropora species, many other branching corals, including most species of Acropora, Pocillopora damicornis, Stylophora pistillata, and Montipora ramosa posses pale zooxanthellae-free areas at the tips of many branches. In addition, plate-forming species in genera such as Pachyseris, Turbinaria and Montipora also posses a white or pale zone along the growing edge of the colony. The illustrations in Faulkner and Chesher (1979) provide many more examples of this phenomenon. These observations suggest that zooxanthellae-free areas may be associated with high growth regions of corals in which rapid extension is characteristically localized within discrete zones of the colony.

One further observation relating to growth in brown and white tips is that at Davies Reef the maximum length of the zooxanthellae-free appears to vary between sites in a regular manner. Although no formal measurements were made, field observations indicate that the zooxanthellae-free zone varies approximately from 1-2 cm at the shallow site, 3-4 cm at an intermediate (10 m) site and 5-8 cm at the deep site. Extension rates show a similar increase with depth (Oliver et al. 1983). Thus there may be some correlation between extension rate and length of the zooxanthellae-free zone.

3.4 Discussion

Evidence presented here indicates that brown tips do not grow in terms of branch extension. Infilling and radial growth however, appear to proceed, and these processes progressively alter the density and profile of brown tips. White tips, on the other hand, exhibit a range of normally distributed extension rates. This study has also shown that tips may change from one form to the other in either direction. Once a tip has remained brown for an extended period, however, changes in the size and structure of the axial corallite occur. It is hypothesized that at some point during this change the axial corallite loses its ability to change colour and extend. Meek (1982) has shown that changes in the axial corallite are accompanied by an increase in the number of tentacles on the axial polyp (from 6 to 12) so that brown axial polyps have the same

number of tentacles as radial polyps. In addition, Oliver (in preparation) has found that the axial polyp of white tips is reproductively sterile and that gonads only develop in mature radial polyps or in the axial polyps of brown tips. Thus the inability of a brown tip to reinitiate extension is associated with the anatomical, physiological and skeletal degeneration of the axial polyp into a radial.

Although conditions in the interior of a colony appear to favour the induction of brown tips, it is not known precisely what factors cause this change. It is possible that the causal factors are entirely endogenous. This seems unlikely, however, in view of the changes in tip colour observed on the fallen colony portion described above. In addition, Oliver (1979) found that many white tips turned brown when exposed to major changes in environmental factors such as decreased light and increased temperature. It is therefore hypothesized that unsuitable micro-environmental conditions, such as are found in the interior of a colony cause tips to turn brown. Two factors which would be expected to become limiting within a colony are light and water motion (Chamberlain and Graus 1975). Both of these factors could be expected to show considerable fine scale variation within a colony. This spatial variation may have been responsible for the variability in the response of the transplanted branches, since branch tips could only be positioned within a centimeter or two of where the original tip had been. Temporal changes in these parameters might also explain the reversals in tip colour seen in several of the directly measured branches at Nelly Bay. A third possibility is that metabolites released by branches reach higher concentrations within the interior of colonies and that this has an inhibitory effect on apical extension. Loomis (1961) has found that a micro-environmental halo of chemically distinct water exists around hydras in culture, while Davis (1966) has found that a substance (possibly a protein) contained in the water from crowded cultures will inhibit the growth of hydras. These results could explain the cessation of branch growth in tips which were growing towards other branches (see above: Field Observations).

If it is accepted that brown tips are formed in response to micro-environmental conditions, the question remains whether conditions actually prevent extension, or if growth is stopped before this point, and energy for growth reallocated to more suitable regions of the colony. This latter possiblity would suggest partial endogenous control and possible translocation of metabolites from brown tips to white tips. If the point at which growth stops is under endogenous control, then genetic differences in this threshold could produce the variations in inter-branch distance and anastamosis found in different Acropora species. Brown tips may therefore represent part of an endogenous control of growth form. Thus while proximate factors controlling the induction of brown tips may be micro-environmental factors near each tip, brown tips could ultimately have arisen in response to pressures towards the adoption of an optimum growth form, and the maximization of growth in regions of the colony where conditions are most suitable.

Density analyses in this study indicate that extension and infilling may be treated as two distinct modes of calcification with different rates. Gladfelter (1982) has found two different types of skeletal deposition in A. cervicornis and relates one to extension and the other to infilling. Radial growth has been included by Oliver et al. 1983 as a third mode of branch growth. However in terms of the physiology of calcification, this mode can be considered a combination of the previous two (e.g. radial extension and radial infilling). The present study provides further evidence for this bipartite model and further suggests that the rates of infilling and extension do not change in direct proportion to each other. Infilling appears to be less variable than extension. This results in a spectrum of tip morphologies and extension rates, from rapidly extending, lightly calcified white tips, to non-extending densely calcified brown tips.

Since hermatypic corals exhibit light enhanced calcification (Goreau 1959; Goreau and Goreau 1959) which is the result of zooxanthellar photosynthesis (Vandermeulen et al. 1972, Chalker and Taylor 1975), it is a paradox that the region of maximum calcification in arborescent Acropora species (Goreau and Goreau 1959) should be devoid of zooxanthellae. Pearse and Muscatine (1971)

investigated this phenomenon in A. cervicornis and established that light-enhanced calcification in the zooxanthellae-free tip was dependent on the translocation of photosynthetically fixed metabolites from proximal zooxanthellae-bearing tissues. Although this work shows how enhanced calcification is maintained in the absence of zooxanthellae, it does not explain the reasons for their absence.

It is possible that the absence of zooxanthellae from the apical region is due to the inability of the algae to reproduce at a fast enough rate to keep up with a rapidly extending tip. If this was the case, however, the length of the zooxanthellae-free zone would be expected to increase with time. This does not occur. Work on algae-coelenterate symbioses also indicates that the host is capable of regulating the algal densities (Muscatine and Pool 1979). Pardy (1974), for instance, found that algae in the process of reinfecting an aposymbiotic hydra exhibited growth rates four times higher than those found in normally infected hosts growing at the same rate.

A second possible explanation is that the conformation, or conformational changes of cells and tissue layers in rapidly calcifying regions is such that algal cells are physically incapable of invading these areas due to their large size and spheroidal shape. Alternatively, the cells may be capable of invading these areas but are actively prevented from doing so by the host, since they prevent the tissue from adopting the appropriate conformation. Barnes (1972) and Meek (1982) have shown that substantial expansion and contraction of tissues, together with changes in the shape and orientation of individual cells, occurs during tissue and skeletal growth. Although this second hypothesis is more plausible than the first, direct evidence is lacking. Histological studies of tissue-algae interacations during the transformation of a brown tip to a white tip could provide further insight into this problem. Counts of brown and white tips indicate that the majority of tips within a colony are not actively extending. This is an important feature to consider when estimating the growth and carbonate productivity of arborescent corals. Estimates of mean tip growth based only on the growth of white tips would drastically over-estimate the productivity of a colony. If brown tipped branches

contribute, through translocation, to the growth of white tips, then tissue or area specific calcification rates for Acropora species may prove to be much lower than is presently assumed (Buddemeier and Kinzie 1976). Clearly there are significant morphological and physiological differences between brown and white tips which should be recognised by future workers. Further, more detailed studies of these differences may lead to a greater understanding of coordinating processes within a colony, and provide clues to the relationship between the different modes of calcification in corals.

Addendum to Chapter 3

For the purposes of the examination of this thesis, it should be noted that the data presented in Table 3.2, and the basic morphological descriptions in the results section are extracted from Oliver (1979). These items should not be considered part of the original content of the thesis.

At approximately the same time as Chapter 3 was published, two highly pertinent papers appeared in other journals. These papers examined intra-colony growth in Stylophora pistillata (Rinkevich and Loya, 1985), and density variations in Acropora branch tips (Brown et al., 1985). These two papers will be briefly reviewed here, and their relevance to the results and conclusions of the preceding chapter discussed.

Brown et al., (1984) examined growth and density (expressed by them as porosity) variations in Acropora pulchra at four different sites around an island complex in Indonesia. They showed that the thickness of the skeletal elements and the density of the branch tips, were significantly greater at exposed reef sites compared to sheltered ones. In addition they found that extension rates also varied according to the degree of exposure of the site, with the highest extension rates occurring in the most sheltered locations. Although it is not explicitly stated, their results indicate that extension and tip density are inversely related. This trend agrees well with the results presented for extension and density within a single colony in Chapter 3. The inverse relationship described in Chapter 3 however, occurred at one site, where the variation in water motion would be much less than between the sites in the study of Brown et al.(1984). Consequently it is possible that the density variations recorded by Brown et al. are a consequence of the variation in extension alone, rather than being due to a change in water motion. In order to distinguish between a possible density/extension relationship, and any additional effect on density due to water motion, it would be necessary to perform an analysis of covariance on the density values, using site as the main factor and extension as a covariate.

In the study by Rinkevich and Loya (1985) extension and calcification rates are shown to vary between different tips in a colony. Side branches in the interior of a colony calcify at a lower rate than upward growing branches at the top of a colony. They also note that internal side branches virtually never grow into each other and fuse, even though fusion is readily induced if two branches are manually brought into contact. In experiments on colony fragments placed adjacent to each other, they showed that upward growing branches frequently grew away from each other, while side branches lower down would cease extending if they were in close proximity to another branch. No observations on the tip colour of upward growing branches compared with inactive internal side branches were made. However, it is still possible that there are two types of branches, analogous to the white and brown tipped branches described in Chapter 3. The density of zooxanthellae in the tissues of many corals including S. pistillata can vary enormously depending on the ambient light levels. If the corals studied by Rinkevich and Loya were very pale, then the colour difference between the two tip forms may not have been particulary distinct.

Despite the similarity in the observations presented by the two studies the interpretation of the results varies considerably. Rinkevich and Loya (1985) conclude that their results indicate the possibility of a new class of biologically active chemicals which is secreted into the external environment but acts on other parts of the same organism. They coin the term "isomone" for this hypothetical chemical.

Although the existence of an isomone is an intriguing possibility, the observations reported both in Chapter 3 and by Rinkevich and Loya (1985) can also be explained in terms of variations in the microenvironment near a branch tip. Such variations could result from the passive presence of a nearby branch (reduction in light or water motion) or due to the excretion of waste metabolites into a boundary zone surrounding the branch. Some of the field and laboratory observations of changes in tip colour presented in Chapter 7, occurred

independently of the presence of other branches. It would therefore be instructive to conduct an experiment where branches were placed so that they grew at various angles into an inanimate object. If retreat growth or a cessation of growth occurred, then this would suggest that purely physical factor may be responsible for the responses recorded by Rinkevich and Loya.

Chapter 4
In Situ Growth: Bathymetric Variations

4.1 Introduction

Hermatypic corals are restricted to the upper euphotic zone with the majority of species occurring in the first sixty meters. It has been shown that light and zooxanthellar photosynthesis directly enhance short term calcification rates (e.g. Kawaguti & Sakumoto 1948, Goreau 1959a, Vandermeulen et al. 1972, Chalker & Taylor 1975). As a consequence of light-enhanced calcification, corals would be expected to calcifiy less rapidly with depth. Field studies to date, however, have not consistently supported this predicted trend. In some corals growth has been shown to decrease with depth (Shinn 1961, Buddemeier et al. 1974, Dustan 1975, Bak 1976, Highsmith 1979) while in others growth increases with depth (Bak 1976, Neudecker 1977, Wellington 1982). Gladfelter and Monahan (1977) and Gladfelter et al. (1978) found that the extension of Acropora palmata branches increased with depth but that the weight of newly deposited skeleton decreased.

These variable responses may be caused by other parameters, particularly water motion, which vary considerably with depth. In addition, photosynthetic adaptation might enable calcification to remain relatively constant through most of the depth range of any one species (Wethey & Porter 1976, Titlyanov et al. 1980, Falkowski & Dubinsky 1981, Dustan 1982). Although photoinhibition of photosynthesis and calcification is another factor which could obscure the predicted depth response, Barnes & Taylor (1973) present the only data which suggest significant inhibition. Buddemeier & Kinzie (1976) have suggested that this inhibition might be a result of the long incubation periods used, and Muscatine (1980) concludes that photoinhibition has never been shown to occur in corals. Inhibition of growth in P. damicornis by ultraviolet radiation in shallow water has been demonstrated by Jokiel & York (1982).

A variety of secondary factors may therefore mask the expected decrease in calcification rates with depth in hermatypic corals, particularly in the first 10 to 15m (Buddemeier & Kinzie 1976),

where other environmental factors tend to show pronounced fluctuations. In spite of this variability, a knowledge of the depth responses in calcification is still of considerable interest because it permits predictive models of population dynamics and reef growth to encompass different depth ranges.

Skeletal growth or calcification of individual coral branches may be subdivided into three separate, measurable processes. These are: 1) linear extension of the apical corallite; 2) radial growth, or increase in the diameter of each branch; and 3) internal calcification, or infilling of the spaces within each branch. In order to establish differences in calcification rates from different environments, it is necessary to measure each of these processes. In addition, the growth of newly initiated branches should also be measured. In virtually all previous studies on branching corals, growth has been measured only as linear branch extension. In fact, the third process (infilling) has only recently been quantitatively described (Gladfelter 1982). In the present study indirect methods were used to estimate the rates of infilling and radial growth. It is also important, when comparing rates of calcification, that the rates should be expressed in terms of tissue biomass or the area of calicoblastic epidermis (Goreau & Goreau 1959). If this is not possible (as is often the case in field experiments) it is desirable that some attempt be made to establish that observed differences in calcification rate correspond to similar differences in tissue or area specific rates.

Finally, consideration must also be given to the fact that the apical region of Acropora tips calcify much more rapidly than more basal areas (Goreau & Goreau 1959, Pearse & Muscatine 1971). Pearse & Muscatine (1971) showed that photosynthetically fixed carbon was translocated towards the apical corallite in A. cervicornis branches. Taylor (1977) found that translocation in this species can occur over a distance of 10cm. Excised tips calcify slowly and do not show light-enhancement of calcification (Pearse & Muscatine 1971). If the amount of zooxanthellae-bearing tissue which supports apical calcification is variable between colonies, then any comparison of branch growth rates should include these measurements.

The staghorn coral, Acropora formosa, and the closely related Caribbean species, A. cervicornis, are major components in many reef systems, often forming vast monospecific stands (Mergner and Scheer 1977, Wallace 1978, Goreau 1959b, Geister 1977). Furthermore, Pichon (1982) has hypothesized that arborescent Acropora species were predominant on the upper zones of vertically growing reefs during the period before they reached the surface. In spite of their obvious biological and geological importance, there have been no long term, in situ, studies on the skeletal growth rates of arborescent Acropora species over an appreciable depth range. In this study, the growth rate of Acropora formosa was investigated at three different depths over a period of one year. In addition, reciprocal transplant experiments were conducted between the deepest and shallowest stations.

4.2 Materials and Methods

This study was conducted on the the colonies at Davies Reef (5, 10 and 15m deep) described in Chapter 1. The period of the study was March 1980 to January 1982.

Environmental Parameters

Light intensity was measured at one metre depth intervals in the hole with a Licor LI-192S underwater quantum sensor and a Licor LI-185 meter. This meter measures photosynthetic photon flux density (PPFD) from 400nm to 700nm.

Temperatures were recorded in the hole during each sampling trip and water samples were collected for later salinity measurement using an inductive salinometer (Autolab model 601-MKIIIB).

Water motion was measured at each site in the hole using plaster of paris clod cards (Doty 1971). Three replicate cards were left in place at each site for twenty-four hours. In addition, three cards were placed in a closed twenty litre bucket at the deep site for still water controls. Winds during this 24 hour period were approximately twenty knots and wave heights outside the hole were 1

to 1.5 metres. Following collection, the cards were rinsed in freshwater, dried for 72h at 70°C and then weighed to the nearest 0.01 gram.

Growth Measurements

Seven consecutive growth samplings, of between 40 and 70 days duration, and spanning a total of 373 days were obtained. The mean extension rates for each sample were summed and the total standardized to a one year interval. New lateral branches were not included in the measurements since the majority were very small and poorly calcified. However, radial corallites present on newly extended portions of each stained branch were counted for each sample except the first and used as an index of the rate of polyp addition and overall polyp density.

Radial growth rates were estimated by measuring the diameter of several branches at 5cm intervals from the tip. The age of the branch at each position was estimated from the mean values for linear extension at each station. The rate of radial increase was determined from a plot of branch width on age.

Skeletal bulk density (see Chapter 1) was used as a direct measure of the extent of internal calcification. Branch portions were cut at regular intervals along several different brances at each site. The age of each portion was estimated from the relationship between branch width and age described below. Density values were then plotted against age to determine the rate of internal accretion.

Transplants

Two transplant experiments were carried out using single branches. The base of each branch was embedded in "Plasticene" modelling clay and fitted into small sections of 20mm diameter P.V.C. tubing. These were in turn fitted into alternate openings in a 50cm by 30cm steel expansion mesh rack. Pieces of polypropylene tubing were used as spacers to ensure a tight fit between the mesh and the P.V.C. tubes. Previous experiments, using A. formosa from an inshore fringing reef

showed that "Plasticene" does not affect corals (Oliver, unpublished data).

In the first experiment, two racks, each containing twenty 10 cm long branches, were prepared at each of the shallow and deep sites. One rack was left near its colony of origin as a control and the second rack was transferred to the opposite site.

In the second experiment, branches of various length were used in order to determine the effect of branch length on growth. The same experimental design was used (one control and one experimental group at each site) but in this case five branches of 5cm, 15cm and 20cm each per rack were prepared from both sites, with one exception. Since very few 20 cm unbranched lengths could be found at the shallow site, only two branches in each group (control and experimental) were prepared.

All racks were fastened to steel stakes near the deep or shallow colony and left for approximately two months to allow the corals to acclimate. The corals in each rack were then stained for three hours by placing the rack in a plastic box into which alizarin (12mg per litre) was introduced. After a period of 143 days, the racks were collected, bleached, and each branch measured for growth increment. Because of the destructive nature of the method for density analysis, and the need to preserve the branches for future study, estimates of internal accretion were not made. Similarly radial growth rates were not obtained since these rates are too slow to be measured accurately over the experimental time period. A qualitative visual assessment of the two processes revealed no major differences between experimental treatments.

Although there was only one tip per branch at the start of the experiment, some branching had occurred by the time of staining and continued during the period of growth determination. Thus three different measures of apical growth were made (see Chapter 1; Fig. 1.4). These were: 1) the total length of all growth, including new and pre-existing secondary branches (Σbr); 2) The extension of the original primary branch tip (1°l); and 3) the mean apical extension of all tips which existed at the time of staining ($\bar{x}$l). If the differences in the rate of internal accretion and radial growth

between treatments are assumed to be small, then the first growth estimate can be used as a relative measure of overall growth for each transplanted branch. The third measure is equivalent to the extension rates obtained from the in situ study.

4.3 Results

Environmental Parameters

Light at the deep (15m) site (expressed as fraction of surface PPFD) is slightly more than 20% of surface values and 50% of values at the shallow site (Fig. 4.1). The light attenuation curve corresponds to those for Jerlov's type II oceanic water (Jerlov 1976). Because field observations indicate that turbidity is variable in the hole, these results are only an approximation of the light regimes at the different stations. Temperature and salinity measurements taken in the hole during sampling trips (Fig. 4.2) exhibit a definite seasonal trend. Temperatures show a 6°C range, from approximately 30°C in the summer to 24°C in the winter. Temperature differences between the shallow and deep site were never more than 0.6°C.

Salinity measurements varied by less than two parts per thousand with lowest values occurring in the February samples. Much lower salinities than those sampled might be expected to occur temporarily after heavy rains during the summer. Observed salinities never varied by more than 0.4 parts per thousand between the shallow and deep sites.

Mean weight losses and confidence intervals for the clod cards at different sites (Table 4.1) indicate that turbulence decreases in the order shallow station > middle station > deep station. Since the 95% confidence intervals do not overlap for any site, these differences may be considered significant.

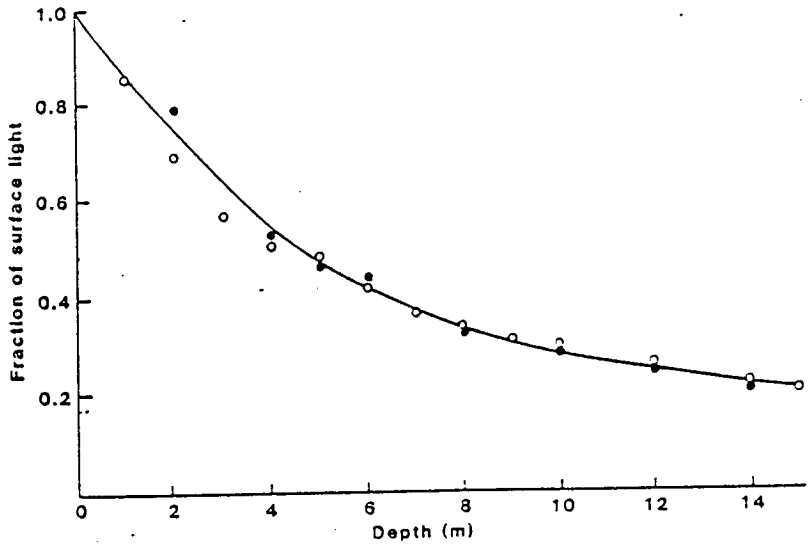


Fig. 4.1 Light attenuation with depth at the study site on 24 October, 1980 (closed circles) and 16 February, 1981 (open circles).

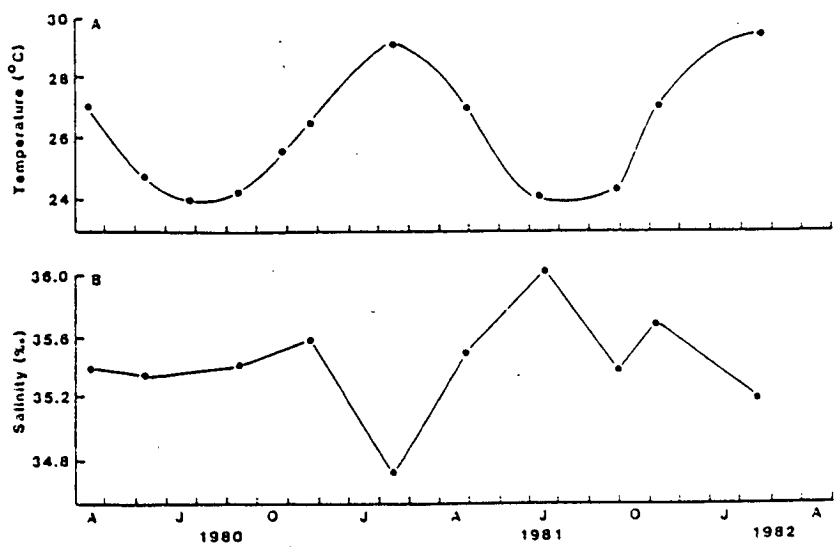


Fig. 4.2 a) Temperature recordings over a two year period at the study site. b) Salinity readings over a two year period at the study site.

Table 4.1
Weight loss of clod cards at different sites

Location	Depth (m)	Mean Weight Loss (g)	95% Conf. Int. (N=3)
Shallow Site	5	6.0	±0.19
Middle Site	10	5.1	±0.12
Deep Site	15	3.9	±0.40
Control	15	2.0	±0.40

However, as discussed by Doty (1971), the exact magnitude of the difference between sites cannot be determined from the weight loss data.

Skeletal Growth Rates

Mean extension rates for in situ coral branches at each site (Fig. 4.3) and standardized yearly rates (Table 4.2), clearly

Table 4.2

Standardized yearly rates for the extension of branches in situ and addition of polyps for seven sample periods spanning one year. Sample sizes for eaach period varied from 27 to 75.

Location	Depth (m)	Extension Rate (cm/yr)	Polyp Addition (polyps/cm
Shallow Site	5	8.0	30.1
Middle Site	10	12.4	26.5
Deep Site	15	16.6	24.1

indicate that extension increases by a factor of two from 5m to 15m. The data were subjected to a non-orthogonal two-way analysis of variance. The statistical package used was SPSS (Nie et al. 1975), in which the default option for a non-orthogonal design involves the successive analysis of A adjusted for B, B adjusted for A, and A x B adjusted for A and B. Since there was no reason to require a more

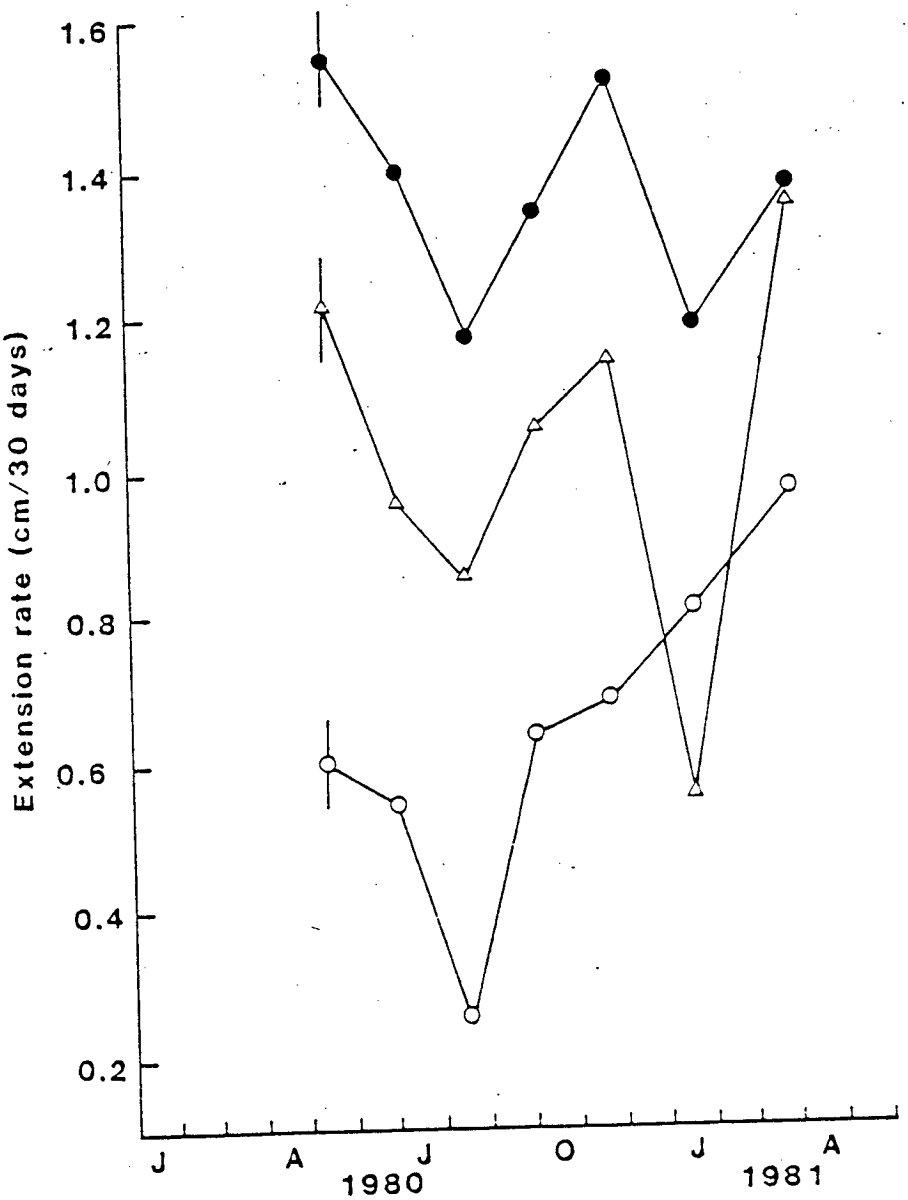


Fig. 4.3 Mean extension rates (standardized to 30 days) at three depths over a period of one year. Error bars represent typical 95% confidence intervals. Sample sizes vary between 31 and 75.

open circles: shallow site (5m)

open triangles: middle site (10m)

closed circles: deep site (15m)

recondite model, the default option was accepted. Owing to the abnormally large number of degrees of freedom for error in the resulting analysis (Table 4.3), the significance tests are weak

Table 4.3

Two-way analysis of variance for extension rate for branches in situ

Source of variance	d.f.	Mean square	F value
Sites	2	41.420	311.3218
Times	6	2.810	21.117
Sites x times	12	1.096	8.238
Residual	902	0.132	

and both and both main effects and interaction are highly significant ($P < .001$). However, comparison of the sites variance with the interation gives $F = 37.792$. This too is significant beyond the $P = .001$ level, so that the site effect can be considered significant independantly of the interaction. In this paper we shall only be concerned with this site effect.

The number of new radial corallites per unit length of newly extended skeleton developed at a steadily decreasing rate with increasing depth (Table 4.2). During analysis, cases with zero values for extension or number of polyps were treated as missing. Of the original 867 cases, 122 cases were excluded from the analysis of variance (Table 4.4) for this reason. Consequently,

Table 4.4

Two-way analysis of variance for addition of polyps on branches in situ

Source of variance	d.f.	Mean square	Variance ratio
Sites	2	2227.452	84.072
Times	6	706.198	26.654
Sites x Times	10	80.256	3.029
Residual	727	26.495	

the results must be interpreted with caution. The interaction in this case is actually significantly less than the site effect. However the variance ratio of the latter is so high that again we conclude that there is a significant depth effect.

Branch width at a given distance from a tip tends to be larger at the shallow site. However, because branches at the deep site had higher extension rates, this difference was reversed when diameter was plotted against age. Figure 4.4a shows the relationship to be markedly curvilinear. Both parameters are essentially growth measurements, so that a log/log transformation appeared appropriate. After transformation to natural logarithms the overall regression accounted for 82.4% of the sum of squares, so that the transformation was regarded as acceptable. Comparison of the two regressions (Fig. 4.4b) is summarized in Table 4.5.

Table 4.5

Comparison of regressions for branch width vs age

Overal regression:	$y = 0.341x + 0.335$
"Deep" regression (n = 136):	$y = 0.329x + 0.384$
"Shallow" regression (n = 61):	$y = 0.397x + 0.186$

Analysis of variance

Source of variance	d.f.	Mean square	Variance ratio
Single regression	1	15.222	1144.695
Improvement for parallel lines	1	0.577	43.369 ***
Improvement for non-parallel lines	1	0.116	8.737 **
Residual	193	0.013	

* P<0.05 ** P<0.01 *** P<0.001

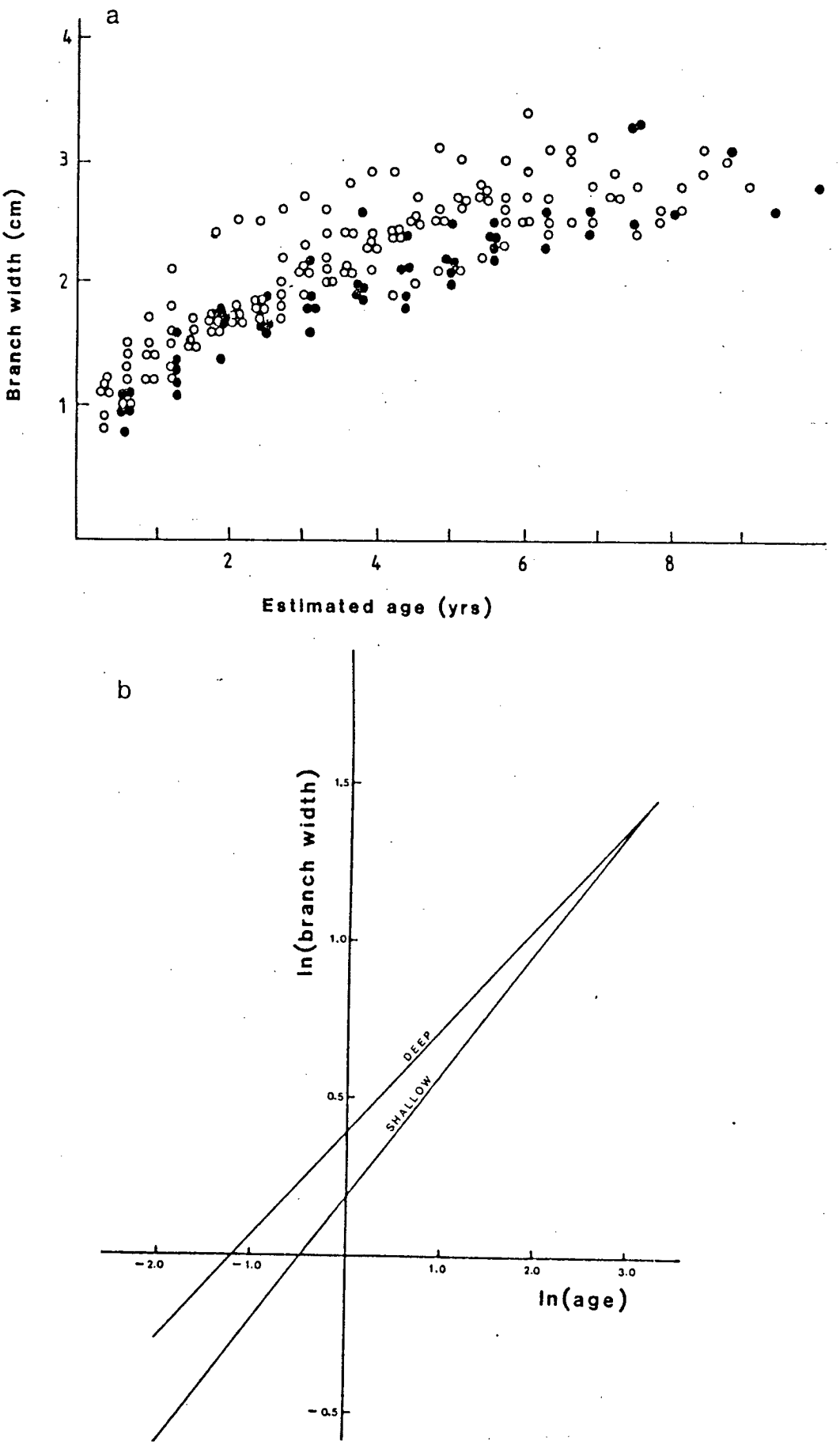


Fig. 4.4 a) Branch width vs age for branches from both the shallow site (closed circles) and the deep site (open circles). See text for calculation of age estimates. b) Regression lines for transformed branch width data.

Since the improvement for non-parallel lines is significant, it is concluded that radial growth is initially faster at the deep site but then proceeds more rapidly at the shallow site. Thus while branch width is initially larger at the deep site, this difference decreases to zero in the oldest branch regions (Fig. 4.4b). The relationship between branch density and age is also curvilinear (Fig. 4.5). Although the apical regions of branches from the deep site tend to be less heavily calcified, when the values are corrected for age there is no difference between the two sites. Since branch density cannot exceed the value for solid aragonite (2.94 gm cm^{-3}) the data were fitted to an asymptotic curve using the general equation: $y = a(1 - e^{-bx})$. The parameters "a" and "b" were estimated using non-linear least squares regression analysis with subroutine BMDP3R from the BMDP statistical package (Dixon and Brown 1977). The resulting regression accounted for 89.3% of the sum of squares (Fig. 4.5). Gladfelter (1982) obtained a similar relationship by recording the proportion of skeleton to empty space in serial cross sections of A. cervicornis branches, although she modelled the relationship with two separate linear regressions.

Transplants

The results of both transplant experiments are shown in Table 4.6. Because the data are highly non-orthogonal, with some extremely small class numbers, analysis of variance was regarded as unsuitable for the analysis of the results. It was decided to categorize the data and adopt manifold contingency techniques. The procedure will be described in detail for one variable (Σbr), and only the final results presented for the others. The complete set of Σbr values was "chopped" hierarchically into 4 groups. The data set is ordered, then dichotomized at the point where the between-group sum of squares is maximum; details of the algorithm are given in Williams and Lance (1977). The progressive fall in the sums of squares is shown diagrammatically in Fig. 4.6. It is clear that the bulk of the fall resides in the first division, which removes approximately 72% of the total sum of squares. It follows that the data need only be dichotomized into "low" and "high" values.

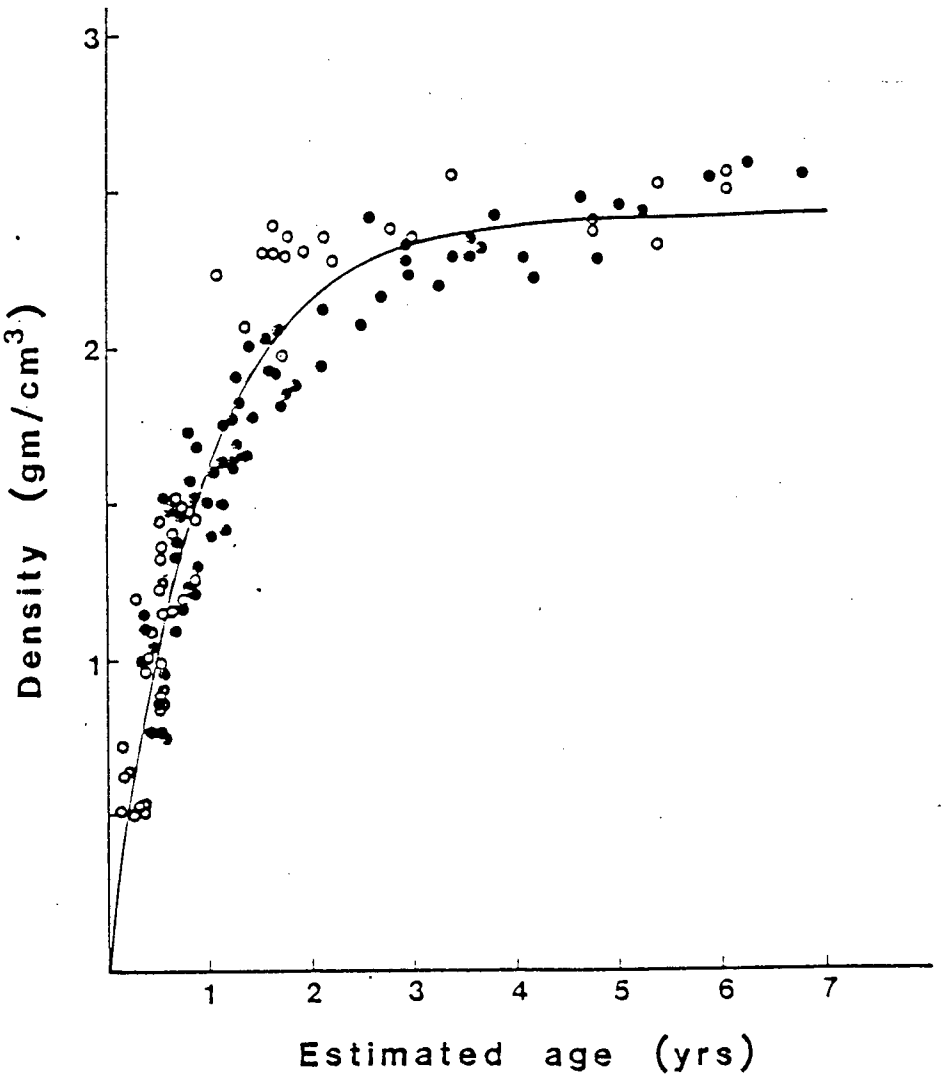


Fig. 4.5 Density vs age for branch portions from the shallow site (closed circles) and the deep site (open circles). Equation for curve is $y = 2.42(1 - e^{(1.12x)})$.

Table 4.6

Mean growth rates for transplanted branches

See Fig. 1.4 for explanation of growth terms.
Note that xl has different sample sizes from the other terms.

Group	Initial Branch Length (cm)	N	No. tips	Σbr (cm)	1°l (cm)	xl (cm)	(N)	length/tip (cm)
SH - SH	5	2	2.5	7.6	4.5	4.4	(3)	5.5
	10	18	6.5	21.4	5.5	4.5	(68)	5.5
	15	5	8.4	32.0	7.2	4.5	(20)	5.9
	20	2	12.5	43.8	6.4	4.7	(11)	5.4
SH - DP	5	4	1.0	0.3	0.3	0.3	(4)	5.3
	10	18	2.2	4.0	2.1	2.1	(22)	7.2
	15	5	2.4	4.9	2.4	2.5	(6)	8.9
	20	2	2.5	5.4	2.9	3.0	(3)	11.7
DP - DP	5	1	3.0	3.7	1.9	1.9	(1)	3.2
	10	16	2.0	4.5	3.3	3.3	(17)	8.9
	15	5	3.8	8.9	4.3	3.3	(9)	6.8
	20	5	3.4	9.5	6.1	6.1	(5)	9.7
DP - SH	5	1	3.0	6.1	4.1	4.1	(1)	3.8
	10	8	6.5	17.2	6.6	5.9	(10)	4.6
	15	5	5.4	19.0	7.2	7.2	(5)	6.5
	20	5	8.4	31.2	7.5	7.1	(12)	6.5
SH*						3.7		
DP*						4.7		

* Sum of two in situ measurements spanning the period of the transplant exper

Examination of the main effects (Table 4.7) shows that transplant configuration again exhibits a dichotomy, according to the site into which the branches were transplanted; the site from which they were obtained is evidently unimportant. Thus the treatment may be divided into two final states: shallow or deep. A similar situation is shown for initial branch length in Table 4.7b, so that it is acceptable to dichotomize branch length into short (5 or 10 cm) or long (15 or 20 cm). The χ^2 values in Table 4.7 show that the site effect is

Table 4.7

Analysis of transplant experiment, "Σbr" only

Transplant	Observed low	Observed high	Deviations from expectation	Row contribution to χ^2
(a) Transplant configuration over all initial branch lengths				
SH - DP	29	0	±10.2	15.818
DP - DP	25	2	± 7.5	9.194
SH - SH	5	22	±12.5	25.222
DP - SH	7	12	± 5.3	6.459
Total				56.693 ***
(b) Initial branch length over all transplant configurations				
5 cm	8	0	± 2.8	4.364
10 cm	41	19	± 2.2	0.364
15 cm	12	8	± 0.9	0.194
20 cm	5	9	± 4.1	5.153
Total				10.056 *

* P<0.05 *** P<0.001

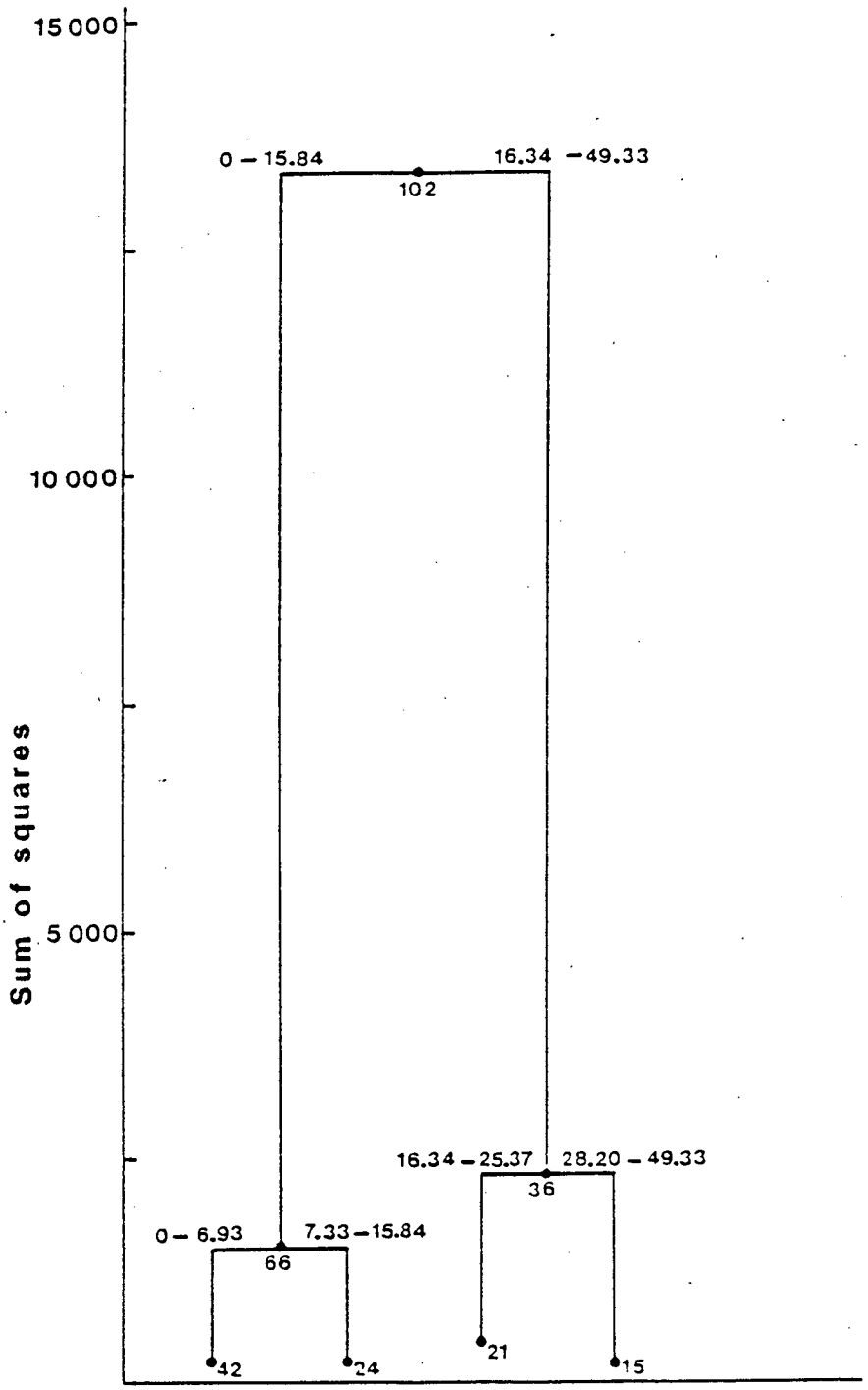


Fig. 4.6 Progressive fall in between group sum of squares for Σbr values in the transplant experiment. Numbers below closed circles are group sizes. Other numbers show limits for each group.

considerably larger than the branch length effect, and exhibits a much higher level of significance. These results do not, however, enable us to determine whether there is any interaction; for this purpose the complete 2 x 2 x 2 contingency table must be analysed and partitioned. The procedure for doing so is set out in Kendall and Stuart (1961). In the results (Table 4.8) the r x c line is

Table 4.8

Analysis of transplant experiment.

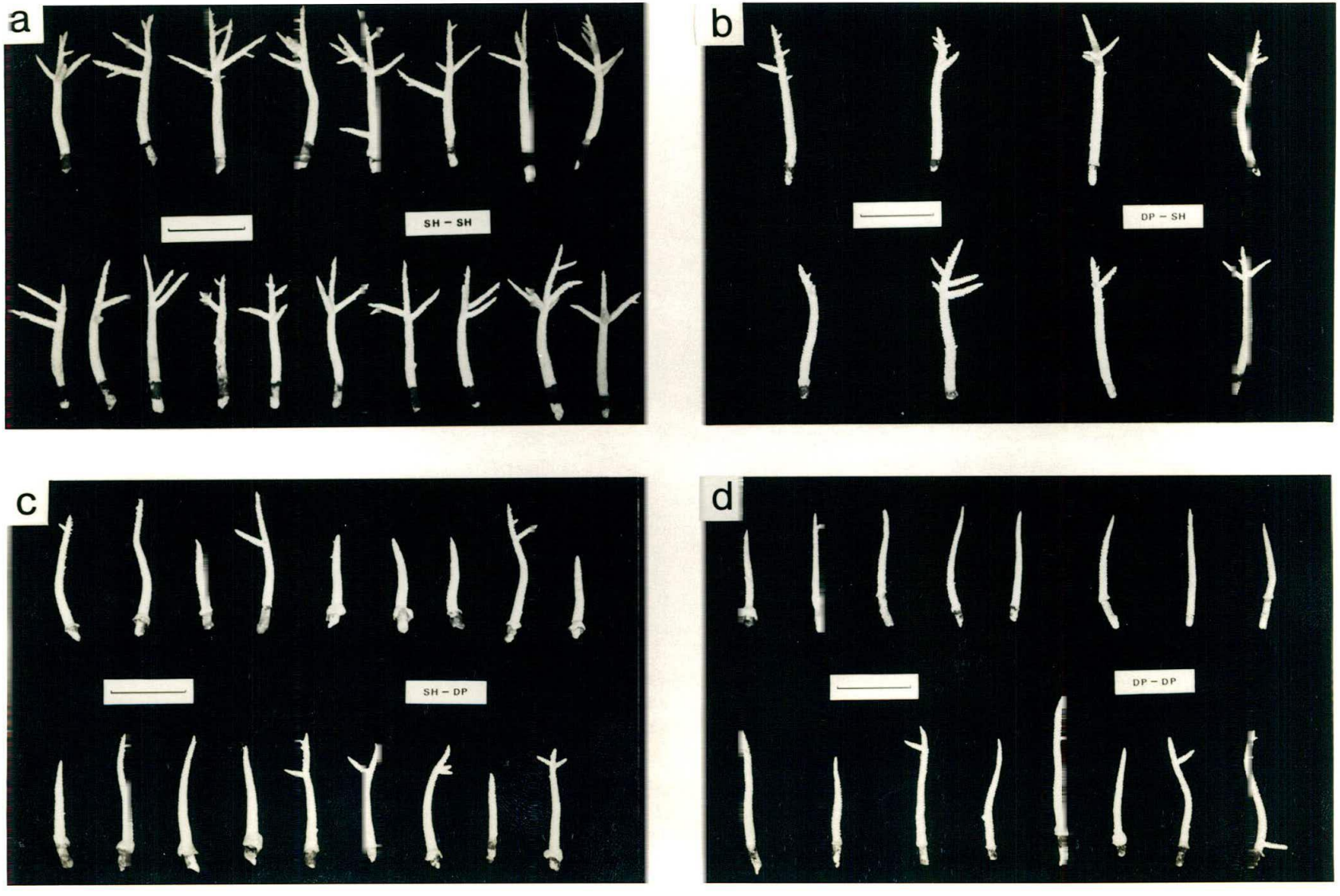
Key: r = site into which transplanted (shallow of deep); c = initial branch length (short, 5 or 10 cm; long, 15 or 20 cm) d = dichotomized variable Table entries are contributions to a 2 x 2 x 2 χ^2; note that contributions of individual elements are always zero, since marginal total were not set by hypothesis.

Source	d.f.	Σbr	1°l	xl	No. tips
r	1	0.000	0.000	0.000	0.000
c		0.000	0.000	0.000	0.000
d	1	0.000	0.000	0.000	0.000
r x c	1	0.495	0.495	0.067	0.495
r x d	1	54.717***	51.957***	38.764***	39.618***
c x d	1	4.830*	9.505*	1.068*	4.474*
r x c x d	1	0.529	0.986	3.751	0.005
Total	7	60.571***	62.943***	43.650***	44.592***

* P<0.05 *** P<0.001

merely a description of the degree of non-orthogonality of the experiment, and is well below statistical significance. The r x d line gives the site of final transfer effect; it is overwhelmingly significant. The c x d line summarizes the initial branch length effect; it is significant for all except xl, but at a much reduced level. The r x c x d line gives the effect of interaction between the two aspects of treatment; it is negligable for all except xl. The variable xl behaves differently from the other growth measurements; the χ^2 value for interaction (3.751) is very nearly significant at the 5% level ($P_{.05}$ = 3.84), while the branch length effect is not significant independent of this interaction. Overall, the transplant results clearly indicate that the number of tips, and all measures of branch growth were significantly greater in corals at the shallow site (Fig. 4.7). This is at variance with the <u>in situ</u>

Fig. 4.7 Transplanted 10cm branches after completion of experiment (143 days). Scale bar is 10cm. a) SH - SH: corals from shallow site retained at shallow site; b) DP - SH: corals from deep site transplanted to shallow site; c) SH - DP: corals from shallow site transplanted to deep site; d) DP - DP: corals from deep site retained at deep site


a
SH – SH
b
DP – SH
c
SH – DP
d
DP – DP

study, which showed that branches at the deep site grew most rapidly. This apparent paradox may be resolved by examination of the initial branch length effect, together with the interaction effect for xl. Long branches (15 - 20 cm) added new tips, increased their total branch length (Σbr) and extended along their primary axis (l°l) at a greater rate than short branches. However, the mean extension of all branches that existed at the time of staining (xl) increased with branch length only at the deep site. As a result, xl values at the deep site approach the values at the shallow site as branch length increases. This suggests that the observed in situ differences in extension rate between depths are only observable in corals which exceed a certain minimum size.

4.4 Discussion

As discussed above, the calcification rate of an individual branch is determined by the rates of extension, radial growth and internal accretion. In situ extension rates for Acropora formosa were significantly greater at 15m than at 5m. In addition, due to an initially rapid rate of radial growth (Fig. 4.4), branch widths at the deep site exceeded those at the shallow site for the range of ages encountered. Thus we conclude that because extension rate and radial growth are higher at the deep site, while internal accretion varies only slightly, branches calcify most rapidly at the deep site.

If comparisons between colonies, as opposed to individual branches are to be made, it is necessary to include growth due to branch initiation. The results from the transplant experiment indicate that growth is higher at the shallow site if new branches are included in the growth measurement (Σbr).

Because direct measurements of surface area or tissue biomass were not made on the experimental branches, it is not possible to calculate the tissue or area specific calcification rates at each site. Measurements of tissue protein in eight 12cm branches from the deep and shallow sites, however, indicate that the mean protein content is significantly greater in branches at the deep site

(Chalker, unpublished). If it is assumed that the differences, between sites, in the rates of internal accretion and radial growth were small compared to differences in extension rate, then it may be concluded that the total amount of calcium carbonate deposited by branches of the same initial size was much greater at the shallow site than the deep site. Furthermore, since the amount of tissue in similar sized branches is greatest at the deep site, the tissue specific calcification rate must also be much greater at the shallow site.

The transplant results also show that initial branch length significantly influences growth rates. The increase in overall growth (Σbr) of all tips in response to increased initial length indicates that calcification is enhanced by the presence of increasing amounts of zooxanthellae-bearing tissue behind the tip. This enhancement is probably due to an increase in the amount of translocated material delivered to each tip. The fact that extension rates ($\bar{x}$l) show a different trend at the shallow and deep stations, however, suggests that the amount of tissue and volume of translocate available to each tip is greater at the deep site. Presumably the smaller number of tips at the deep site (Table 4.6) enables each tip to receive proportionally more translocate than tips at the shallow site.

An estimate of the average amount of tissue available per tip was obtained by dividing the total length of all branches on a transplant by the total number of tips (Table 4.6), and used as an index of the amount of translocatable material which each tip could potentially draw upon. The length per tip showed little or no increase with initial branch length at the shallow site, while at the deep site, the values increased with initial length and exceeded the values at the shallow site at all lengths except 5cm. This further supports the proposition that branch tips at the deep site sustain their rapid extension rates by drawing upon more translocated material from a greater tissue source than branch tips at the shallow site.

It is interesting that the extension of the primary branch tips (1°l) did not exhibit the same response as the mean extension rates

(xl). This could be due to an unequal distribution of translocated material among branch tips. Primary branch tips of both the transplanted and in situ corals usually extended faster than newly formed lateral branches (Oliver, pers. obs.).

One inconsistency in the transplant results is that the extension rates of all the shallow control branches and of the 20cm, deep control branches exceeds that of the in situ corals. This difference may be due to some effect of colony size. Small juvenile colonies may tend to devote a greater proportion of their energetic resources into growth. In particular, small colonies such as the transplanted pieces may not reproduce. The period of the transplant experiment overlapped with the period of gamete maturation and release (Oliver in prep.) and if the transplanted corals did not reproduce this might explain the discrepancies in extension rates (but see Chapter 6).

In addition to depth-dependent rates of tissue specific calcification, A. formosa also exhibits quite different growth patterns at different depths. Higher extension rates and lower branching rates occur in deep water, while in shallow areas, branch initiation is more frequent and extension rates are slower. Thus, in shallow colonies, branches are short and close together, while in deeper colonies they are longer and more widely spaced (Fig. 1.3).

The mechanism for the decrease in colony growth and tissue specific calcification rates is difficult to determine without some knowledge of the total energy budget of the corals at each depth. For instance, it is possible that the total amount of energy available is less at the deep site or, alternatively, that available energy is the same but less is allocated to calcification and more to some other metabolic process.

Changes in growth form, on the other hand, probably represent an adaptation to one or more environmental factors. The two most likely factors, that vary with depth are light and water motion. Because decreased branching and increased spacing of branches at the deep site enables both light penetration and water flow to be increased

within the colony, the observed morphological changes with depth can be interpreted as responses to either or both of these factors.

Previous work also indicates that both light and water motion can influence growth rates and form, but there have been only two controlled laboratory studies on the effects of light or water motion on the long term growth of corals. Houck et al. (1977) found that linear growth (alizarin method) of Porites lobata and Pocillopora damicornis decreased with decreasing light intensity, although Montipora verrucosa showed the opposite trend. The effect of water motion was studied by Jokiel (1978), who demonstrated that increased turbulence stimulated the growth (weight increment) of P. damicornis and P. meandrina, although very high levels of turbulence were inhibitory in some cases.

Field studies have also implicated light, water motion or simply depth as factors influencing the growth and form of corals. Maragos (1972) showed that transplanted colonies of Porites lobata grew most rapidly in areas of heavy surge, and Dodge (1978) was able to correlate growth rate distributions with broad gradients in wind--wave patterns. Neudecker (1977) found that Pocillopora damicornis colonies extended more rapidly at 15m than 2.4m if they were caged to prevent grazing. Gladfelter et al. (1978) showed that extension of A. palmata branches was greater at 10m than 0.5m and that branch form changed, becoming more flattened in cross section at the deeper site. Furthermore their estimate of overall calcification was greater at the shallow site. Their results correspond quite closely to the present findings, in which extension rates were highest but calcification rates were lowest at the deep site. It is also interesting to note that branches of A. prolifera, which is closely related to A. cervicornis, extended more slowly at 2m than A. cervicornis at 15m (Gladfelter et al. 1978). Possibly most branching corals exhibit increased extension rates with depth, through a reduction in some other mode of skeletal growth, and an increased dependency on translocated products from a larger tissue source. Increased extension rates may represent an adaptation to sub-optimal conditions by increasing the chances of growing into a more favorable environment.

Goreau (1963) and Dustan (1975) showed that the shape of Montastrea annularis colonies changed from hemispherical to plate-like with increasing depth. Similar changes in growth form with depth have been described for Porites astreoides (Roos 1967) and Synaraea convexa (Jaubert 1977). In each case light was considered to be the controlling agent, although the changes were depth related and thus other parameters may also have varied. The nature of the growth form change (flattening of the colony surface in a plane normal to incident light) and the body of corroborative evidence suggest that light is the most likely controlling factor, in these massive or foliose colonies.

In branching corals, the evidence for a controlling factor is less definitive, but may favour water motion. Bottjer (1980), for instance, found that A. cervicornis exhibited less frequent branching in the less turbulent (and also slightly deeper) of his two study sites. Veron & Pichon (1976) state that the enormous intra-specific variability in the growth form of P. damicornis, Stylophora pistillata and Seriatopora hystrix could be largely correlated with the degree of exposure of the collection locality. In each case there was a distinct tendency for corals from more protected sites to possess larger and more widely spaced branches. Wood-Jones (1907) and Mayor (1924) have also claimed that water motion induced similar changes in branching corals.

The precise nature of the effect of water motion is not known, however the changes in growth form, towards increased branching and decreased branch length, have usually been interpreted as an adaptation to reduce mechanical stress in turbulent environments (Wood-Jones 1907, Graus et al. 1977, Bottjer 1980). Although the growth form changes can be seen as a response to mechanical stress, the overall increase in calcification seen in the present study, and by others (Jokiel 1978, Maragos 1972, Dodge 1978), cannot be explained in mechanical terms. Chamberlain & Graus (1975) have shown how different colony designs in model corals and dead skeletons can enhance or reduce water flow through the colony. Presumably, enhanced intra-colony flow increases the supply of limiting water borne substances and removes accumulated inhibitory substances, but this has not yet been experimentally demonstrated.

Neither the literature nor the present study provide sufficient evidence to choose between light or water motion as the primary controlling influence of the growth patterns observed in A. formosa. Possibly a combination of factors are involved. Food availability is one factor that has not been considered, but lack of knowledge concerning the trophic requirements of A. formosa and the depth distribution of various food sources make it impossible to evalute the potential influence of this factor. It is of interest, however, that the rate of polyp addition in the present study decreased with depth and that Chalker et al. (1982), working on the same colonies, have found that the respiration rates at the deep site were less per unit tissue protein than at the shallow or middle sites. Similar decreases in polyp densities and respiration have been found by Lasker (1981) and Davies (1977, 1980). The decrease in polyp density may be the cause of the respiration decrease if polyps are considered to be more metabolically active than coenenchymal tissue. The role, if any, that these changes play in bathymetric adaptation is not certain. Reduced respiration rates may represent an attempt to reduce overall energy expenditures without decreasing skeletal growth. This is particularly likely if food intake by the polyps is not a significant energy source. An increase in polyp density at the shallow site may also represent an increase in reproductive effort in a more favourable environment, since reproductive products are formed exclusively in the polyps.

The present study draws the following conclusions: 1) both the growth form and calcification rate of A. formosa change significantly with depth; 2) failure to include the extension of newly initiated branches can lead to highly misleading estimates of colony growth rates; and 3) differences in extension rates may be due to differences in the amount of zooxanthellae-bearing tissue supplying translocate to each tip. The third finding is based on tantalizing but indirect evidence, and direct experimentation using radio-isotopes would be required for verification. If this phenomenon does indeed exist, it raises some interesting questions concerning the relationship between the basal regions of a colony and its growing tips. First, does all zooxanthellae-bearing tissue, no matter how remote, contribute to the extension of branch tips?

Second, can translocate be preferentially distributed to some tips? If a colony can control the distribution of translocate to its tips, this would provide a mechanism to coordinate its growth and change its growth form to suit specific environmental conditions.

Addendum to Chapter 4

Inadequacies in the Original Experimental Design

Since the material in Chapter 4 has been published, it has become clear that the experimental approach used to examine bathymetric differences in the growth of A. formosa was not strictly valid. Although numerous replicate branches were sampled within the colonies at 5, 10 and 15m, the lack of replicate colonies at each depth, and the restriction of the observations to a single site on one reef means that the overall experimental design suffers from pseudoreplication (Hurlbert, 1983). Thus it is possible that the differences recorded between the three depths are only a measure of the differences which might be found between different colonies at the same depth, or between colonies at different sites with similar depth.

This flaw in the experimental design is mitigated somewhat by other independent experiments and observations which suggest that depth related parameters were indeed responsible for the observed differences. Firstly, the results of the reciprocal transplant experiment which was performed on two of the colonies at 5 and 15m, suggests that a large proportion of the variations between the colonies was due to differences in the environment rather than innate colony differences. Secondly, during the fifth sampling period, an additional colony at 16m, located approximately 5m from the colony at 15m was stained. The results from this second deep colony were not presented in Chapter 4 but are shown below.

The second deep colony extended much more rapidly than the two shallower colonies at 5 and 15m. There was also a small but significant difference between the two deep colonies (T-test, P=.045). This additional result from a separate colony supports the view that the extension rates of the different colonies are influenced by some site related characteristic. Since light and water motion are two depth-related environmental parameters which are known to influence growth, and which were demonstrated to vary significantly between the three sites, there are still grounds for the tentative conclusion that the observed growth responses were

depth related. Nevertheless, further replicated sampling at different site are necessary for a unambiguous analysis of the general effect of depth on the growth of A. formosa .

Table 4A.1

Comparison of extension rates from different sites at Davies Reef (5th Sampling Period). The colonies at 5,10 and 15m are the same as those measured in Chapter 4.

Depth	Sample Size	Mean Extension (cm/30days)	Standard Deviation
5	43	.68	.326
10	35	1.14	.322
15	36	1.48	.475
16	12	1.77	.128

Additional Data Obtained After Publication of Chapter 4

Sampling of branches from the colonies at 5,10 and 15m continued for a year after the last sample presented in Chapter 4. As can be seen in Figure 4A.1, the clear differences between sites which existed during most of the first year deteriorated during the second year. At the end of sampling in the second year, the growth rates had become virtually identical at all three sites. These new results together with the problems in experimental design mentioned above, further weaken the overall conclusion that extension rates increase significantly with depth. However, in view of the very strong and consistent results obtained during the first five samples it seems probable that this initial pattern was in fact a real phenomenon, rather than a sampling artifact. The subsequent growth data may therefore reflect a disruption of this original pattern. This view is also supported by a comparison of data from Nelly Bay during the same period (Figure 4A.1, see also

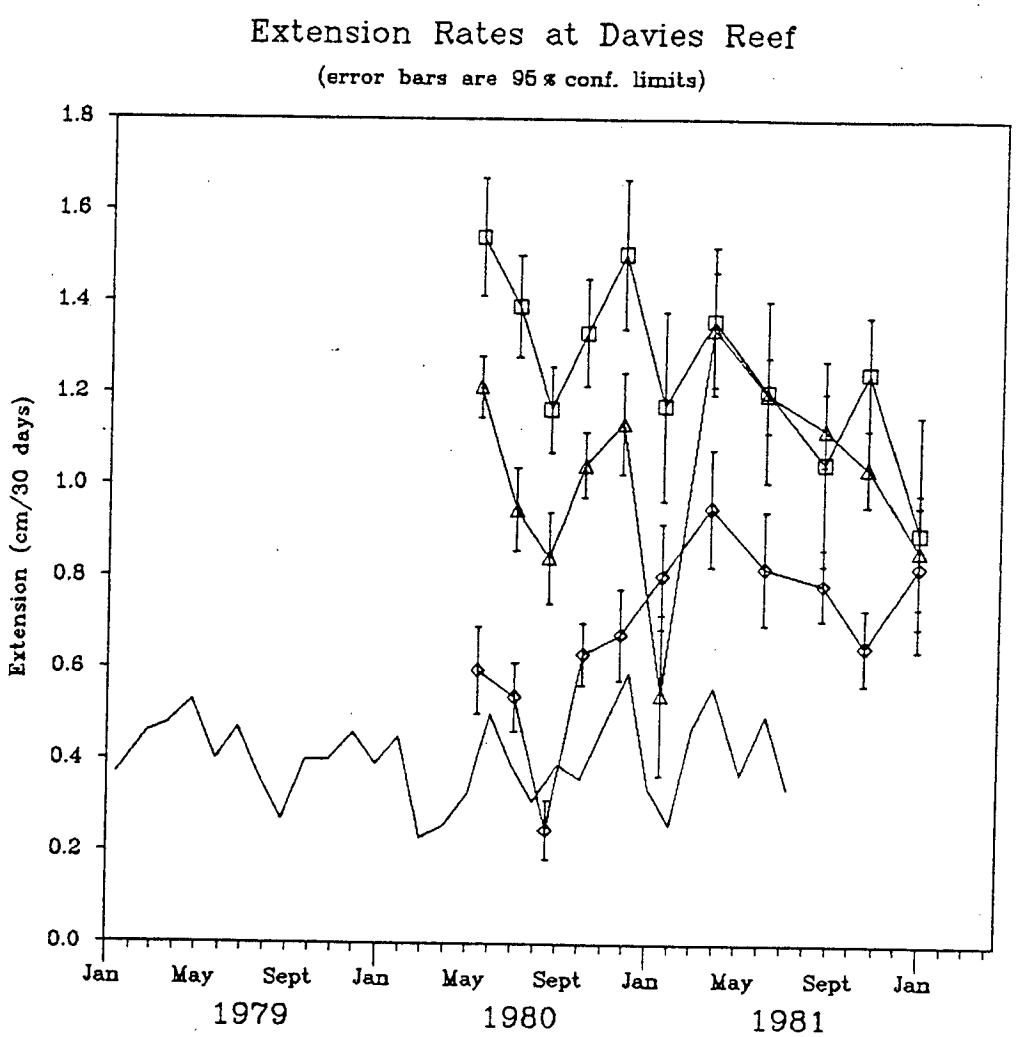


Figure 4A.1 Extension rates for Davies Reef and Nelly Bay, showing extra data not published in Chapter 4. Squares: Deep site. Triangles: Middle Colony. Diamonds: Shallow Colony. Line without symbols is comparative data from Nelly Bay (see Chapter 5).

Chapter 5). These data indicate that during the first seven samples the pattern ofseasonal variation was nearly identical at both Nelly Bay and Davies Reef. This similarity in pattern suggests that the extension rates were indeed reflecting the response of the coral to some broad scale environmental pattern. In subsequent months the seasonal pattern breaks down (see Chapter 5).

The major changes during the second year are a decreasing trend in extension at the deep site and an overall increase at the shallow site. Although the causes responsible for these changes are not obvious, it is suspected that excessive harvesting of branches may have played an important role.

At the deep site, repeated removal of 30 or more branches every two months may have had a significantly adverse affect on the colony. It has been hypothesized that branch extension at this site depends on the translocation of metabolites from a greater volume of tissue than at the shallow site. It is possible that chronic damage to the colony resulted in the increasing diversion of translocate away from undamaged growing tips to damaged area in need of repair. Rapid repair of the broken surface of a colony is important as it prevents colonization of the broken surface by epilithic algae, and subsequent competition for space. This repair response, and the detrimental consequences of algal fouling have been reported by Fishelson (1973), Connell (1973) and Loya (1976). In addition, the results of Loya (1976) and Stephenson & Stephenson (1933) indicate that colonies exhibit higher than normal growth in damaged regions of small colonies. As suggested by Loya (1976) this is probably made possible by the translocation of material from undamaged regions of the colony. Thus at the deep site the decreasing extension rates may have been due to the increasing demands of "repair growth" as more and more branches were harvested.

At the shallow site over-harvesting may not have been a significant problem since branching is much more frequent, and the total volume of coral per unit of reef area is much higher. If, as hypothesized in Chapter 4, each tip at the shallow site depends

on a smaller volume of tissue to sustain normal growth, the effect of harvesting from nearby branches may be minimized. Thus a pronounced decrease in extension might not be expected to occur as a result of the sampling program. However, this does not explain why extension rates should show a substantial increase during the second year. It is possible that a change in the sampling the sampling procedure was partly responsible. During the first year branches were harvested from a relatively small $10m^2$ area at one end of the colony where the depth was consistent at 5m. During the second year the reduction in number of suitable white-tipped branches due to intensive harvesting necessitated sampling over a much larger area of the same colony, and at a slightly greater depths (up to 7m). If the initial area sampled was situated in a slightly favourable area than the rest of the colony, then this might explain the increase in extension rates during the second year.

Despite the apparent disruption of the original growth response during the second year, extension rates at the shallow site were consistently and significantly less than the deep site for all except the last sample (see 95% confidence intervals in Figure 4A.1). Consequently it is still reasonable to conclude that extension rates at the deep colony were, on average substantially greater than the shallow colony.

Recent Literature

The papers published recently on variations in coral growth rate with depth tend to support the conclusion that calcification (but not necessarily branch extension) decreases with increasing depth. Tunnicliffe (1983) measured the extension of A. cervicornis branches at Jamaica and found little variation with depth between approximately 5 and 30m. However because branches at deeper sites were generally thinner, total weight increment decreased with increasing depth. In addition the rate of branch initiation was greater in shallow water, a feature also noted at Davies Reef.

Bablet (1985) measured the weight increment of Fungia paumotensis at Moorea over a two year period. He also found that growth decreased with depth and that the greatest difference was between the 10 and 20m. In addition his data indicate that the difference between depths was greatest during the summer months compared to the winter period.

Growth variations in 6 massive species at Jamaica were studied by Huston (1985) using X-radiography of annual density bands. In 4 out of 6 species there was a significant decrease in linear growth with increasing depth, with a pronounced decrease at about 20m. In the remaining four species there was no trend with depth.

Hubbard and Scaturo (1985) also examined the growth of the massive coral Montastrea annularis at different depths using density band analysis. Their results showed a clear and significant decrease with increasing depth. However, the trend was not linear, with growth exhibiting the greatest decrease between 12-18m. At shallower stations it was high but variable, while at deeper stations it was relatively constant and low. They suggested that the 12-18m zone may represent the depth beyond which calcification cannot compensate for reductions in available light. The results of the studies cited in previous paragraphs tend also to support this view. Photoadaptation is the most likely mechanism by which this compensation would occur and is well in reef corals (e.g. Falkowski & Dubinski, 1981; Chalker et al., 1983; Porter et al., 1984). Indeed, Chalker and Dunlap (1983) have calculated that photoadaptation enables gross diel photosynthesis in Acropora species to remain constant down to 35m (5.8% of surface illumination) at Davies Reef.

All of the above studies report significant decreases in growth rate with depth, but in almost all cases, the trend is manifested primarily at depths between 10 to 20m. In the present study growth was examined over a narrower depth range (5-15m) but the results, especially those of the transplant study, clearly indicate that calcification is reduced at the deep site compared to the shallow site. It was concluded that either light or water

motion were the most likely parameters responsible for this reduction. However the calculations of Chalker and Dunlap (1983), which were base on measurements from the same colonies as this thesis, suggest that light is not a limiting factor at the deep site. Consequently it now seems more likely that reduced water motion is the cause of the reduction in both calcification and branching frequency. This possibility should be investigated further.

There are two other recent studies which, although not directly related to bathymetric growth variations, are relevant to this study. As mentioned above it was hypothesized in Chapter 4 that the higher extension rates at the deep site may have been made possible by translocation of material from tissues at some distance from the tip. Gladfelter (1983) has now described the morphology and circulation rates of fluids within the gastrovascular canals in A. cervicornis. Her results suggest that fluids can rapidly transport a variety of both particulate and dissolved material both up and down a branch. In addition, Rinkevich and Loya (1983) have shown that photosynthetically fixed carbon is concentrated at the branch tips of Stylophora pistillata, and can even be transported across graft zones between different genotypes. These results support the suggestion that the translocation of material is a potentially important means of coordination of growth within a large arborescent colony.

Chapter 5
In Situ Growth: Seasonal Variations

5.1. Introduction

Although lacking the temperature extremes of many temperate regions, reefs and other tropical ecosystems experience significant seasonal variations in several environmental variables. On the Great Barrier Reef seawater temperatures can vary over a range of 10°C or more in shallow areas (Walker, 1981a; Potts & Swart, 1984). Reef zones exposed to open water exhibit a somewhat smaller range of 5-8°C (Wolanski *et al.*, 1981; Andrews, 1983; Potts & Swart, 1984). Other important parameters which exhibit significant seasonality include solar radiation (Oliver, 1978), salinity (Walker, 1981b), winds (Walker & Collins, 1985) and dissolved nutrients (Hatcher & Hatcher, 1981; Hatcher & Larkum, 1983). Even in equatorial regions, the shift between wet and dry monsoons causes seasonal fluctuations in rain, winds and solar radiation which can influence sea temperature, salinity and turbidity levels, especially on fringing reefs (Charuchinda & Hylleberg, 1984; Brown *et al.*, 1985). The annual range in sea temperatures, however, is less (3-4°C) than in more subtropical regions.

This annual fluctuation in environmental parameters, directly or indirectly induces a similar seasonal variation in many biological processes on coral reefs. These can include algal growth and biomass (Hatcher & Larkum, 1983; Atmadja & Sulistijo, 1981; Morrissey, 1980), changes in plankton abundance (McWilliams *et al.*, 1981), reproductive cycles in diverse phyla (Willis *et al.*, 1985, Caspers, 1984; Conand, 1981; Braley, 1984), community metabolism (Kinsey, 1983; Wilkinson *et al.*, 1984), and growth of calcium carbonate producing organisms such as corals (Buddemeier & Kinzie, 1976; Gladfelter, 1984), molluscs (Erlenkeuser & Wefer, 1981) and foramniferida (Wefer & Berger, 1980).

Previous long-term studies on seasonal growth rates of corals have emphasized the predominant importance of two parameters as correlates of growth. These are water temperature (Shinn, 1966;

Glynn, 1977; Crossland, 1981,1984; Charuchinda & Hylleberg, 1984; Yap & Gomez, 1981, 1984; Brown et al., 1985, Bablet, 1985) and light (Bak, 1974; Maragos, 1972; Gladfelter, 1984). In these studies, light consistently has a positive correlation with growth. The effect of temperature is more complicated. In studies where water is consistently warm but exceeds 30°C during part of the year, growth is negatively correlated with temperature (Charuchinda & Hylleberg, 1984; Brown et al., 1985). In subtropical regions with cooler water and winter minima near or below 20°C there is a positive correlation (Crossland, 1981; Glynn, 1977; Shinn, 1966; Bablet, 1985). In other regions where temperature fluctuation is minimal, the relationship with growth, if detectable, is not very pronounced (Lewis et al., 1968; Charuchinda & Hylleberg, 1984; Gladfelter, 1984). These long-term field studies confirm the findings of short-term laboratory and field studies on the effects of temperature and light on corals (see review by Buddemeier & Kinzie, 1976). In particular, the studies of Clausen & Roth (1975), Jokiel & Coles (1977) and Houck et al., (1977) indicate that maximum growth occurs at approximately 26-27°C and is increasingly inhibited at temperatures above and below this level.

On the near shore fringing reefs at Nelly Bay, Magnetic Island, North Queensland, the temperature range is quite high (19-32°C) and encompasses both the upper and lower extremes which appear to cause growth reductions in the previous studies. For this reason, it might be expected that, growth would exhibit a bimodal seasonal pattern with depressed rates in both the summer and winter. However, the marked seasonal fluctuations which also occur in salinity, light and other factors might tend to obscure this pattern. In this chapter the growth of a single colony at Nelly Bay over a period 2.5 years is analysed, together with subsidiary data from other colonies at both Nelly Bay and Davies Reef. It is demonstrated that there is indeed a bimodal seasonal growth curve at Nelly Bay, and a suggestion of a similar pattern at Davies Reef, despite the much lower temperature range at this offshore site, and the loss of a clear pattern during the last year of the study.

5.2. Materials and Methods

Study Sites and Experimental Colonies

All experiments and observations were carried out at the Davies Reef and Nelly Bay study sites described in Chapter 1. At Davies Reef, the colonies used were located at 5, 10 & 15m depths, while at Nelly Bay, repeated measurements were made on four different colonies at approximately 6m depth. The first colony (Colony 1) was the same as that used by Oliver (1979) and was chosen in order accumulate a continuous series of measurements for as long as possible. The three other colonies (Colonies 2-4) were located within 100m of the first, and were chosen in order to determine the degree of variability in growth between colonies in the same habitat.

Environmental Parameters

During each sampling trip, temperatures were measured (0-50° thermometer), and water samples were taken for subsequent salinity determination on an Auto-Lab inductive salinometer. Although maximum/minimum thermometers were kept at both Nelly Bay, and at the 5 and 15m sites at Davies reef, they were repeatedly lost or broken by storms or large grazing scarids, so that these data are incomplete. Data on total daily solar irradiance (pyroheliometer) and daily number of sun-hours were obtained from the Bureau of Meteorology, Townsville. Maximum daily air temperature, 9am wind speed, and rainfall data were obtained from the Cape Cleveland lighthouse. This latter station was chosen for most data since it is located on an exposed headland which juts out into Cleveland Bay. It is closer to Nelly Bay than the Townsville station, and is less influenced by land induced meteorological effects such as land and sea breezes (Walker & Collins, 1985).

Growth Measurements

Growth measurements were taken approximately every month at Nelly Bay, and every two months at Davies Reef. In each case 25-30 plastic bags were placed over branches possessing one or more actively growing (white-tipped) terminal corallites. The bags were injected with alizarin and incubated for 3-4 hours. The branches were then tagged with plastic coated wire, and harvested an average of 32 days later (see Chapters 3 & 4 for more detailed methodology). Linear growth was determined from the bleached specimens using calipers to measure the distance between the alizarin stained skeleton and the tip of the apical corallite. Only those branches which were greater than 1cm in length at the time of staining were measured.

At Nelly Bay, a total of 19 monthly samples were taken from Colony 1. For the sake of completeness, the results obtained by Oliver (1979) on monthly growth of A. formosa at Nelly Bay will be included and re-analyzed as a component of the present more extensive study. Thus for Colony 1, monthly growth measurements cover a period of 2.5 years, from December 1979 to June 1981. Measurements on Colonies 2-4 at Nelly Bay began in September, 1980 and continued until June 1981 (10 samples).

At Davies reef, sampling began in April, 1980 and continued until February 1982, during which 11 samples were taken from each of the three colonies. The first 6 samples are the same as those referred to in Chapter 3.

5.3. Results

5.3.1. Environmental Parameters

Meteorological Records

Figure 5.1 shows the mean weekly values for solar irradiance, sun hours, air temperature, rainfall and wind during the study period. In general two distinct seasons can be identified. The

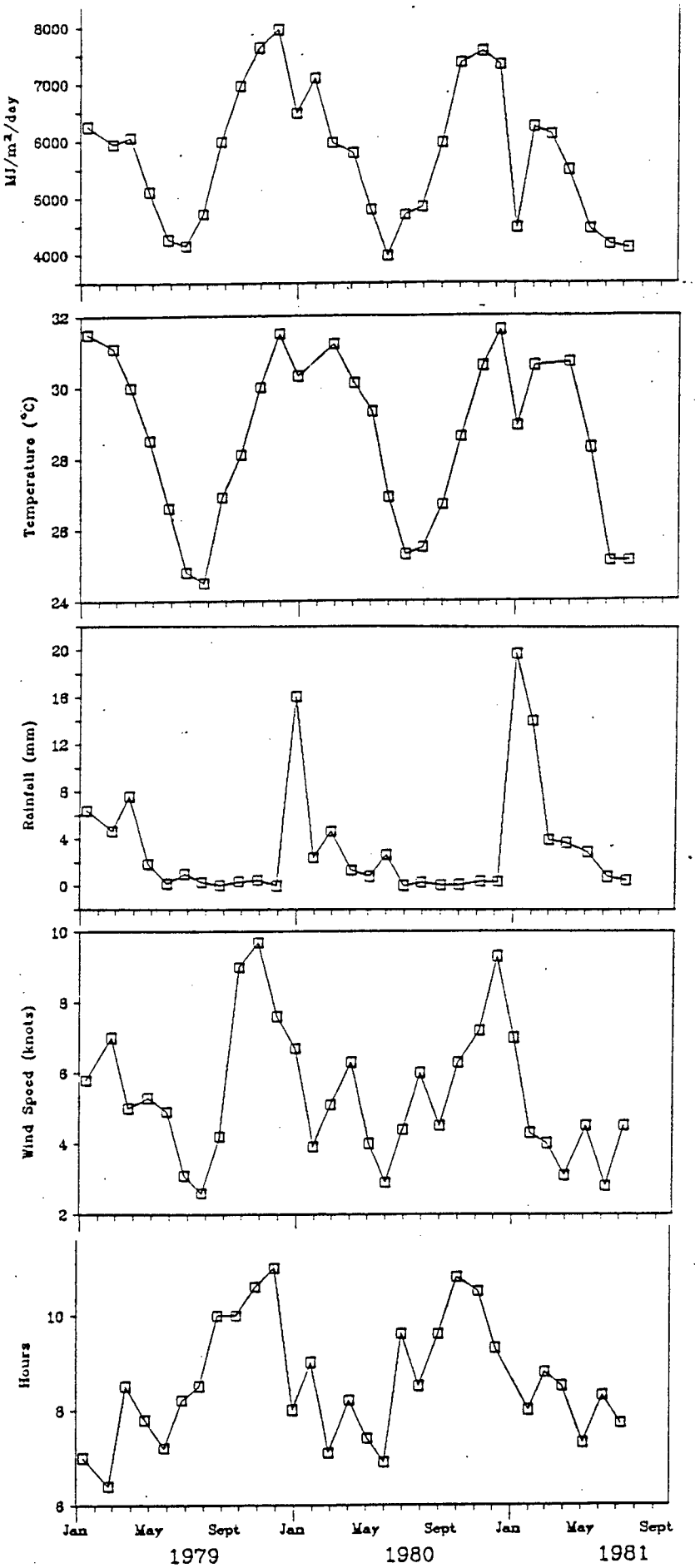


Figure 5..1 Seasonal variations in environmental parameters. Values at each point are means for each of the monthly growth periods at Nelly Bay. a) solar radiation at Townsville airport; b) air temperatures at Cape Cleveland; c) rainfall at Cape Cleveland; c) 9am wind speed at Cape Cleveland; d) Number of hours of sunshine at Townsville airport.

rainy season (December - March) is characterized by warm temperatures, heavy but sporadic rainfall, and light and variable winds. The dry season (May - October) has lower temperatures, almost no rainfall, and moderate to strong south-easterly winds. The intervening months are less predictable and may exhibit characteristics of either season. Solar irradiance and sun hours reach a maximum just before the rainy season, when the sun angle is high but cloud cover is minimal.

In situ Measurements

Temperatures at both Nelly Bay and Davies reef exhibit a definite seasonal trend (Fig. 5..2), although the difference between summer and winter values is much greater at Nelly Bay. Temperatures ranged between 19.3-32 °C (mean=26.1) at this inshore site, while the range at Davies was restricted to 22.5-30.5 °C (mean=26.3). The coldest months were July and August, while the warmest periods were during January to March.

Salinity values also show a distinct seasonal trend, which was again more pronounced at Nelly Bay (Fig. 5..3). During the rainy season (January to March) direct rainfall and runoff from nearby creeks and rivers cause substantial fluctuations and an overall reduction in salinity, which then gradually increases to its previous level during the dry winter months.

5.3.2. Extension Rates

Mean monthly extension rates for the 4 colonies at Nelly Bay are shown in Figure 5.4, and descriptive statistics are presented in Appendix 1. There are two features of the graph in Figure 5.4 which are apparent on close inspection. Firstly, in the long-term growth record for Colony 1, there is a pattern of successive growth minima which correspond roughly to the mid-summer and mid-winter periods. Thus the annual growth curve is bimodal. The second feature of significance is that the three other colonies, measured in 1980-81 exhibit an almost identical pattern of maxima and minima, despite

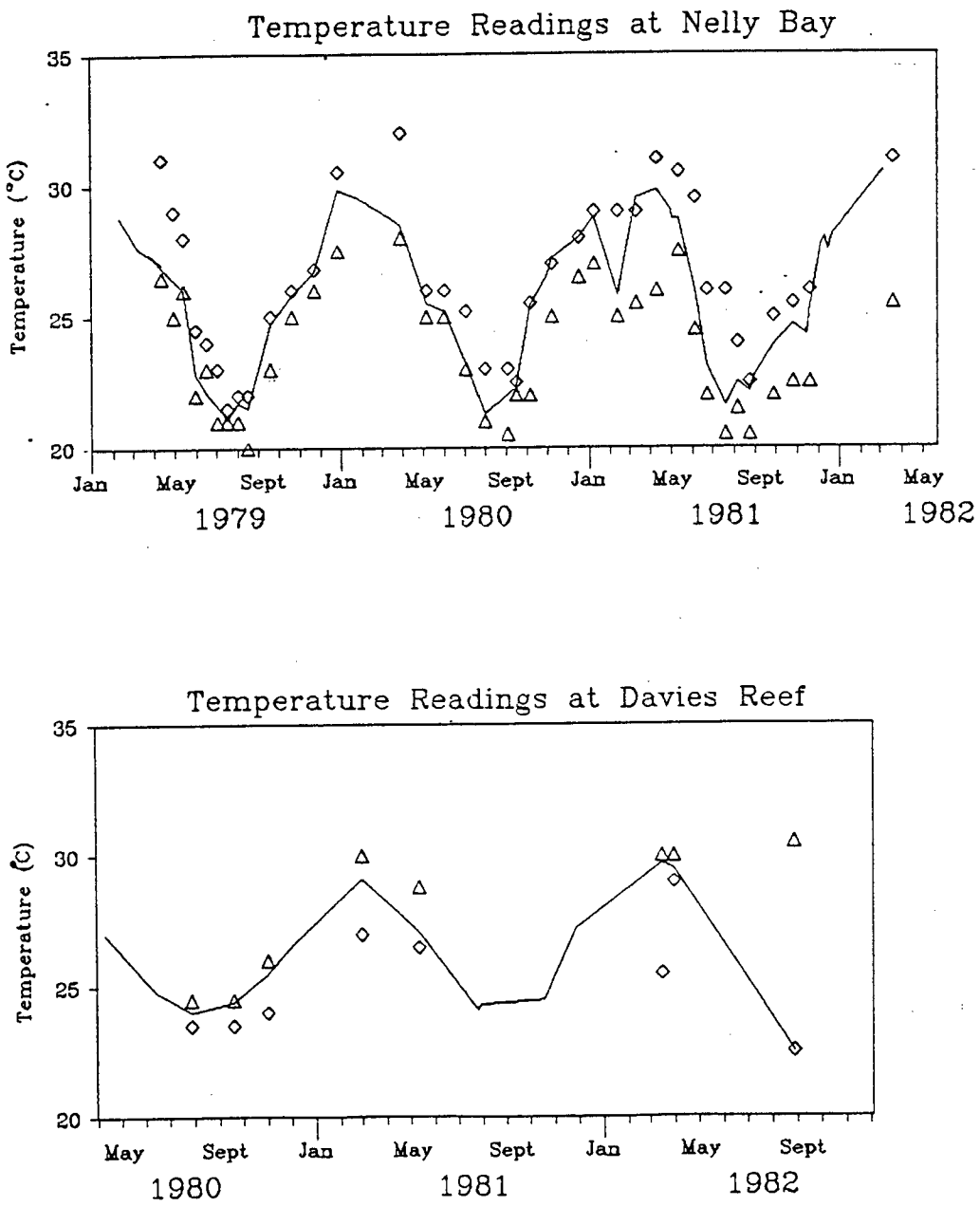
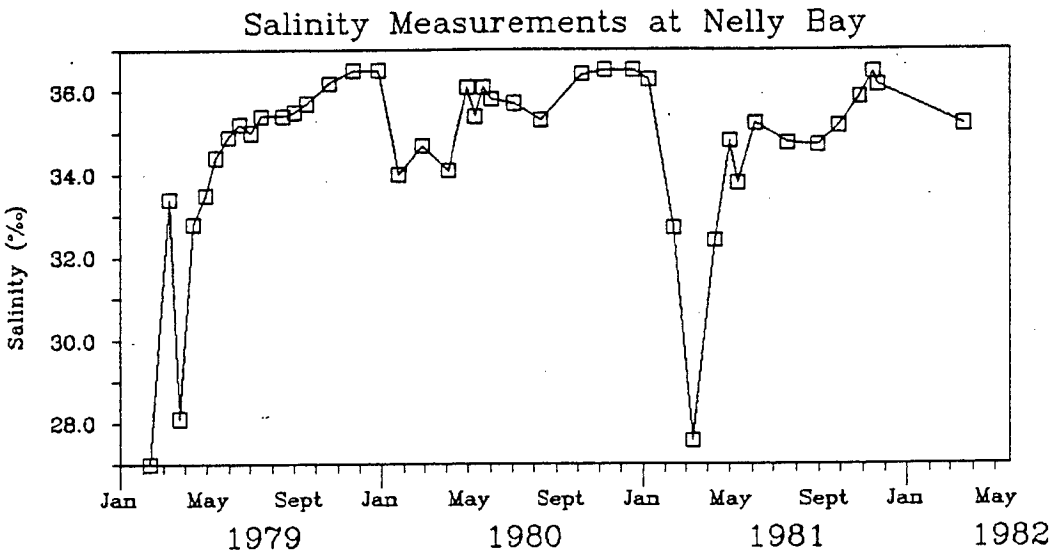


Figure 5.2 In situ temperature readings at Nelly Bay (a) and Davies Reef (b).



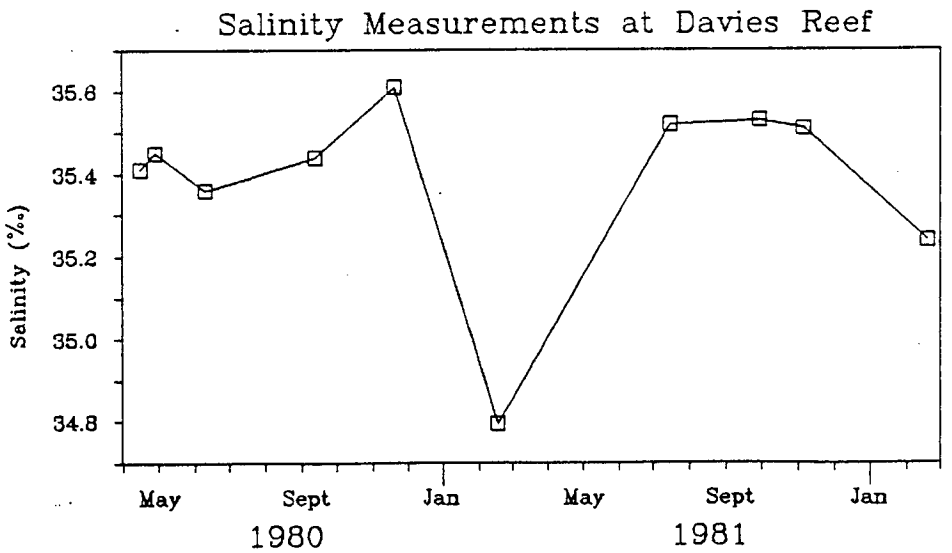


Figure 5.3 In situ salinity mesurments at Nelly Bay (a) and Davies Reef (b).

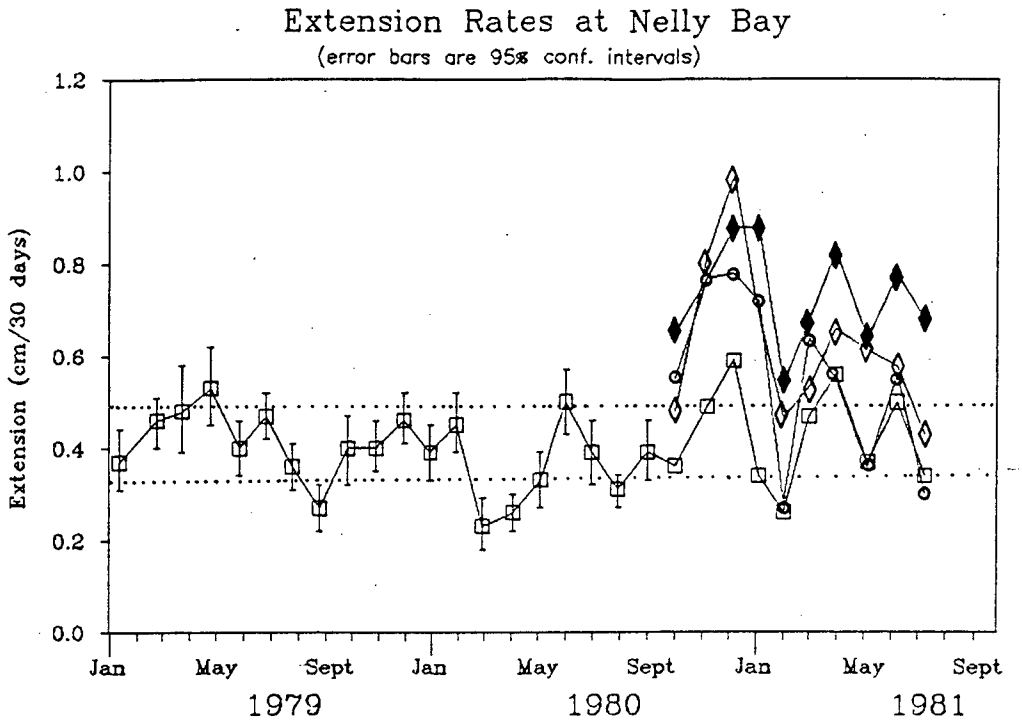


Figure 5.4 Mean extension rates at Nelly Bay. Square = colony 1; open diamond = colony 2; circle = colony 3; closed diamon = colony 4.

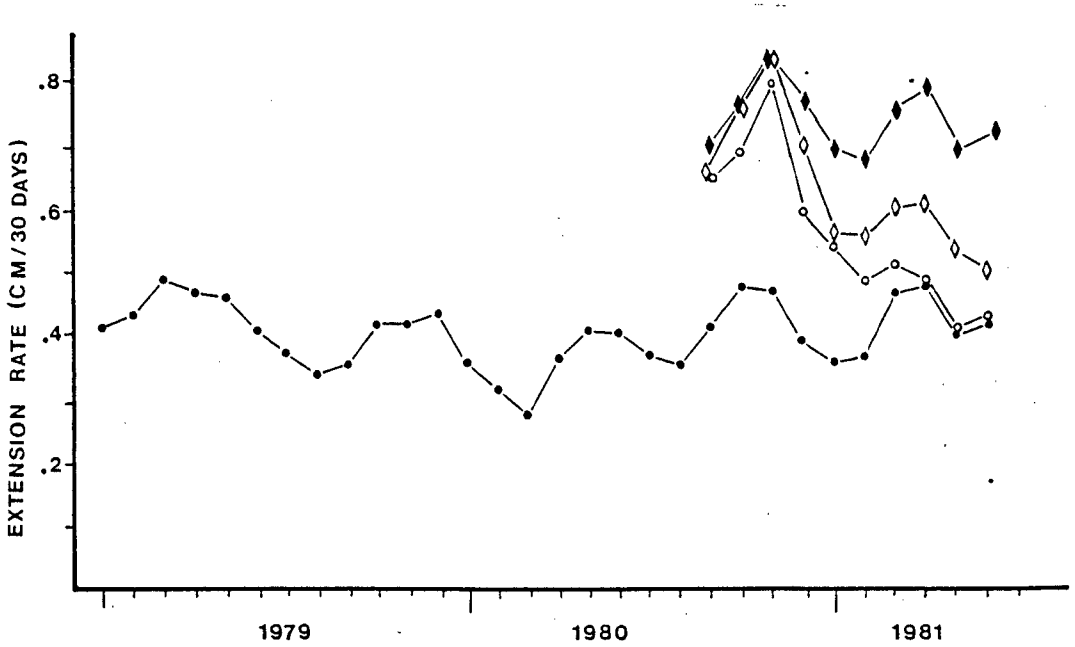


Figure 5.5 Smoothed (3 point running mean) extension rates at Nelly Bay. Symbols definition is the same as Figure 5.4.

differences in their absolute growth rates, and in their performance relative to each other.

Since the bimodal growth pattern in Figure 5.4 appears to be based on a quarterly seasonal cycle, a 3-point running average was applied to the data. This has the effect of filtering out any variation in the data which occurs with a frequency shorter than three months (ie. within season variation). The running mean data (Figure 5.5) again indicate clearly that there is a consistent seasonal pattern to the growth rates of all 4 colonies, and that both the summer and winter periods represent times of reduced growth.

Extension rates for the three colonies at Davies Reef are shown in Figure 5.6, and descriptive statistics presented in Appendix 1. Growth data for Colony 1 at Nelly Bay has also been included for comparative purposes. During the first 5 samples, there is a clear depression of extension rate for all colonies during the winter of 1980, followed by a rise in the spring and early summer. This initial pattern closely follows the trend seen at Nelly Bay. In subsequent samples there is a lack of coherence between colonies, which will be discussed in more detail later. Nevertheless, the deep site continues to exhibit a seasonal pattern which is nearly identical to that seen at Nelly Bay. The other two colonies show varying degrees of departure from this pattern during the last year of sampling.

5.3.3. Analysis of Seasonality

In order to test the statistical significance of the seasonal pattern demonstrated in the growth rate data, two different procedures were followed: 1) Analysis of Variance to test for differences among the sample means, followed (where possible) by an *a posteriori* test to determine which samples were significantly different from each other; and 2) Time Series Analysis to determine whether there was any significant periodic cycle in the growth record from Colony 1 at Nelly Bay.

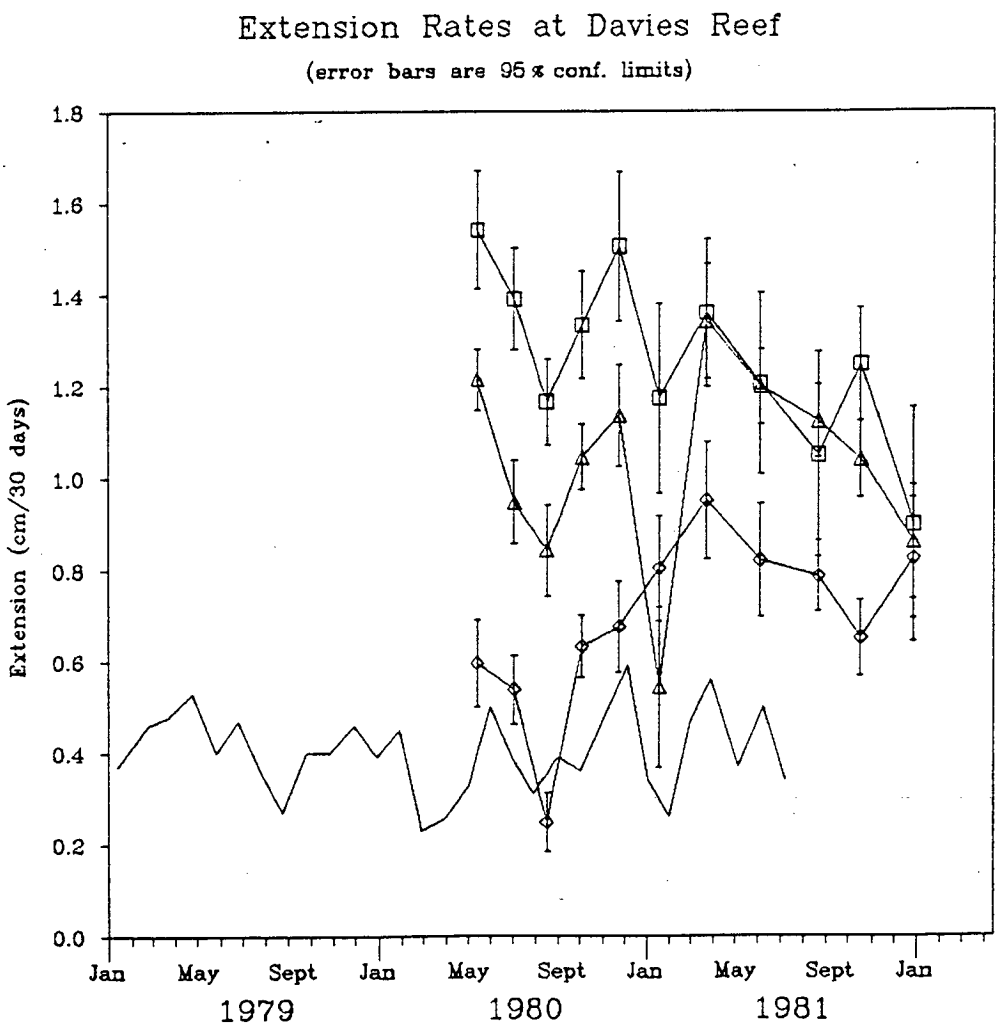


Figure 5.6 Mean extension rates at Davies Reef. Square = deep colony; triangle = middle colony (10m); diamond = shallow colony (5m). Line without symboles is data for colony 1 at Nelly Bay.

Since homogeneity of variances is a requirement of the Anova procedure, the data for each colony were tested using the F_{max} test (Sokal & Rohlf (1969). The colonies at Davies reef exhibited significantly unequal variances between samples ($P<.05$), and since this was not ameliorated by a log transformation, a non-parametric Kruskal-Wallis Anova was used to test for differences among sample means. The results (Tables 4.1 & 5.2) indicate that in all cases there were significant differences among the means. These tests do not indicate which pairs, or subgroups of samples are significantly different. This information is most readily derived from an a posteriori test, which was performed on the most complete growth sequence (Colony 1). The results (Table 5.3) indicate that there are numerous pairs of significantly different samples. In particular, there is a block of comparisons (outlined in Table 5.3) which are consistently different (with one exception). The upper and lower

Table 5.1

Oneway Anova for Seasonal Variation
in Extension Rates at Nelly Bay

Colony	d.f.	F	Prob.
1	29,1027	7.99	<.001
2	9, 144	12.95	<.001
3	9, 152	9.14	<.001
4	9, 96	3.36	.001

Table 5.2

Kuskal - Wallis Test for Seasonal Variation

Colony	Number of Samples	Total Cases	Chi-Square	Prob
Shallow	11	449	103.56	<.001
Middle	11	468	116.83	<.001
Deep	11	440	52.20	<.001

Table 5.3
Multiple Range Test

Student-Newman-Keuls Procedure, (*) Denotes pairs significantly different at the .050 level

Mean	Group	FEB80	MAR80	JAN81	AUG79	JUL80	APR80	DEC80	JUN81	JUL79	SEPT80	APR81	JAN79	JUN80	DEC79	AUG80	SEPT79	MAY79	OCT79	JAN80	FEB79	NOV79	JUN79	FEB81	MAR79	OCT80	MAY80	MAY81	APR79	MAR81	NOV80
.2332	FEB80																														
.2603	MAR80																														
.2645	JAN81																														
.2688	AUG79																														
.3072	JUL80																														
.3286	APR80																														
.3371	DEC80																														
.3398	JUN81																														
.3602	JUL79																														
.3605	SEPT80																														
.3664	APR81																														
.3733	JAN79	*																													
.3911	JUN80	*																													
.3922	DEC79	*	*																												
.3944	AUG80																														
.3954	SEPT79	*																													
.3980	MAY79	*	*																												
.4018	OCT79	*	*																												
.4522	JAN80	*	*		*																										
.4556	FEB79	*	*		*																										
.4631	NOV79	*	*	*	*	*																									
.4683	JUN79	*	*	*	*	*	*																								
.4749	FEB81	*	*	*	*	*																									
.4819	MAR79	*	*		*																										
.4899	OCT80	*	*	*	*	*	*																								
.4989	MAY80	*	*	*	*	*	*																								
.5001	MAY81	*	*	*	*	*																									
.5342	APR79	*	*	*	*	*	*	*	*	*	*			*		*			*												
.5638	MAR81	*	*	*	*	*	*	*	*	*	*		*	*	*	*			*	*											
.5868	NOV80	*	*	*	*	*	*	*	*	*	*		*	*	*	*			*	*											

bounds of this block are shown in Figure 5.4, and indicate that, in general, the growth minima during both summer and winter seasons are significantly different from the maxima of intervening periods.

Although similar tests could not be applied to the colonies at Davies Reef due to inequality of variances, the similarity in timing and scale of the minima and maxima indicate that the observed seasonal pattern occurred (particularly during the first year of observation) to some extent on mid-shelf as well as near-shore reefs.

The second analytic approach (Time Series Analysis) was applied only to Colony 1 at Nelly Bay since it was the only one in which there was a reasonably long growth record, covering approximately five of the apparent 6- monthly cycles. The analysis was carried out on the smoothed data (Figure 5.5) in order to eliminate any sub-seasonal noise. This approach is justified in view of the a priori assumption that a seasonal cycle would be present in the data (see Introduction). Two different tests were carried out. In the first, an autocorrelation was performed. In this test the growth series was tested for a correlation with itself (period=0) and with other series formed by shifting (i.e. lagging) all values by one or more periods. Thus in a time series with a perfect 6 month cycle, there would be a correlation of 1 at 6 months, and a correlation of -1 at 3 months. The results of the autocorrelation are presented in Figure 5.7. The dotted lines represent plus and minus the large lag standard errors for each coefficient. These limits provide an indication of the critical significance level of each coefficient, but may underestimate the significance at small lag periods (Box & Jenkins, 1970). The results (Figure 5.7) indicate that there is some evidence for a 6 monthly cycle, with negative and positive correlations at 3 and 6 months. The coefficients at these periods are not particularly significant. By 12 months however, the correlation has become negative, which indicates that the cycle is only approximate in its 6-month periodicity.

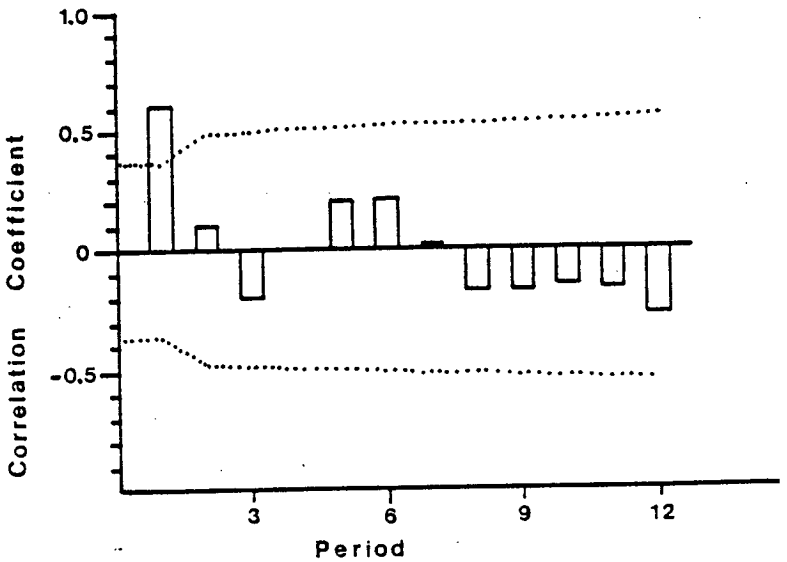


Figure 5.8 Results of autocorrelation analysis on data from colnyl at Nelly Bay. Strength of the autocorrelation at each period is indicated by the height of the bar. Dotted lines represent "large lag" standard errors (see text).

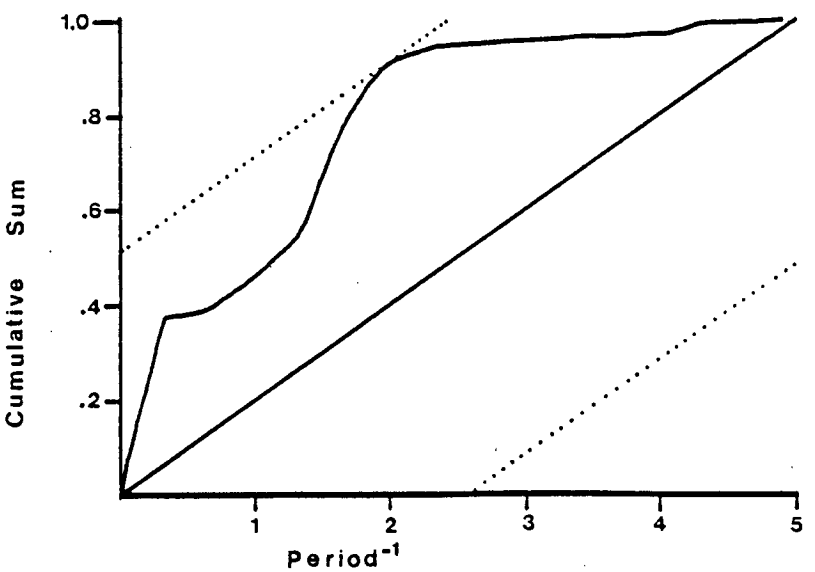


Figure 5.8 Periodogram for extension of colony 1 at Nelly Bay. Deviations from the diagonal line represent periodicities in the data. Dotted lines represent 95% Komolgorov-Smirnov limits.

The second test involved spectral analysis of the time series. In this method the variance of the data is decomposed into contributions of a series of sinusoids over a range of frequencies. The results of this analysis (Figure 5.8) are presented as a cumulative periodogram. Departures from the diagonal in figure 5.8 represent deviations from a random sequence with no periodicity. The dotted lines represent the 95% Komolgorov-Smirnov limits, and again provide an indication of the critical significance limits for each frequency (Box & Jenkins, 1970). It can be seen that there is a significant periodicity in the Nelly Bay series with a frequency of 2 (period of 5 months). Given the small number of total cycles in this sample, these results can be considered to support a conclusion that there is an approximately 6-month cycle in the growth data.

In addition to exhibiting significant seasonal variation in extension rate, there also appear to be differences between the individual colonies at Nelly Bay and Davies Reef. The differences between colonies at Davies reef has already been analysed in detail in Chapter 4, and is primarily related to the different depths at which the colonies were growing. At Nelly Bay, however, depth and other environmental parameters were not noticeable different between colony sites. This suggests that the colonies may have inherently different extension rates. The statistical significance of the differences between colonies at Nelly Bay was tested using a two-way ANOVA. The results (Table 5.4) indicate that there was a significant interaction effect

Table 5.4

Two-way ANOVA for Extension vs Colony and Date at Nelly Bay

Source of Variation	Sum of Squares	df df	Mean Square	F	Prob.
SITE	7.84	3	2.613	21.2	<.001
DATE	10.08	9	1.120	9.1	<.001
SITE x DATE	3.19	26	.526	11.67	<.001
Residual	27.31	606	.045		

between site and date. However the main effects for site and sample taken independently were of a sufficient magnitude that they were also significant, even when compared with the interaction effect. Thus there was a significant difference between sites. Inspection of Figures 5.4 and 5.5 indicates that Colony 1 was consistently slower growing than Colony 4, while Colonies 2 & 3 were more variable, and exhibited a tendency to decrease during the sampling period.

5.3.4. Relationship to Environmental Parameters

The existence of a bimodal annual growth cycle supports the proposition that a large seasonal temperature range may cause inhibition of growth in both summer and winter. In order to test this hypothesis, and to determine the possible role of other environmental variables, mean values for the environmental parameters described in the previous section (5.3.1) were calculated for each of the monthly growth periods at Nelly Bay. Since growth rates were depressed during the summer season, and since high temperature has been shown to have an inhibitory effect on coral growth (Coles & Jokiel 1977), an artificial parameter, termed "Temperature with Inhibition" (T_i) was calculated in the following manner. It was assumed that the optimum temperature for growth was 26°C. This corresponds to maxima observed in Hawaiian corals growing at a similar latitude (see section 5.1). In addition it was assumed that the effect of increased temperature above the optimum was the same as decreasing temperature below the optimum. Consequently T_i was calculated by replacing all seawater temperatures above 26° with values an equivalent distance below 26°.

Correlations between extension rates and seawater temperature, T_i, air temperature, salinity, rain, 9am wind speed, sun hours and total solar radiation are presented in Table 5.5. It can be seen that there were no significant relationships between growth and any environmental factors, so no further analysis was carried out. The above results suggest that environmental parameters have little predictive power in determining concurrent extension rates. However it is possible that there may be a lag effect between growth and one

or more of the environmental factors which, if incorporated into a multiple

Table 4.5

Correlation Coeffients for Extension with Environmental Factors at Nelly Bay
Coefficient and Significance are Displayed, Sample Size=30

	LIGHT	TMAX	SEATEMP	TINHIB	WIND	SALIN	RAIN	SUN
EXT'N	.1059 P= .289	.1499 P= .215	.1853 P= .163	-.0345 P= .428	.0415 P= .414	-.0400 P= .417	-.1876 P= .160	.1584 P= .202

regression analysis, would yield more significant results. In other words, growth may be influenced by the values of a parameter one or more months before. Analysis of variables lagged for one period resulted in a significantly increased correlation for several of the previously analyzed environmental parameters. Two mutually uncorellated parameters with the highest correlation coefficients (Table 5.6) were selected for

Table 5.6

Correlation Matrix for Extension and Lagged Environmental Parameters at Nelly Bay

Number of lag periods are shown in parentheses.
Correlation coefficient and significance are displayed.
" . " is printed if a coefficient cannot be computed. Sample size=28.

	EXT'N (0)	TINHIB (1)	SALIN (1)
EXT'N	1.0000 P= .	.3573 P= .031	-.3330 P= .042
TINHIB	.3573 P= .031	1.0000 P= .	.1170 P= .277
SALIN	-.3330 P= .042	.1170 P= .277	1.0000 P= .

analysis using multiple stepwise linear regression against smoothed extension. Other parameters were either strongly correlated with the first two, or showed no appreciable improvement when expressed as a lag variable. Table 5.7 indicates that the use of lagged variables produced an equation

Table 5.7

Summary Table for Multiple Regression
of Lagged Variables on Extension

Multiple R	.53096
R Square	.28192
Standard Error	.08164

Analysis of Variance

	DF	Sum of Squares	Mean Square	F value	Prob.
Regression	2	.06803	.03402	5.104	.014
Residual	26	.17329	.00666		

Regression Parameter Estimates

Variable	B	SE B	T	Prob.
TINHIB	.02857	.01155	2.473	.0202
SALIN	-.01564	.00688	-2.272	.0316
Constant	.26634	.34307	0.776	.4446

which included both terms as significant parameters: T_i (1 lag); and Salinity (1 lag). The overall equation was significant (P=.014) and explained approximately 28% of the variance. T_i was the most significant of the two parameters, and was positively correlated with extension, indicating that both high and low temperatures during the previous month had an inhibitory effect on growth. Salinity, on the other hand was negatively correlated with extension during the subsequent month.

In order to determine whether the residual variation in the multiple regression model was caused by a generally poor fit, or by the failure of the model to predict a specific features of the observed growth pattern, the observed and predicted extension rates were plotted and are shown in Figure 5.9. Overall their predicted

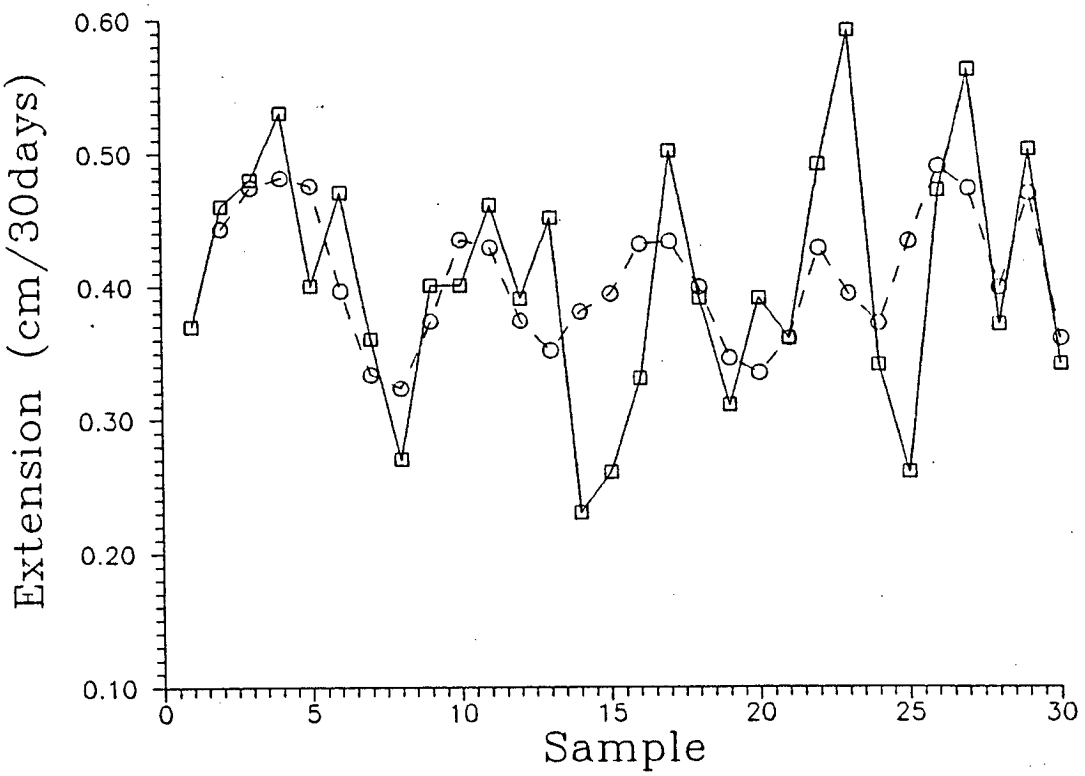


Figure 5.9 Comparison between observed growth rates (squares), and those predicted form the multiple regression model (triangles).

values provide a good approximation of the pattern of maxima and minima during the study period. The major discrepancies occur during the two summer minima (samples 14-15 and 25) and during one of the spring maxima (sample 23). This inability of the model to account for the extreme high and low period of growth could be due to a non-linear relationship between growth and the two independent environmental parameters.

A possible explanation for the failure of the model to account for the extreme summer minima is that the late summer months are times when the corals at Magnetic Island are occasionally stressed to the point where they expel their symbiotic zooxanthellae. This bleaching phenomenon has been described by Oliver (1985). In 1980, during the first, and lowest growth minima in Figure 5.9, a minor bleaching event occurred. Although the experimental colonies did not bleach during this period, they were severely affected during a subsequent bleaching event in 1982. All except one of the experimental colonies died during this latter event. Although the periods of bleaching correspond to period of high water temperature, and light levels, no direct cause of the bleaching could be unequivocally identified (Fisk & Done, 1985; Harriott, 1985; Oliver, 1985). As suggested by Oliver (1985), it is possible that the corals are stressed every summer period by a synergistic combination of high light and temperature. Very small increases in these two or even other factors could provide the small additional stress necessary to trigger bleaching and subsequent mortality. The multiple linear regression model used in this study can not take synergistic or other non-linear effects into account, and this may explain, to some extent, its inability to predict the growth extremes in Figure 5.9.

5.4. Discussion

The results presented above have demonstrated a clear and statistically significant seasonality in the growth of A. formosa at Nelly Bay. As hypothesized in the introduction (section 5.1), growth appears to be reduced in mid summer and mid winter when temperatures are alternately at their maximum and minimum values.

However, there is some uncertainty as to the principal factors causing this seasonality. Analysis of several environmental parameters showed significant correlations with growth only when considered as lag variables. The multiple regression equation produced from analysis of lagged variables was significant, but still left a large proportion (67%) of the total variance in the growth data unexplained. Nevertheless, T_i, a computed parameter designed to mimic the non-linear response of growth to temperature emerged as the most significant parameter. This lends support to the hypothesis that temperature may be an important driving force behind the bimodal seasonal response observed at Nelly Bay.

Salinity, was also a significant parameter in the multiple regression model, with a negative correlation. This result is difficult to interpret since it suggests that the drop in salinity during the summer months (the only period when salinity varies) causes an increase in growth during the next month. Since salinity is only one of several parameters which show marked fluctuations during periods of heavy rainfall, it is possible that growth is responding to some other parameter, such as input of nutrients during river runoff. Although the nutritional requirements of branching Acropora are not fully known, growth might be enhanced either directly through the supply of inorganic and dissolved organic nutrients (eg. Meyer & Schultz, 1985) or indirectly by stimulating secondary production and increasing the supply of zooplankton or particulate organic matter (Lewis & Price, 1975).

The severe depression of extension during one summer period coincides with a bleaching event which affected several other corals. Although neither light nor sun hours were significantly correlated to extension, and did not contribute significantly to a multiple regression model, the role of light in the bleaching phenomenon, and the death of the experimental colonies during the a subsequent bleaching event suggest that high light levels may also play an important role in causing the observed seasonal extension pattern.

In general the correlation of extension with environmental parameters in this study is rather low compared with that achieved in other areas where such parameters exhibit a distinct seasonality.

For instance, Glynn (1977) obtained a high correlation (r=.83) between extension and sea temperature at one site off Panama, and a significant inverse correlation (r=-.586) with cloud cover at a second site. Yap & Gomez (1984) also found significant correlations between temperature and day length for A. formosa in the Philippines. In this case both parameters were inversely correlated with extension, presumably due to the inhibitory effects of excessively high light and temperature at this tropical location. Temperature accounted for between 83-86% of the total variance in branch extension. In a slightly cooler location, Bablet (1985) showed a high positive correlation (r=.9) between temperature and the weight increment of Fungia paumotensis at 10m. The correlation decreased in deeper water, probably due to the fact that the deeper water temperature deviated somewhat from the surface water measurements used in the correlation analysis.

These studies, and others cited in the Introduction all point to the importance of temperature and light in controlling in situ growth rates. The low correlations found in the present study may be due to inadequate measurements of in situ environmental parameters. Temperature readings were only obtained every second week, on the average, while light data was obtained from aerial measurements. Light levels at 6m depth in Cleveland Bay would be subject to wind induced turbidity which can cause order of magnitude fluctuations in ambient light compared to surface values. In addition, the failure of the multiple regression model to account for the severe growth depressions during the late summer months has also resulted in a low overall correlation with environmental parameters. This failure may again be due to the lack of an accurate index of ambient light levels, since light is believed to play an important role in coral stress and subsequent bleaching. On the other hand, once severely stressed (by whatever means), corals may require a recovery period of one or more months before they are capable of exhibiting a normal growth response. A simple multiple regression model using environmental parameters could not predict such a recovery process.

Reproduction is further parameter which could be important in causing the seasonality in growth. Although reproductive condition

was measured at Nelly Bay and Davies Reef, the period of measurement did not overlap sufficiently with growth measurements to permit reproduction to be included as a variable in the multiple regression analysis. Reproduction and its possible relationship to growth is examined in detail in Chapter 6. No striking correlation with growth was found.

Gladfelter (1984) in a recent study on seasonal coral growth in the Caribbean, concluded that extension is unlikely to exhibit seasonal variation if the ambient temperature range is between 26-29°C. Outside this range growth would decrease. The results of this study support this general hypothesis, although the exact temperature range over which growth is constant may vary between sites due to local acclimation. A more general hypothesis is that growth is constant when the annual temperature range is approximately 3°C or less, with a mean near 26°C, and shows marked decrease with increasing departure from this optimal range. In regions with a temperature range approaching 10°C or more growth would be expected (as in this study) to exhibit a bimodal response due to inhibition of growth in both summer and winter. Although not stated explicitly, the data of Shinn (1966) suggest that growth of Acropora in Florida follows such a pattern. In addition, Acropora colonies in western Australia also exhibit a bimodal seasonal response (C.J. Simpson, pers. comm.). At both locations the temperature range is very high, and exceeds 10°C.

Gladfelter (1984) also suggests that calcium carbonate accretion is more sensitive to environmental parameters, and may exhibit a seasonal response where none is evident in the records of linear extension. As discussed in Chapter 2, however, it is possible that her measure of carbonate accretion is not a realistic one, and merely accentuates subtle differences in the linear growth measurements. Further work, using a more accurate measure of calcification is required to resolve this issue.

At Davies Reef, the seasonal pattern of growth is less obvious than at Nelly Bay. During the first year of observations, when there was some overlap in growth periods, there was quite good concurrence in the growth trends between Nelly Bay and the middle

and deep sites at Davies Reef. This similarity in response appears too striking to be coincidence, and suggests that the same parameters which cause the seasonal pattern at Nelly Bay are also operational on offshore reefs. Given the much lower annual temperature range at Davies Reef, it is possible that light or some other seasonal factor plays a synergistic role with temperature in reducing growth during certain periods. Alternatively corals at Davies may be more stenothermic than those at Nelly Bay, and thus show a similar growth response despite the smaller scale temperature fluctuations. Evidence for temperature acclimation between sites with different thermal regimes has been previously presented for reef corals by Clausen & Roth, 1975 and Coles et al., 1976.

The similarity in A. formosa growth responses between Davies Reef and Nelly Bay, however, disappears at the shallow site during the first summer period, and at the middle and shallow sites during the second year. The reasons for this are not clear, and have been discussed to some extent in Chapter 2. It would appear that there was no inhibition of growth at the shallow site during the summer months, despite the fact that its shallower location would have exposed it to higher levels of both light and temperature than the deeper sites. Although might be possible to speculate on possible causes for this difference, the overall loss of a coherent response during subsequent months raises the possibility that some other disrupting factor was influencing growth at all sites. As discussed in Chapter 2, this may have been due to extensive experimental manipulations carried out on the colonies. Alternatively, some other unmeasured environmental parameter may have shifted during the second year and exerted a disrupting affect. Manipulations carried out on the colonies at Nelly Bay were not quite as extensive or destructive. It is possible that the larger range of most environmental variables (especially temperature) at this site overwhelm other factors which disrupt the seasonal growth response at Davies Reef.

To summarize, this study has established that extension rates at Nelly Bay exhibit significant seasonality, with two maxima and minima each year. Extension is reduced during mid-winter and mid-summer, but analysis of several environmental parameters was not

able to indicate any single parameter, or group of parameters which could account for the majority of the annual growth variation. An artificial parameter, which was designed to mimic a postulated inhibition of extension at temperatures above or below 26°C, was significantly correlated to extension rates measured one month earlier. Salinity exhibited a significant negative correlation at a similar lag of one period, however the causal nature of this correlation is regarded as uncertain. Consideration of the pattern and timing of a recurrent summer bleaching phenomenon lends support to a conclusion that temperature, possibly acting in concert with other parameters such as high light levels, is (as in other areas) the most likely factor causing the observed seasonal patterns. There is a suggestion of a similar seasonal pattern at an offshore reef where both temperature and light are less variable, but this pattern is not the same at all depths, and appears to have been disrupted during the latter part of the study.

It is proposed that in areas with mean temperatures near the apparent optimum of 26°C, and with a range less than approximately 3°C, there will be no appreciable seasonal variation in extension rates. In regions with a larger range but a similar overall mean, extension will exhibit a bimodal seasonal pattern. Areas with only moderate annual temperature variation, but with mean temperatures substantially above or below 26°C will exhibit a unimodal pattern which will exhibit, respectively a negative or positive correlation with temperature.

The degree to which calcification follows this proposed pattern in extension rates has not been ascertained in this study. The results of the analyses in Chapter 2, however suggest that the weight of newly extended branch material exhibits an identical pattern. Other studies (Brown et al., 1984; Gladfelter, 1984) have concluded that trends in weight increment and extension are not the same. As discussed in Chapter 2, there is a need to more rigorously define "calcification" in coral "growth" studies and to devise more meaningful estimates of this elusive physiological process, for long-term studies of arborescent coral growth.

Chapter 6
Sexual Reproduction

6.1 Introduction

In previous chapters coral growth rates have been examined with a view to understanding the relationships between growth and various exogenous parameters (e.g. season, depth, position within a colony etc.). Although some consideration has been given to the possible role of endogenous controls over the coordination of growth within a large, and geometrically complex colony, one other endogenous factor, reproduction, could possibly have a major influence on growth.

Since reproduction and growth represent the two most important sinks for excess metabolic energy (after catering for basic metabolic requirements) they may thus compete during periods of limited energy availability. The proportion of a calorific content which is reproductive material can be very high. For instance Richmond (1983) estimates that planulae represent between 50 and 180% of the calorific content of the non-reproductive tissues of P. damicornis.

It is also possible that during the time when gonads are mature, their volume fills the gut cavity and prevents feeding. The importance of this feature is difficult to determine, since it is not known to what extent A. formosa depends on the ingestion of particulate food.

The general reproductive patterns of corals have not been studied until recently. Consequently, there is almost no previous work on the relationship between growth and reproduction. Buddemeier & Kinzie (1975, 1976) first raised the possibility of competitive interactions between these two processes as a possible explanation of variations in growth, and density banding patterns. Wellington & Glynn (1983) found that high density band formation occurred in Pavona gigantea at the same time as a high proportion of the colonies were in reproductive condition. They then suggested

that this correlation may indicate that reproduction draws energy away from tissue growth and linear extension, and causes high density growth to occur.

The work of Loya (1985), and Rinkevich & Loya (1985) provide the best evidence so far that reproduction and growth may compete and that, depending on the circumstances, one process or the other may dominate. In Stylophora pistillata colonies with a geometric mean radius of less than 2cm there was significantly faster growth in summer than in winter. But in larger, reproductively mature colonies there was no seasonality. Loya (1985) hypothesizes that the energy which would normally be allocated to increased summer growth is diverted into gonad growth. However his data are somewhat ambiguous since in absolute terms summer growth remains approximately constant in both large and small colonies, while winter growth appears to have increased in the larger colonies. In order for Loya's conclusions to be valid, a more circuitous set of reasoning (not explicitly stated) must be applied to the data. It must be assumed that the larger colonies normally grow faster than small colonies, a feature observed in many corals (e.g. P. damicornis Oliver 1985; Harriott 1983a; and other species Babcock 1985). Under such circumstances, the failure of the larger corals to increase their growth rate in the summer as well as the winter, may be construed as evidence of allocation of energy away from growth and into reproduction. The necessity for such "negative" logic tends to weaken the conclusions somewhat. Nevertheless, his results are the best indication, to date, that in corals, reproductive processes may divert energy away from growth.

The work of Rinkevich & Loya (1985), suggests that the alternative process, in which energetic investment in growth is at the expense of reproduction, may also occur in corals. In the same series of experiments, they show that the number of polyps containing female gonads is drastically reduced near the contact zone of intra-specific grafts. Even in areas further away there is a significant reduction in reproductive polyps compared with non-interacting colonies. These results are significant because they indicate that the allocation of resources to growth and reproduction can be varied in response to changing environmental conditions, rather than being

constant, or varying predictably through time. Richmond (1985) also provides evidence of this phenomenon in the case of Pocillopora damicornis which grows more rapidly but does not reproduce in the biogeographic extreme of its range (Panama) compared to a site closer to the centre of its distribution (Enewetak).

In other invertebrates there is also evidence that: 1) the energy allocated to reproduction can vary under different conditions; 2) that reproduction and growth can directly compete for limited supply of available energy; and 3) that the outcome of such competition may also vary under different conditions. For instance, an increase in food supply results in increased reproductive output in gastropods (Spight & Emlen, 1976), and ctenophores (Reeve & Walter, 1978), while starvation can lead to a marked reduction in freshwater snails (Bohlken et al., 1986). The flexibility of energy allocation into reproduction vs growth is evidenced in the experiments of Calow (1977). If starved, the freshwater bug Corixia draws upon energy reserves in both storage organs and non-replaceable structural musculature in order to maintain levels of egg production. However, if the bugs were prevented from mating, energy was drawn from the gonads and storage organs but not musculature. The importance of the reproductive context in determining the response to limiting energy supplies is also seen in the results of Calow & Woodhead (1977) who found that starvation led to an increase in reproductive effort in semelparous but not iteroparous triclads. Similarly, Crisp & Patel (1961) found that the barnacle Elminius modestus grew faster if it was prevented from spawning by isolation from conspecifics.

Injury is a relatively common event for many organisms, and subsequent regeneration could place extra demands on energetic reserves. It might thus be expected that regenerating individuals would divert energy away from reproduction in order to effect repairs. Evidence for this phenomenon has been found in bivalves (Trevaillon et al., 1970) bryozoans and sponges (Jackson, 1979; Jackson & Palumbi, 1978) and zooanthids (Karlson 1981, 1983). On the other hand, Wahle (1983) could find no significant reduction in rates of regeneration between reproductive and non-reproductive gorgonians.

The relationship between growth and reproduction also changes with ontogeny. Most organisms go through a juvenile growth phase when no reproduction occurs. This can be followed by either a cessation of growth with surplus energy being directed entirely into reproduction, (Corkette & Mclaren, 1978) or to continued growth together with reproduction. In the latter case reproductive output frequently increases with age since the amount of gonad material in an organism is usually closely correlated with body size (Calow, 1977).

In corals, studies on the relationship between age and reproduction are hampered by the fact that age cannot be readily determined from measurements of size. Fragmentation can lead to chronologically old but very small colonies (Connell, 1976; Hughes & Jackson, 1980). Kojis and Quinn (1985) and Szmant-Froelich (1985) have examined the relationship between age, size and reproduction in Goniastrea australiensis and Montastrea annularis respectively. They found that naturally occurring small colonies were non-reproductive. If small colony portions were broken from large colonies, there was a reduction in the fecundity or reproductive status of the portions, but not to the level of naturally occurring colonies of similar size.

In this chapter some of the basic aspects of reproductive behaviour, which have a bearing on growth, will be examined. It is not within the scope of this study to undertake a quantitative examination of the reproductive energetics of A. formosa. Rather, this study will apply the techniques and hypotheses addressed by Loya (1985), Rinkevich & Loya (1985), Kojis & Quinn (1985) and Szmant-Froelich (1985) to a coral with a very different growth form and life history from those previously studied. Specifically, the following questions will be addressed: 1) Is there a seasonal gametogenic cycle in which investment of energy into the growth of gonads is higher than at other times of the year? If so then how does this seasonality relate to the previously described pattern in seasonality in skeletal growth? 2) Are there differences in reproduction patterns within or between colonies? 3) Is there a relationship between reproduction and size and if so is this related

only to size, or to physiological age? 4) Is there any evidence that a trauma such a branch breakage and subsequent repair will affect the gametogenic cycle?

6.2 Materials and Methods

All measurements of gametogenic cycles were carried out at Nelly Bay and Davies Reef on the colonies described in Chapter 1. At Nelly Bay, Colonies 2 was not sampled regularly, and is not included in the reulsts. However, a 5th colony in the same area (Colony 5) was also included in the sampling.

Experiments on the effect of isolation of small fragments, and measurements of reproductive activity within different size categories were carried out at Geoffrey Bay, Magnetic Island. This bay is adjacent to Nelly Bay, and is very similar in terms of environmental regime and coral community structure.

Determination of Gametogenic Cycles

Nelly Bay: During the first year of this study (1980) 3-5 branches of A. formosa were collected haphazardly from different colonies within the study site. These colonies frequently included the 4 principal experimental colonies, and always included one branch from Colony 1. During the second year 1-3 white tipped branches were sampled from each of the 4 experimental colonies. Collections were made at approximately monthly intervals.

Davies Reef: At this site, 3-5 white tipped branches were collected at approximately 60 day intervals from each of the three experimental colonies. Sampling ran from April 1980 until February, 1982.

Intra-colony Variation in Reproduction

In a previous chapter, it has been shown that there are significant differences in growth and skeletal characteristics between brown and white tipped branches. In brown tipped branches, extension has stopped, and the pattern of a large apical corallite surrounded by small developing radial corallites is gradually replaced by a uniform distribution of normal radial corallites. In addition, the gradual increase in branch width and skeletal density away from the apical corallite is replaced by a pattern of nearly uniform width and density.

In this section in situ observations of spawning in brown and white tips are compared. The reproductive condition of polyps at different positions along white tipped branches was also examined in order to determine whether there are reproductive variations which correspond to the density and branch width variations. Variation along white tipped branches was studied at the deep site, at Davies Reef using samples collected on Sept 30, 1981. On two branches, samples of five polyps each were taken at .5, 4, and 8 cm on each branch. On a third, longer branch, additional samples were also taken at 12 and 16cm. A fourth branch was sampled only at 8cm. The branches and polyps were decalcified and inspected as described below.

Size vs Reproduction

Two different types of colonies were sampled in order to determine the size at which mature gonads could be found: 1) new colonies derived from planular settlement; and 2) colonies which were obviously isolated remnants of larger, mature colonies. In the first type, colonies were selected which were small, had a conspicuous central vertical branch, with secondary branches symmetrically arranged around it, and had a single large "holdfast" zone at the bottom of the primary branch which attached the colony to hard substrate. The second type of colony was identified by a region of dead skeleton near the base of the colony, lack of

attachment to the substrate together with an asymmetrical appearance. In some case colony remnants were still part of a much larger colony, but physiologically isolated by a region of dead skeleton at least 8cm long which, together with the degree of algal fouling suggested that the live portion had been isolated from the main colony for at least 9 months.

For small colonies the entire coral was sampled. For larger colonies, the length, width and height of the colony was measured, to give an index of overall size, and a portion of the colony was then sampled. For the purposes of analysis, "coral size" was regarded as the mean of the length, width and height of small colonies, or simply the length of single or slightly branched corals. Although this method tends to underestimate the true size of colonies with several main branches compared to a single branch, the trend evident in the results meant that this bias did not exert a confounding influence.

Effect of Isolation of Small Fragments from the Parent Colony

In this experiment, small lengths of branch from a large A. formosa colony were broken off and attached to a nearby steel mesh rack. Three different branch lengths were used: 5cm, 10cm, and 20-50cm. Ten replicates of each size class were collected. The two smaller size classes consisted of a single white tipped branch, while the third size had a variable number of secondary branches which together did not exceed 50cm in total length.

The experiment was initiated on August 13th 1984, approximately half way through the gametogenic cycle, just prior to the period of maximum increase in gonad size. Ten 8cm long branches were removed from the parent colony at this time in order to determine the precise stage of gametogenesis, and level of fecundity.

Approximately one week before spawning, seven of the ten replicate branches of each size category were collected for analysis (see below for processing and analysis procedure). At the same time, 10 branches from the parent colony were also sampled. During the night

of mass coral spawning, underwater observations were carried out on both the remaining experimental branches, and the parent colony.

Sample Processing and Analysis

Branches from all colonies were fixed in 10% seawater formalin and then decalcified in 10% HCl. In decalcified specimens, the individual polyps form discrete structures within a spongy matrix of coral tissue. Between five and 10 polyps were haphazardly removed from this tissue matrix, and dissected using fine forceps and a stereo microscope. Counts were made of the number of oocytes on each ovigerous mesentery, and the number of mesenteries with testes. In addition, the length and width of three randomly selected oocytes, and two randomly selected testes was measured using an ocular micrometer. Volume was then estimated from these measurements assuming that both oocytes and testes were prolate spheroids (during early months of gametogenesis) or solid rectangles (during the last two months of gametogenesis). The change in formula use for volume estimation was based on the visual appearance of the gonads within the decalcified polyps. For determination of gametogenic cycles, all polyps were taken between 5-10 cm from the branch tip.

Selection of a Reproductive Index

In this chapter primary interest will be focussed on an estimate of energetic investment in reproduction. Total gonad volume per polyp was considered to provide the most appropriate index of this parameter. It is readily measured compared to other possible indices (e.g. total calorific value) and this permitted fairly rapid analysis of large samples. Total gonad volume was derived by first multiplying the average testes and oocyte volume per polyp by the number of testes or oocytes respectively in that polyp. Total oocyte and testes volumes per polyp were then summed to obtain total gonad volume per polyp.

Consideration will also be given to two measures of reproductive condition: mean testes and mean oocyte volume. These indices differ from the previous one in that they are independent of fecundity and can thus provide a more accurate estimate of the state of reproductive readiness of a colony. These two measures were obtained by taking the mean of the two testes and three oocyte measurements for each polyp.

Since fecundity (number of oocytes per polyp) is a parameter which has a major influence on total gonad volume per polyp, and which can vary independently of oocyte or testes size, it is also considered in some comparisons between colonies. The number of testes in a polyp was found to be virtually constant at 4, and was therefore not included in such comparisons.

6.3 Results

Reproductive Seasonality

The annual variation in total gonad volume per polyp at Davies Reef and Nelly Bay is shown in Figures 6.1 and 6.2 respectively. It is obvious from these figures that there is an annual gametogenic cycle with a rapid increase in gametogenic activity during October and November. Although there were striking differences between colonies, in the volume of gonad material produced (e.g. Figure 6.1), the seasonal pattern was similar in all cases. The inter-colony differences will be discussed in more detail below. Spawning of gametes occurs during the 4th or 5th nights after a full moon between late October and early December, and can be synchronous for entire populations on a reef. A detailed account of the synchronous mass spawning of reef corals, including A. formosa has been published elsewhere (Harrison et al., 1984; Willis et al., 1985; Babcock et al., 1986). For the purposes of this investigation, the salient features of the data are the consistent annual cycle

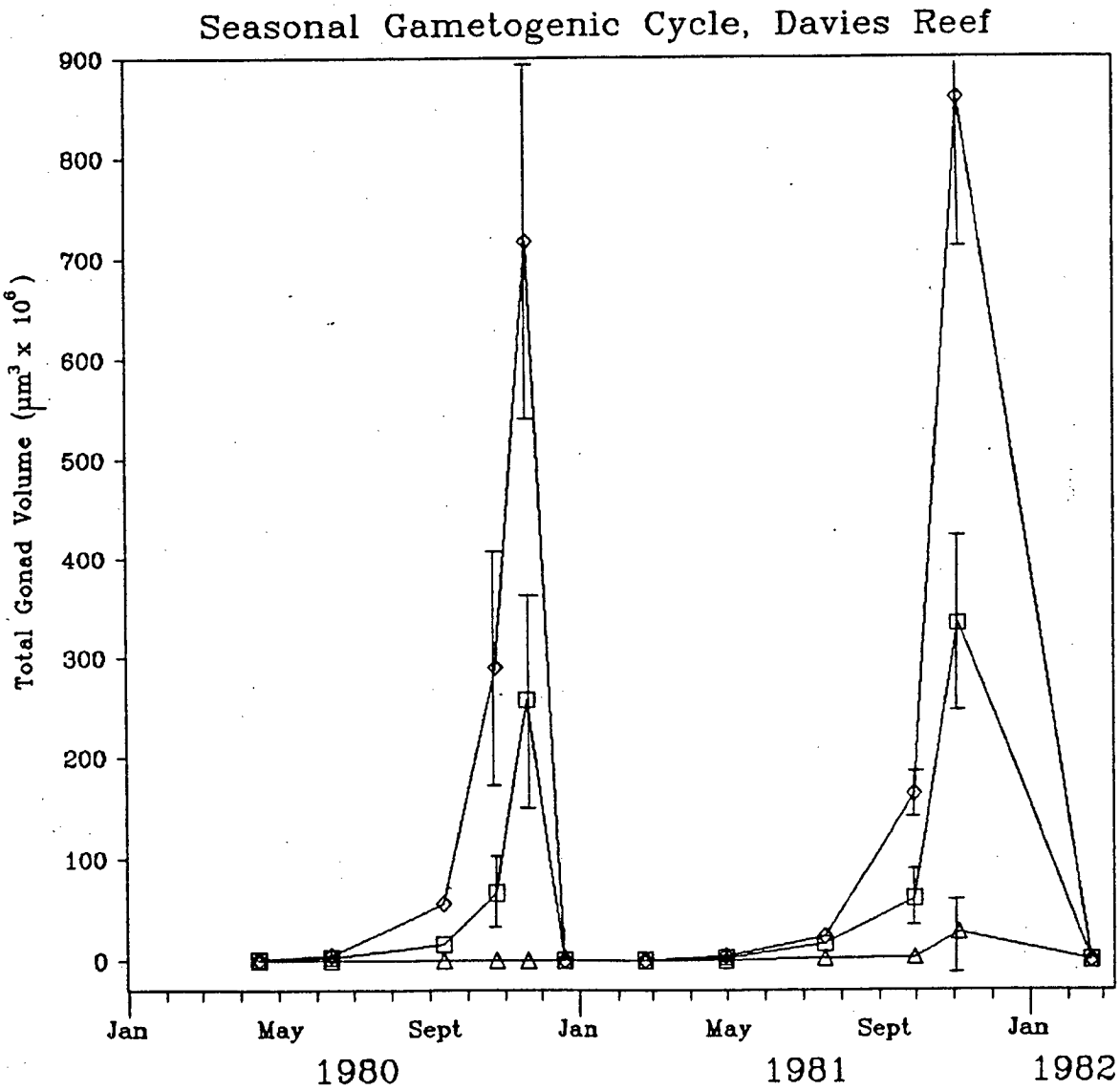


Figure 6.1 Seasonal variation in total gonad volume per polyp. Total gonad volume represents the summed volume of all oocytes and testes per polyp. Diamonds = deep colony; squares = shallow colony; triangles = middle colony.

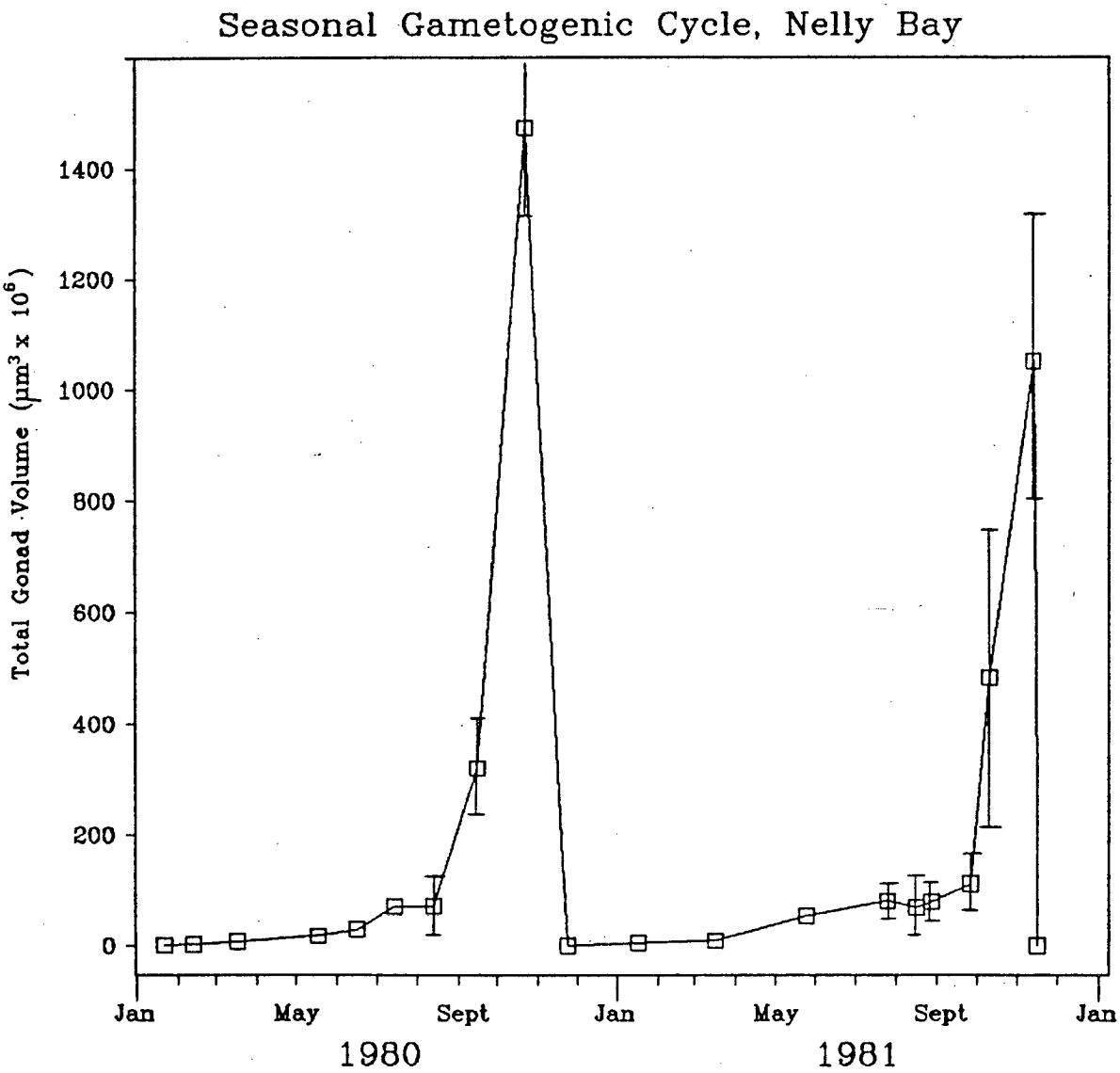


Figure 6.2 Seasonal variation in total gonad volume per polyp at Nelly Bay (Colony 1).

at both locations, and the rapid increase in gonad volume during the month before spawning.

Mean gonad volume also shows a nearly identical pattern. Figure 6.3 shows representative annual cycles of oocyte and testes volume for Nelly Bay. Oocytes begin to increase in size during April or May, and then show a rapid rise in volume from September onwards. Testes, although visible from about March, do not start to increase in size until September and are, on average smaller than oocytes throughout the gametogenic cycle.

Relationship Between Gametogenic Cycle and Seasonal Growth Curve

It has been shown that there is a predictable and significant increase in gonad volume during the months of September through until spawning. Since this is presumably accompanied by an increase in energetic expenditure on reproduction, there exists the possibility that this energy is obtained through the diversion of resources from other non-essential processes such as growth. Figures 6.4 and 6.5 show the superimposed seasonal curves for skeletal extension and total gonad volume per polyp at Davies Reef (deep site) and Nelly Bay. This comparison must be considered rather crude, since the exact energetic relationship between both extension and gonad volume is not known. Nonetheless, it is evident from the figures that the period of peak gametogenesis is not coincident with a minimum or any decreasing trend in skeletal extension. On the contrary, it would appear that growth is either at a maximum, or is on the rise. These results suggest that gametogenesis is not correlated with a period of reduced growth.

Spatial Variations in Reproduction

Inter-colony Variations at Nelly Bay

The seasonal changes in total gonad volume between the 4 colonies studied at Nelly Bay are shown in Figure 6.6. There are two major features which should be noted. Firstly, Colony 5 shows

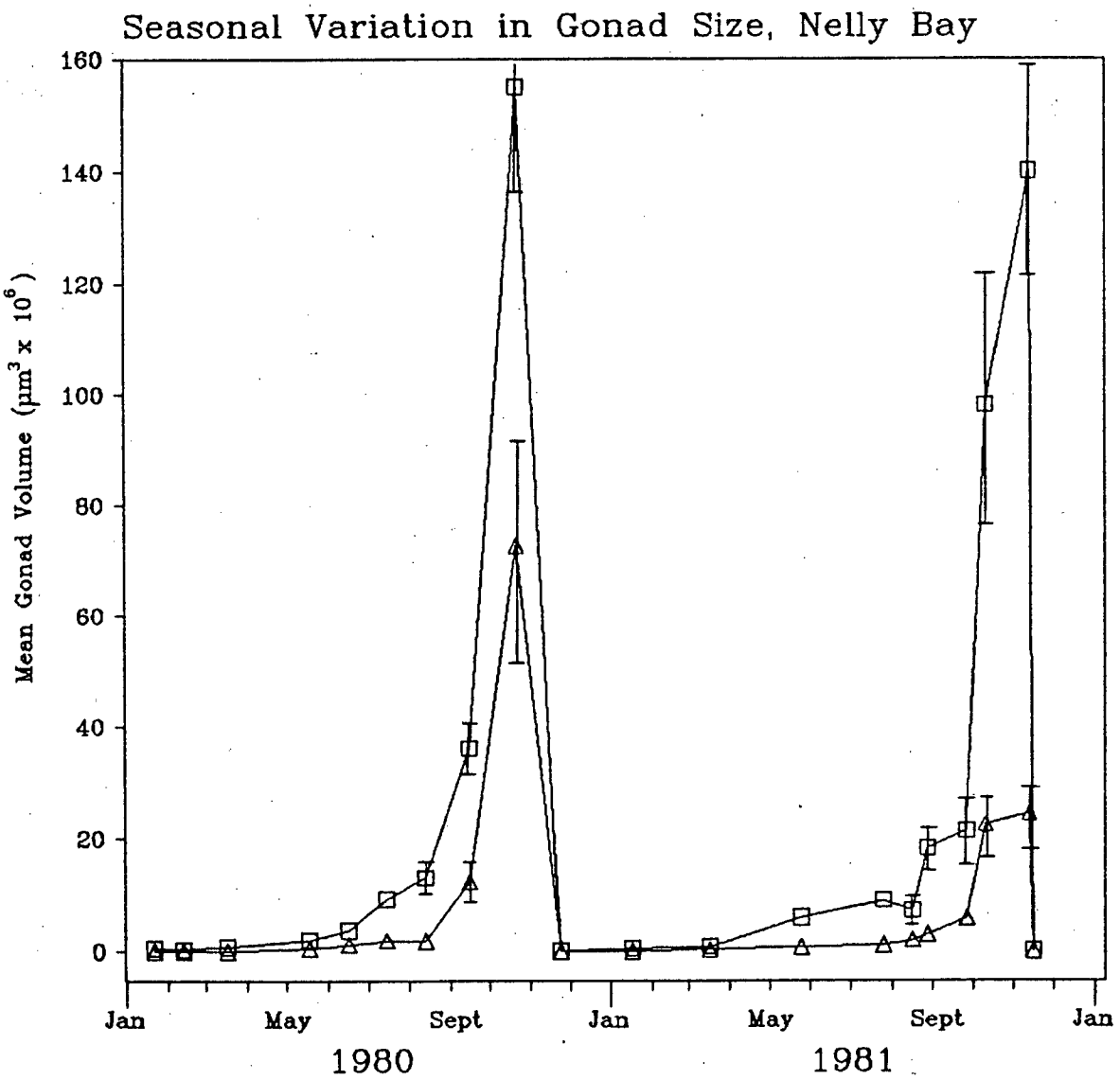


Figure 6.3 Seasonal variation in mean gonad size at Nelly Bay. Squares = mean oocyte volume; triangles = mean testes volume. Error bars are 95% confidence limits

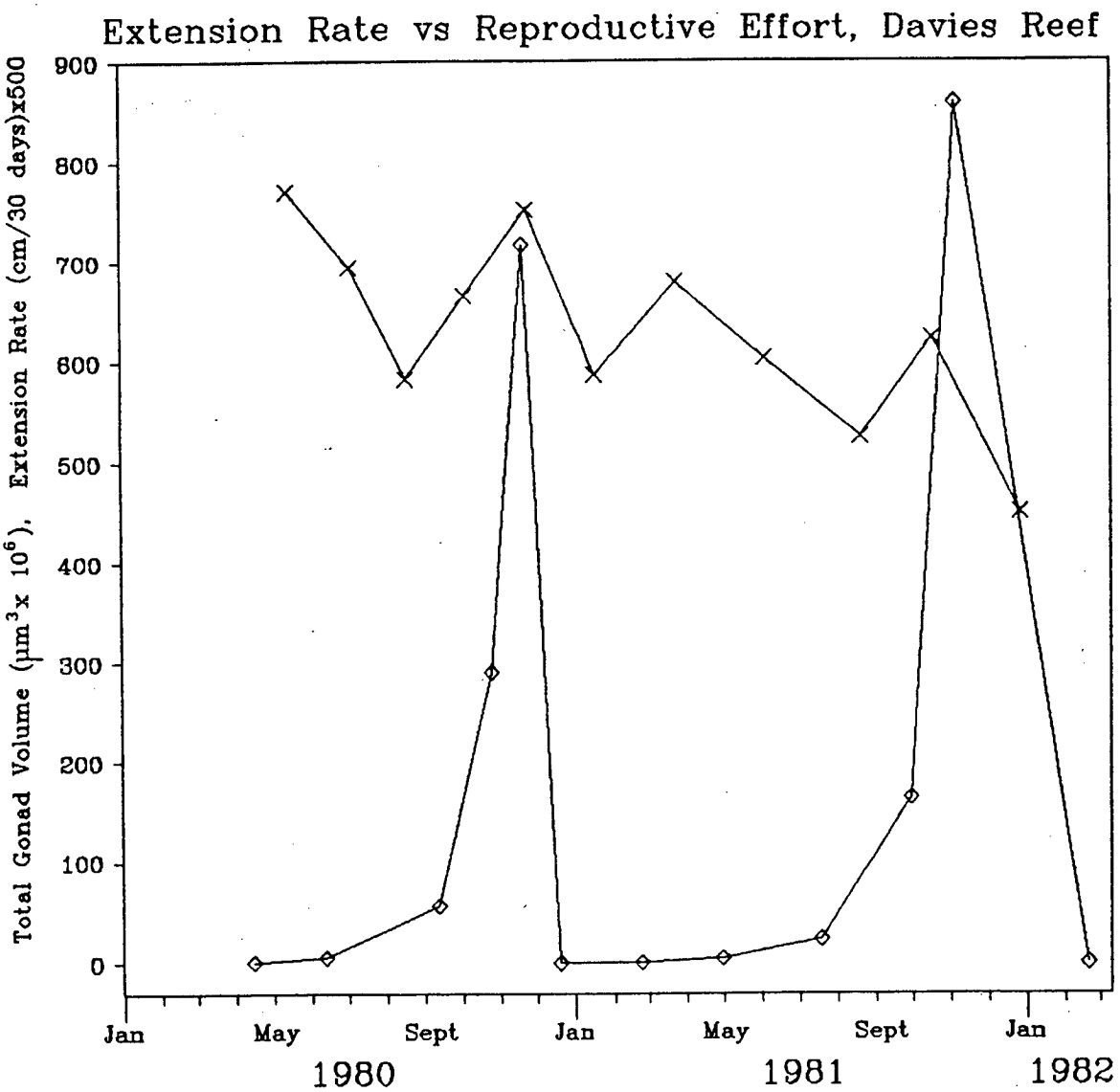


Figure 6.4 Comparison of extension rates with total gonad volume per poly at Davies Reef (Deep Colony). Diamonds = total gonad volume; crosses = extension rate.

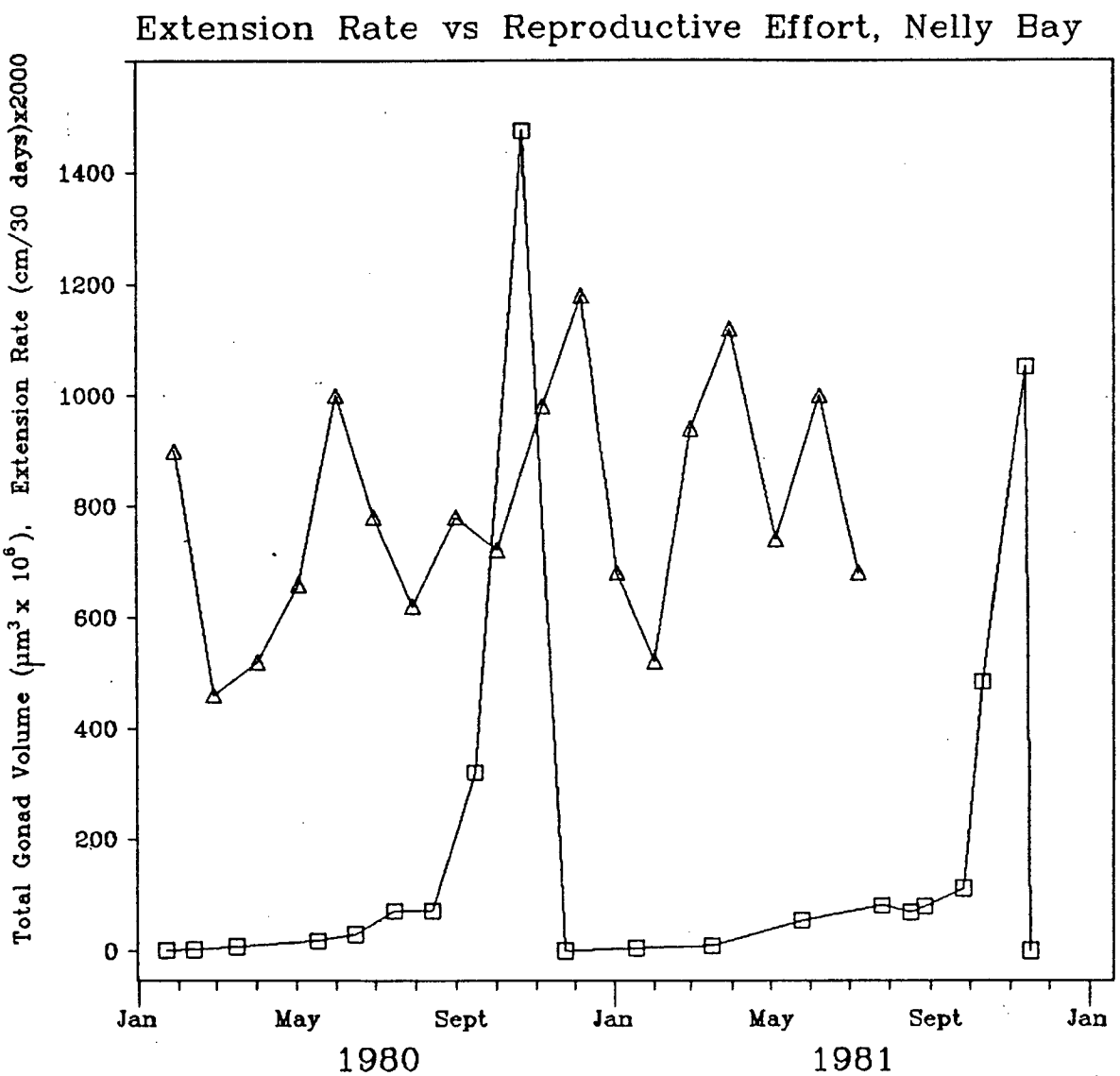


Figure 6.5 Comparison of extension rates with total gonad volume per polyp, Nelly Bay (colony 1). Squares = total gonad volume; triangles = extension rate.

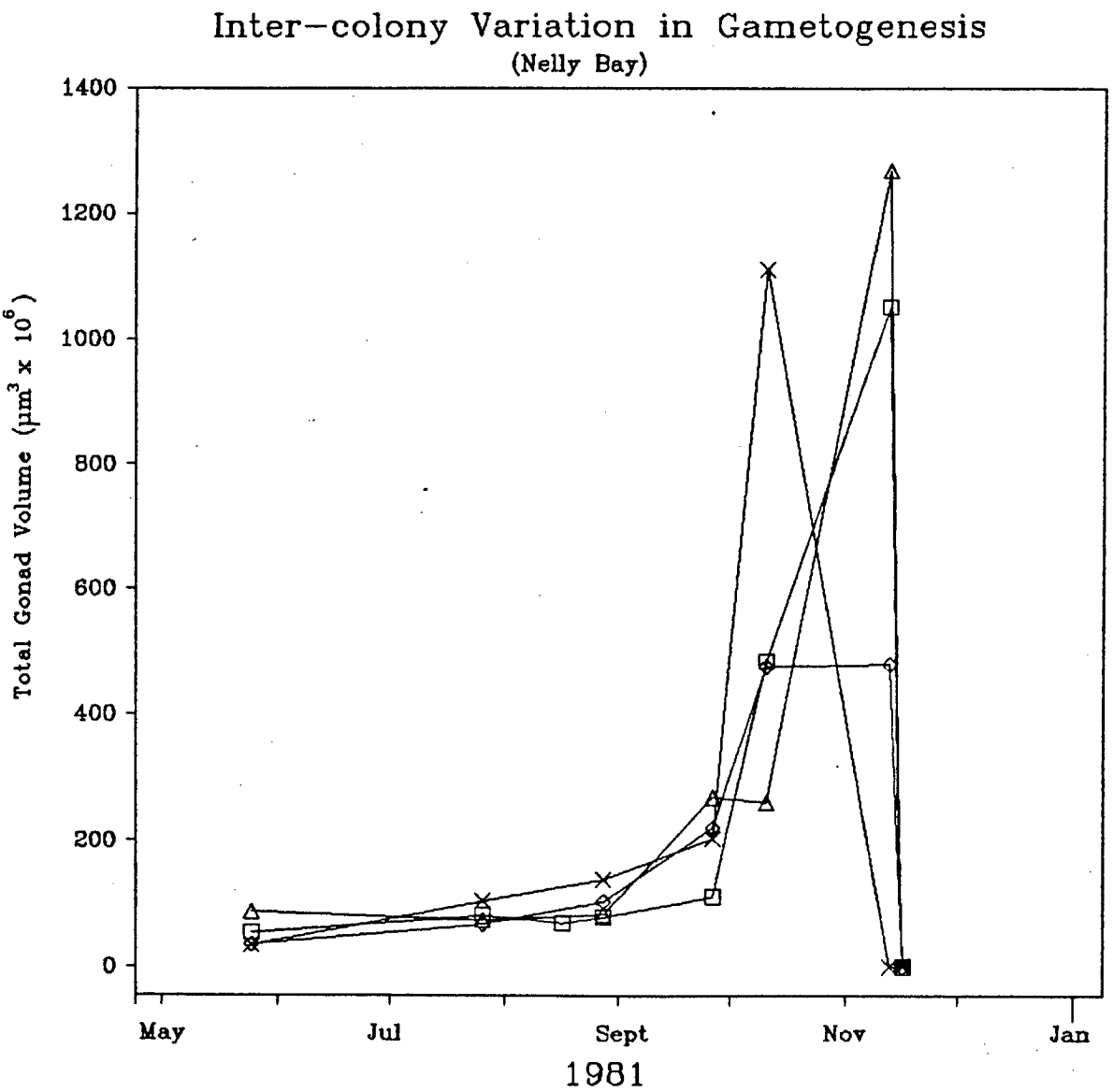


Figure 6.6 Variations in gametogenic cycles between different colonies at Nelly Bay. Data points represent total gonad volume per polyp. Squares = colony 1; triangles = colony 3; diamonds = colony 4; crosses = colony 5.

a peak, and subsequent fall in total gonad volume one month before the other colonies. Field inspections indicated that this colony spawned one month before the others. In 1981, mass coral spawning was split between two episodes, exactly one lunar month apart (Willis et al., 1985). Secondly, Colony 4 shows a much lower peak volume than the other colonies. This appears to be due to a cessation in gonad growth during the last month (Table 6.1).

In order to test for differences in reproduction between colonies, an ANOVA was carried out on the samples taken from each colony just before spawning (i.e. when gonads had reached maximum size). Thus the sample used for Colony 5 was for Oct. 12, 1981 while for the remainder it was the Nov. 12, 1981 sample. This was because Colony 5 reached reproductive maturity and spawned one month before the other colonies (Figure 6.6). The ANOVA was carried out for four different reproductive indices: total gonad volume per polyp; mean oocyte volume; mean testes volume; and fecundity. Since the number of replicated branches varied from 1 to 3, observations were pooled over all branches in a colony. Log transformations were used for fecundity and testes volume measurements in order to alleviate heterogeneity of variances (Bartlett-Box test). The results of the analyses, and group means, are presented in Tables 6.1 and 6.2 respectively. The full analysis of variance table is presented for total gonad volume, while only the F-values and associated probabilities are shown for the remaining variables.

It can be seen that there were significant differences between colonies in terms of total gonad volume and testes size, but no difference for fecundity or egg size. Closer inspection of the group means indicates that Colony 4 had consistently lower values than the other Colonies for all 4 indices (although this was not significant in some cases). As noted above, Colony 4 is anomalous in that gonad volume did not continue to increase during the last month, as it did in the other colonies. A second analysis with Colony 4 excluded was conducted to see if there were significant differences among the remaining 3 colonies. This analysis indicated that there were no significant differences between colonies in any of the indices (Table 6.2b).

Table 6.1

Group Statistics for Reproductive Indices in Different Colonies at Nelly Bay
(volume units are $\mu m^3 \times 10^6$)

Variable	Colony	N	Mean	Std Dev.
Total Gonad Volume	1	10	1,050	471.6
	3	5	1,268	548.8
	4	5	479	214.0
	5	15	1,111	231.7
Fecundity	1	10	6.8	.633
	3	5	7.2	1.924
	4	5	5.4	.548
	5	15	6.3	1.291
Oocyte Volume	1	30	140.1	69.7
	3	15	177.2	116.9
	4	15	78.8	46.7
	5	45	146.2	41.2
Testes Volume	1	30	24.5	16.7
	3	15	33.8	20.2
	4	15	10.8	4.8
	5	30	46.8	31.8

Table 6.2

ANOVAs for Differences in Reproduction Between Colonies at Nelly Bay

a) Variable: Total Gonad Volume per Polyp

Source of Variation	Sum of Squares	df	Mean Square	F Value	Prob.
Colony	1.905×10^{12}	3	634.9×10^{9}	4.57	.009
Residual	4.304×10^{12}	31	138.9×10^{9}		

b) Summary Results for ANOVAs with Other Variables

Variable	Factor	F Value	Prob.
Fecundity	Colony	2.35	.092
Log(Oocyte Volume)	Colony	2.32	.115
	Polyp	4.08	<.001
Log(Testes Volume)	Colony	8.31	.001
	Polyp	1.25	.254

c) Summary Results for ANOVAs with Colony 4 Excluded

Variable	Factor	F Value	Prob.
Total Gonad Volume	Colony	0.52	.601
Fecundity	Colony	1.05	.365
Log(Oocyte Volume)	Colony	0.29	.752
	Polyp	4.24	<.001
Log(Testes Volume)	Colony	2.60	.115
	Polyp	3.50	.001

Inter-colony Variations at Davies Reef

The striking differences in total gonad volume between colonies at Davies Reef (Figure 6.1) has already been noted. In particular, the deep colony exhibited consistently higher values than the other two colonies, while the middle site showed almost no reproductive activity during the entire study.

A comparison of reproductive indices similar to that carried out for Nelly Bay is presented in Tables 6.3 and 6.4. In the ANOVA designs for fecundity and reproductive effort, values for each polyp were considered to be the fundamental replicated unit, while replicate branches for each colony were treated as a nested factor. In the case of oocyte and testes volume, polyps were also treated as a nested factor since individual oocyte or testes measurements within each polyp formed the basic replicated unit. Since the available data covered two years, "Year" was also included as a independent factor in the ANOVA. Heterogeneity of variances was tested using Cochran's and the Bartlett-Box tests and the ANOVA considered to be valid unless both statistics were significant beyond P=.04. Testes volume was one such case, and log transformation did not alleviate the problem. However due to the overwhelming significance obtained ($F=38.0$, $P<<.001$), it was considered reasonable to accept, with caution, the results of the analysis.

Table 6.3 shows that there were significant differences between the three colonies at Davies Reef in terms of total gonad volume, fecundity and both oocyte and testes size. Since the middle colony is obviously strikingly different from the other two, it was decided to repeat the analysis without the middle colony. In this case a significant difference was still found between the shallow and deep colony in terms of all the above indexes. The general pattern was for the deep colony to have many more eggs than the shallow colony, but smaller ones. Numbers of testes were constant at 4 but tended to be larger at the deep colony (Table 6.4).

It can be seen from Table 6.3 that differences between years were not generally significant, with the exception of egg volume.

Table 6.3
ANOVAs for Differences in Reproduction Between Colonies at Davies Reef

a) Variable: Total Gonad Volume per Polyp

Source of Variation	Sum of Squares	df	Mean Square	F Value	Prob.
Colony	7.703×10^{12}	2	3.852×10^{12}	12.8	.001
Year	0.041×10^{12}	1	0.041×10^{12}	.13	.717
Col x Yr	0.015×10^{12}	2	7.412×10^{9}	.03	.976
Branch	3.609×10^{12}	12	0.301×10^{12}	10.9	<.001
Residual	2.124×10^{12}	77	0.028×10^{12}		

b) Summary Results for ANOVAs with Other Variables

Variable	Factor	F Value	Prob.
Fecundity	Colony	18.97	<.001
	Year	3.98	.069
	Col x Yr	0.79	.477
	Branch	24.95	<.001
Oocyte Volume	Colony	8.74	.013
	Year	44.42	<.001
	Col x Yr	0.27	.621
	Branch	0.82	.575
	Polyp	1.76	.01
Testes Volume	Colony	19.27	.001
	Year	2.66	.147
	Col x Yr	5.27	.055
	Branch	1.33	.262
	Polyp	1.42	.112

c) Summary Results for ANOVAs with Middle Site Excluded

Variable	Factor	F Value	Prob.
Total Gonad Volume	Colony	5.49	.047
	Year	0.09	.770
	Col x Yr	0.02	.879
	Branch	11.75	<.001
Fecundity	Colony	9.24	.016
	Year	3.62	.094
	Col x Yr	0.09	.768
	Branch	29.80	<.001
Oocyte Volume	Colony	17.41	.004
	Year	44.42	<.001
	Col x Yr	0.27	.621
	Branch	0.82	.575
	Polyp	1.75	.012
Testes Volume	Colony	38.00	<.001
	Year	2.66	.147
	Col x Yr	5.27	.055
	Branch	1.33	.262
	Polyp	1.40	.123

Table 6.4

Group Statistics for Reproductive Indices in Different Colonies at Davies Reef
(volume units are $\mu m^3 \times 10^6$)

Variable	Year	Colony	N	Mean	Std Dev.
Total Gonad Volume	1980	SH	30	257.1	254.5
		MD	15	0	0
		DP	25	717.5	422.4
	1981	SH	20	333.3	118.0
		MD	23	27.7	84.4
		DP	20	859.1	256.9
Fecundity	1980	SH	30	3.1	2.80
		MD	15	0	0
		DP	25	10.8	5.56
	1981	SH	20	7.7	1.81
		MD	23	0.6	1.62
		DP	20	16.0	1.97
Oocyte Volume	1980	SH	52	59.0	23.7
		MD	15	0	0
		DP	63	50.0	17.6
	1981	SH	59	39.3	13.6
		MD	15	0	0
		DP	60	33.0	12.0
Testes Volume	1980	SH	33	35.8	22.6
		MD	15	0	0
		DP	42	56.2	39.2
	1981	SH	37	8.7	8.3
		MD	4	19.3	10.8
		DP	39	81.3	49.9

Similarly, no significant interactions between the various factors were found.

Intra-colony Variation in Reproduction

Brown vs White-tipped Branches

Observations of over 50 branches during spawning, both in aquaria and *in situ*, consistently demonstrated that white tipped branches are sterile near the tip, while brown tipped branches develop and spawn eggs and sperm over the entire branch tip, including the apical corallite if it is still discernable. Figure 6.7 show a

typical example of a brown and white tipped branch during the period of gamete release. There is a clear zone of approximately 1-2cm on the white tipped branch where no gametes are being released. On the brown tipped branch pink egg-sperm bundles are clearly visible over the entire surface.

Variation along a White-tipped Branch

The results, expressed in terms of total gonad volume per polyp are shown graphically in Figure 6.8. In all branches from the deep colony at Davies Reef, there were no gonads visible in the .5cm sample. This confirms numerous observations on other tips at the deep site in which no polyps within the top .5 - 1cm were ever found to have gonads. At 4cm, two of the three branches were virtually non-reproductive, while the third had a gonad volume comparable to all the samples further along the branch. Gonad volume appears to then reach a maximum at approximately 8cm. If the three data points in Figure 6.8 with zero or nearly zero gonad volume are excluded, then there is no significant trend towards increasing gonad volume with distance along the branch (ANOVA on regression; $P>.1$). It would thus appear that there is a transition zone at approximately 4cm, where gravid polyps first start to appear. Within this zone polyps appear to be either fully gravid, or non-reproductive, rather than exhibiting a progressive increase in reproductive maturity.

White tipped branches from the deep site at Davies Reef tend to have large white (zooxanthellae-free) zones (2-4cm) compared to the other corals at both Davies and Magnetic Island. At Geoffrey Bay, for instance, the white zone is only approximately .5-1cm long. It is interesting to note that gonads also start to appear closer to the tips of branches from Nelly and Geoffrey Bays. For instance, in a sample of six branches, the mean distance at which fecund polyps first appear is 1.62cm (95% conf. limits of .58-2.20) This is much nearer the tip than at Davies Reef, where fecund polyps were first detected at about 4cm (Figure 6.8, and pers. obs.). This suggests that the length of the sterile zone in A. formosa branches is variable, and may be correlated with the length of the zooxanthellae-free zone in white-tipped branches.

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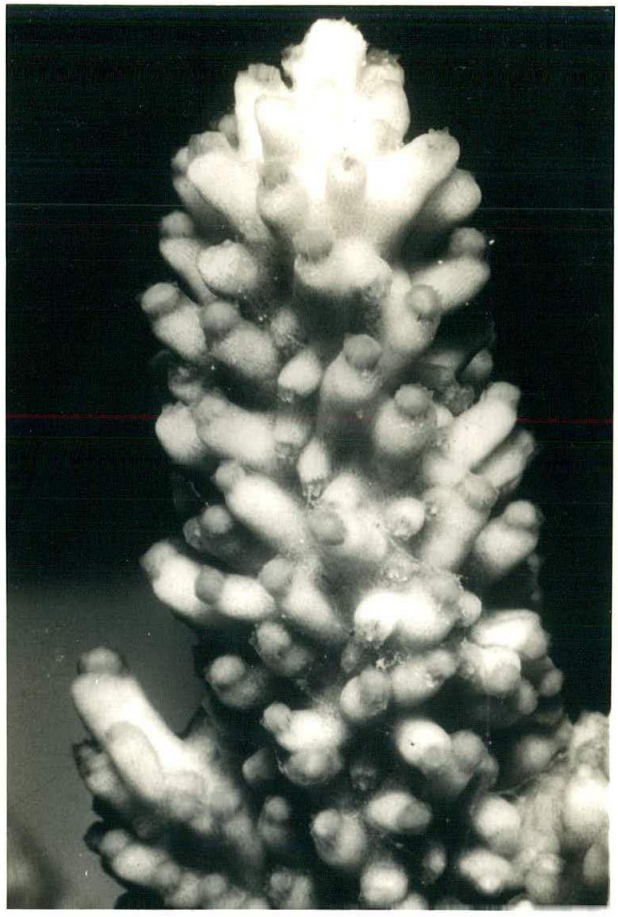
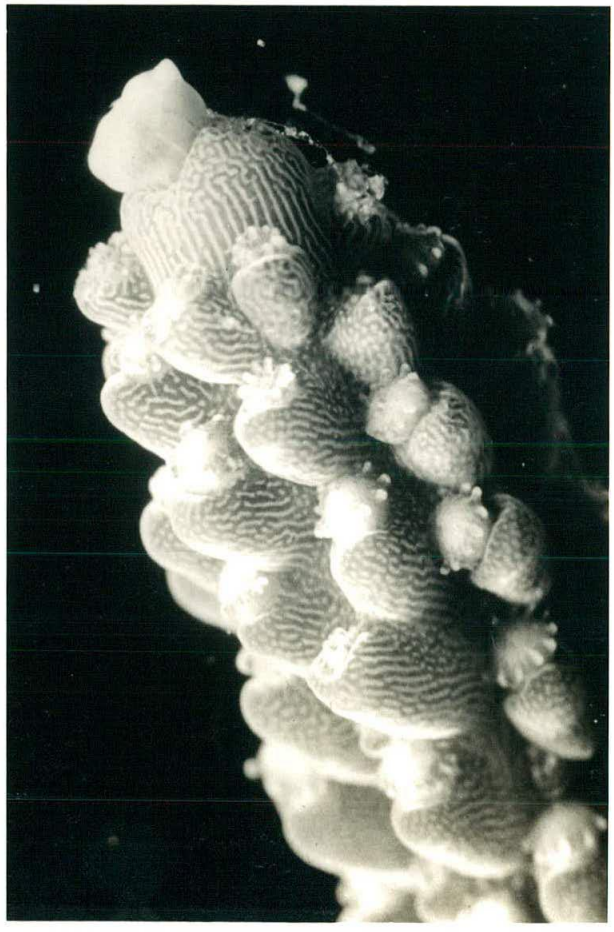
Figure 6.7 Photographs of a white tipped (a) and an brown tipped (b) branch of A. formosa spawning. Note the absense of egg-sperm bundles in the apical region of the white tipped branch.





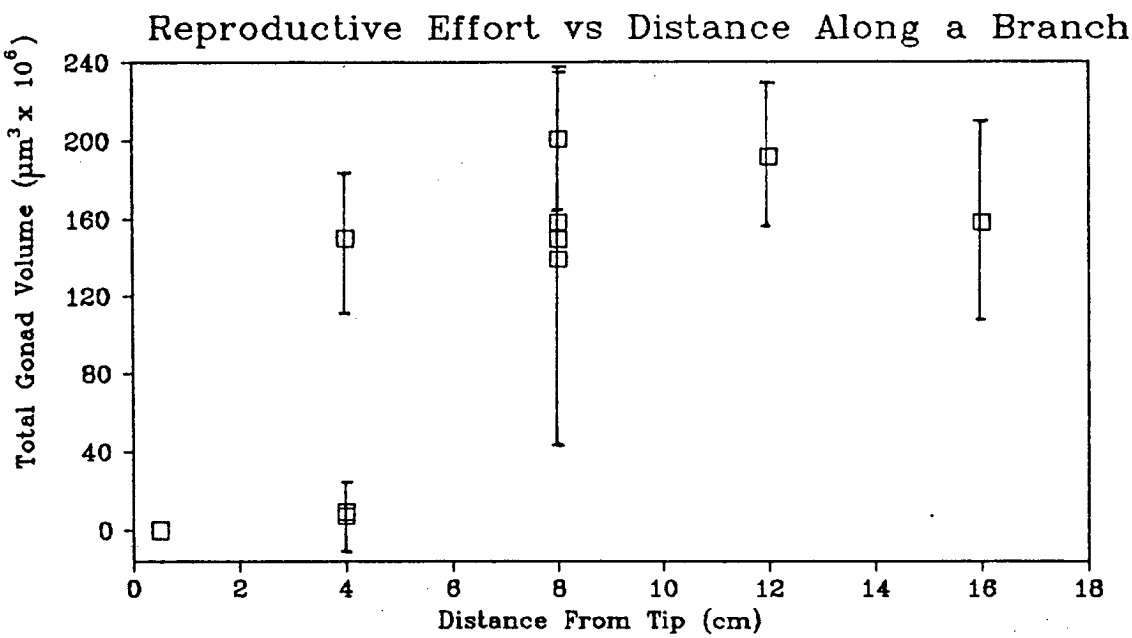


Figure 6.8 Variation in mean total gonad volume per polyp, along a white tipped branch. Error bars are 95% confidence Intervals.

Reproduction vs Colony Size

There was a striking difference in the reproductive status of juvenile corals compared to isolated remnants of larger colonies (Figure 6.9). All juveniles between 17 and 143mm mean diameter were sterile, whereas isolated remnants between 35 and 110mm in length showed a range in total gonad volume

Among the isolated remnants, the data are highly variable but there was a statistically significant trend for larger remnants to have a higher total gonad volume (ANOVA on regression line; $F=15.2$, $P<.01$). Fecundity also increased significantly with remnant size ($F=19.5$, $P<.01$). However, if branches with no gonads are excluded from the analysis, there are no significant trends in fecundity with increasing size ($F=.7$ with 1 x 10 df: $P>.05$).

If non-zero (i.e. reproductive) remnants from Figure 6.9 are compared with the large parent transplant colony (see below, and also Materials and Methods), then the remnants are seen to have significantly lower fecundity (T-test, $t=7.41$; $P<.01$) and total gonad volume ($t=6.63$; $P<.01$). Oocyte size was not significantly different.

Effect of Fragmentation and Transplantation

The design of this experiment resulted in three groups of corals: 1) An "Initial Control" group from the parent colony providing information on the reproductive status at the beginning of the experiment; 2) A "Control" group on the parent colony taken at the end of the experiment; 3) and an "Experimental Fragments" group from the experimental branches (i.e. isolated fragments) taken at the same time as group 2 in order to determine whether gametogenesis had been affected by the experimental procedure. Table 6.5 shows the summary statistics for total gonad volume per polyp for each of the above groups. Each mean is derived from 5-8 replicate polyps sampled from a branch. Figure 6.10 shows a plot of the means as a function of branch size. Although formal growth measurements were not taken,

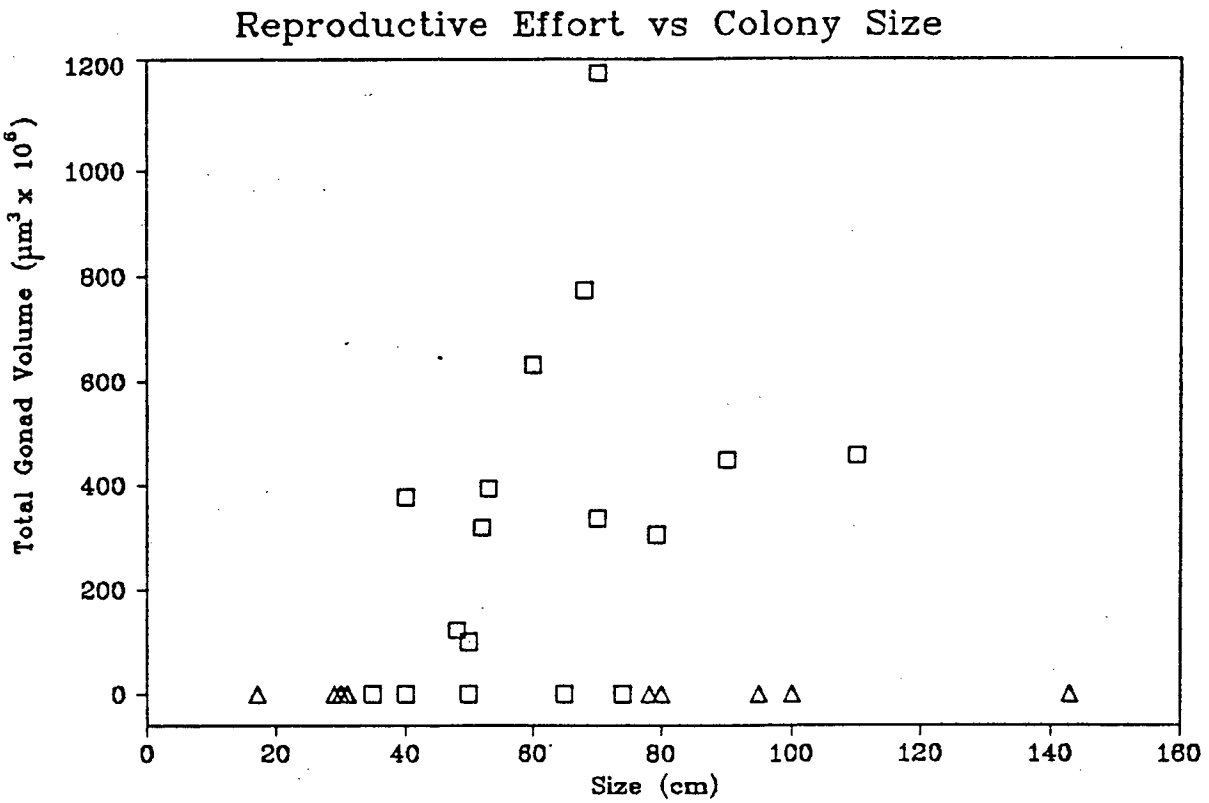


Figure 6.9 Variation in mean total gonad volume per polyp in colonies of different size. Triangles = juveniles; squares = isolated fragments.

all except the smallest fragments had normal white growing tips, and many fragments had produced new lateral branches. All fragments showed significant addition of skeletal material around their bases. This is a normal repair response which serves to create a new "holdfast" at the point of attachment to the mesh rack.

In situ observations during spawning indicated that virtually all transplanted fragments spawned at the same time and in a similar manner to the parent colony. The only exceptions were 2 very small fragments of about 30-50mm which had begun to die off near the base.

Dissection and examination of the gonads of the transplanted fragments indicated that all except 3 of the branches had oocytes and testes. Of those 3 exceptions, two were very small (30 and 36mm) and had obviously experienced die off during the experiment, while the third was small but not obviously stressed or damaged. The very small gonad volume for this branch (Branch 7, Table 6.5) was due to the presence of a single testes in one polyp.

A comparison of the means for control and experimental groups with the initial controls indicates that gonads continued to develop in both parent colony and on transplant racks, and that the total gonad volume per polyp is significantly greater at the end of the experiment compared to the beginning (T-tests, Table 6.6).

There were also significant differences between the control and experimental groups at the end of the experiment. Table 6.5 indicates that the experimental branches had significantly less total gonad volume per polyp than the control branches. However, this significant difference does not persist if the branches with no gonads are omitted from the comparison (Table 6.5). In addition, there is no significant trend for increasing total gonad volume with size in the transplants if the non-reproductive branches are excluded (ANOVA of regression line; $F=1.7$ with 1x19 df; $P>.05$).

Table 6.5
Descriptive Statistics for Branches from Transplant Experiment
Meaurements are for Total Gonad Volume per Polyp ($\mu m^3 \times 10^6$)

a) Group 1 - "Initial Control"

Branch	n	Mean	Std Dev.	Max	Min
1	5	90.3	22.1	107.4	56.5
2	5	130.1	30.7	162.2	79.5
3	5	170.6	33.3	213.3	121.1
4	5	175.1	50.6	257.7	129.5
5	5	124.1	30.4	167.7	91.3
6	5	107.4	47.8	187.2	63.5
7	5	61.1	15.6	78.8	35.9
8	5	95.2	23.5	130.0	73.8
9	5	97.5	22.0	125.0	66.7
10	5	132.0	20.2	167.0	118.9
11	5	113.9	32.4	132.5	56.7
Overall:	55	118.0	43.4	257.7	35.9

b) Group - "Controls"

Branch	n	Mean	Std Dev.	Max	Min
1	5	340.9	26.3	375.7	304.8
2	5	1106.7	470.3	1848.3	673.5
3	5	1089.6	118.8	1252.5	991.7
4	5	988.2	253.0	1266.6	641.4
5	5	686.9	94.1	812.8	554.8
6	5	757.2	114.9	875.9	633.0
7	5	799.2	325.8	1353.7	566.1
8	5	978.7	99.1	1091.4	851.3
9	5	720.0	79.5	785.2	587.3
10	5	1079.1	174.8	1366.0	898.3
11	5	795.2	211.6	1018.9	519.0
Overall:	55	849.3	295.7	1848.3	304.8

c) Group 3 - "Experimental Fragments"

Branch	Size	n	Mean	Std Dev.	Max	Min
1	30	5	0.0	0.0	0.0	0.0
2	36	6	0.0	0.0	0.0	0.0
3	55	6	740.4	241.3	1100.5	438.7
4	57	6	584.5	71.5	718.5	509.3
5	57	6	385.3	114.8	528.1	242.1
6	58	8	525.9	113.5	655.3	348.6
7	59	6	0.5	1.4	3.5	0.0
8	64	6	1110.9	185.9	1385.1	816.0
9	66	6	588.6	113.5	802.4	487.9
10	77	6	630.9	185.8	885.7	396.2
11	81	5	941.3	118.1	1076.0	781.1
12	96	5	721.4	173.2	953.1	519.4
13	96	5	458.3	284.4	768.2	89.6
14	105	5	842.8	108.1	1000.6	735.0
15	109	5	1106.6	272.6	1565.0	854.8
16	109	5	844.0	110.3	957.0	713.7
17	110	5	1026.4	262.2	1442.6	756.1
18	111	5	182.0	192.2	425.6	0.0
19	112	5	896.3	471.4	1409.7	404.5
20	113	5	1234.5	87.9	1374.1	1145.1
21	115	5	1176.0	216.0	1487.3	936.3
22	124	5	956.6	218.3	1258.5	717.5
23	145	5	294.4	89.5	423.0	183.7
24	185	5	1093.9	225.7	1330.9	795.9
Overall		131	666.7	412.6	1565.0	0.0

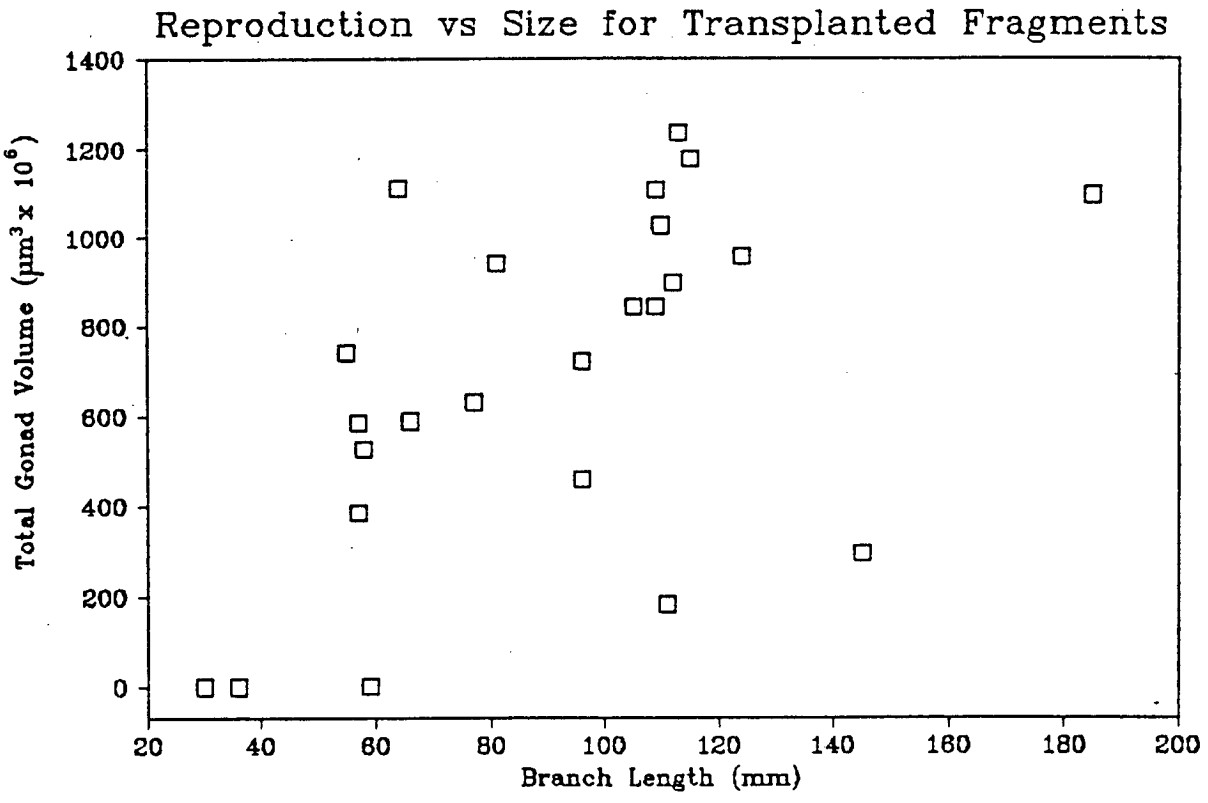


Figure 6.10 Relationship between mean total gonad volume per polp, and branch size for transplanted branches at Geoffrey Bay, Magnetic Island.

Table 6.6
T-tests for Comparisons Between Groups in Transplant Experiment
(values in parentheses are group means)

Comparison			T-value	d.f	P
Initial Control (118.0)	vs	Control (849.3)	18.15	108	<.01
Initial Control (118.0)	vs	Experimental (666.7)	9.82	184	<.01
Control (849.3)	vs	Experimental (666.7)	2.98	184	<.01
Control (849.3)	vs	Experimental (0's excluded) (766.0)	1.54	167	>.05

In summary, there appears to be a significant and dramatic effect on reproduction when very small fragments (3-5cm) are isolated. In other larger branches, isolation from the parent colony, and transplantation onto racks does not appear to have significantly disrupted the reproductive cycle.

6.4 Discussion

Reproductive Seasonality

The data presented here clearly show that A. formosa has an annual gametogenic cycle with final gonad maturation and subsequent spawning occurring in the spring (October - November). The spawning behaviour of this species has been described elsewhere (Harrison et al., 1984; Babcock et al., 1986). It is a broadcaster, releasing bundles of eggs and sperm on the evening of the 4th or 5th nights after the full moon. Spawning is synchronous over a large area with all or most of a population spawning within the space of an hour. The seasonal pattern in A. formosa agrees with the results of numerous previous studies on other broadcasting corals in Australia (Kojis & Quinn, 1981,1982; Harriott, 1983b; Harrison et al., 1984; Willis et al., 1985; Babcock et al., 1986; Simpson, 1985). Brooding species such as

P. damicornis, however, tend to spawn on a monthly basis, although a significant seasonal peak may still occur (Harriott, 1984; Kojis, 1986).

The other major feature of the reproductive cycles in Figures 6.1-6.3 is the dramatic rise in total gonad volume just in the month or two before spawning. This indicates that there is a brief annual period of intense energetic investment in reproduction rather than a constant low investment rate throughout the year.

Interaction between Seasonal Growth and Seasonal Gametogenesis

At both Nelly Bay and Davies Reef, there is no indication that skeletal extension is reduced during the period of maximum increase in gonad volume. On the contrary, extension appears to be either increasing or at a maximum during this period. Although it is possible that skeletal extension might still be inhibited from attaining an even higher level than observed, the results do not suggest that reproduction has a marked effect on skeletal growth. Further experimental work on the differences in seasonal growth between juvenile and similarly sized mature fragments would permit more definite conclusions to be drawn.

Inter-Colony Differences

Colonies at both Nelly Bay and Davies Reef exhibited significant differences in their reproduction. At Nelly Bay the colonies were all located at the same depth and in a similar environmental regime. The results indicate that only one of the 4 colonies studied was significantly different in terms of reproductive investment (total gonad volume). The remaining colonies all had similar volumes of gonad material at maturation. There were no obvious differences in location or history which can help account for this difference. It is interesting to note, however that the difference occurs only during the last sample. In previous samples the colony showed no difference from the others (Figure 6.4). It would appear that normal maturation of gametes in this particular colony was interrupted by some factor,

resulting in a lack of gonad growth in the last month. Since in situ observations were not obtained from this colony, it is not known if the gametes were sufficiently developed for spawning to occur, or if gonad resorption was responsible for the disappearance of reproductive material in the subsequent sample.

The other major inter-colony difference found at Nelly Bay was the development and release of mature gonads by one colony one month earlier than the others. This "split spawning" phenomenon has been recorded previously in a number of corals engaging in the annual mass spawning event (Harrison et al., 1984; Willis et al., 1986), and involves members of a population spawning on two different occasions exactly one lunar month apart. The data presented here (Figure 6.6) are of interest since they show that the differences in time of spawning are matched by differences in the timing of the gametogenic cycle. In other words, the "early" coral in this study not only spawned a month early, it also underwent its period of rapid increase in gonad volume a month early. It would be instructive to monitor the behaviour of individual colonies over several years to determine if the same colony consistently spawns early.

At Davies Reef the three colonies were situated in very different environments, along a depth gradient. As discussed in Chapter 4, there were substantial differences in at least 2 important physiological parameters: light and water motion. Differences in reproduction between colonies in this situation were striking. Although all sites were significantly different from each other, the middle site should probably be considered independently of the other two since it was almost completely inactive reproductively, while the other two colonies showed normal gametogenic cycles. Furthermore, its lack of normal gonad development does not match its intermediate position in terms of the depth related environmental parameters (light and water motion). The reasons for this lack of reproduction at the middle site are not clear. There was no obvious difference at this site in terms of colony appearance or environmental parameters which might explain failure to develop gonads.

Energetic investment in reproduction was much greater at the deep site compared to the shallow site. This was due principally to a much higher fecundity at the deep site. Oocytes were actually slightly smaller here than at the shallow site. Skeletal extension rate at the deep site was greater than the shallow site, but overall calcification (including initiation of new branches) was estimated to be lower. If Acropora is considered to be primarily autotrophic, then the results of Chalker and Dunlap (1983) indicate that as a result of photoadaptation to lower light intensities at the deep site, the amount of daily energy available for metabolic processes is approximately the same at both sites. Thus at the deep site, the colony appears to be investing less energy in calcification but more into reproduction. The reasons for this difference in strategy are not immediately obvious. However it is interesting to note that the deep colony, which is near the limit of its depth distribution, and thus possibly in a sub-optimal environment in terms of water-motion and perhaps other factors, chooses to use what energy it has available to it to 1) extend its branches as far as possible; and 2) to produce large numbers of dispersive propagules. This could be an adaptation to unfavourable conditions (i.e. growing out of an unsuitable habitat, and dispersing propagules away from it).

Within Colony Variation

The lack of gonad development in white tips of A. formosa supports the findings of Wallace (1985) for other Acropora species. As she points out, this sterile zone is probably due to the presence of immature radial corallites at the branch tip. The lack of reproduction of the apical corallite cannot be similarly explained however. Although the exact functional role of the apical corallite in Acropora is not known, its status as the growing point of the branch may preclude it from developing gonads. For instance Gladfelter (1983) has shown that the apical canal is a major avenue of internal fluid transport. The presence of gonads in this canal would undoubtedly interfere with such transport.

In brown tips, lack of branch extension results in the tip being surrounded by mature radials which are fully reproductive. In addition, the degeneration of the apical corallite into what is morphologically indistinguishable from a radial, is paralleled by the development of gonads.

Although the distance between samples along white-tipped branches in this study (4cm) does not permit a detailed examination of the transition from sterility to maturity, it is interesting to note that the samples at 4cm from the tip showed a high degree of variance. Polyps from 3 branches contained virtually no gonads, while a few contained nearly normal gonad volumes in most polyps. This suggests that the transition zone between sterile and fully reproductive polyps on a white tipped branch occurs (in this colony) at approximately 4cm, and that the transition does not involve a large number of polyps with intermediate levels of fecundity and gonad volume. Since new polyps are continually being produced at the tip, these results suggest that newly developing radial polyps may need to a attain a specific size, or stage of development by a particular time if they are to develop gonads. It is interesting to note that if the average growth rate at the deep site (1.27cm/30 days) is assumed to have applied to the branches sampled, then the polyps at 4 cm would only have begun to develop some 3 to 3.5 months before spawning (i.e. in August). Thus the polyps would have had to compress the entire gametogenic cycle into a much shorter period than fully developed polyps further down the branch.

From the point of view of competition between growth and reproduction along a tip it is interesting to note that infilling, and to a lesser extent radial growth, proceeds at a decreasing rate away from the tip (see Chapters 3 and 4), reaching a minimum at about 30 cm from the tip. This decreasing energetic investment in calcification is not reflected in any appreciable increase in reproductive output per polyp.

Age/size differences

The results of this study indicate that small recently settled (i.e. chronologically young) colonies do not develop gonads. The size at which gonads first appear could not be determined since even the largest colonies (143mm mean diameter) of this type sampled were devoid of gonads. Larger colonies were not sampled since it became difficult to distinguish between recently settled colonies and fragments from larger colonies. Future studies, in which known juveniles were tagged and monitored through several years as they grew, might provide more detailed information on the size and approximate age at first reproduction.

Although chronologically young colonies did not have gonads, most isolated remnants of larger colonies which were similarly sized, but were obviously much older chronologically, possessed both eggs and sperm. Total gonad volume in these remnants was slightly less than the large intact colony used for transplants at Geoffrey Bay, but it is uncertain whether this is a slight size effect, or a manifestation of innate differences between colonies. Overall, these results suggest that chronological age rather than size is the most important factor in determining the reproductive status of a colony, and that in reproductively active corals, there is no obvious trend for larger colonies to invest more in reproduction.

Previous studies on massive corals have drawn somewhat different conclusions. For instance, Kojis & Quinn (1985) found that both isolated fragments and naturally occurring small colonies of Goniastrea favulus showed a significant increase in fecundity per polyp with increasing size. However the slopes of the two regression lines were significantly different, so that experimentally fragmented portions tended to have a higher fecundity for their size, than the naturally occurring colonies. They concluded that both age and size were important determinants of fecundity, although size was obviously the most important of these two factors.

Szmant-Froelich (1985) also carried out a similar series of experiments on Montastrea annularis. She found that at one site isolation of fragments from the parent colony some 6-9 months before spawning caused a significant reduction in reproductive status compared with their colony of origin. There was no appreciable difference in reproductive status between the experimentally isolated fragments and small naturally occurring colonies, although it could not be determined whether these latter colonies were juveniles, or natural isolates of larger colonies. These results again suggest that size, more than chronological age is the most important factor determining reproductive status. At a second site, Szmant-Froelich (1985) found only a slight reduction in reproductive status after fragmentation. The fragments at this site had a much higher proportion of reproductive polyps for their size compared to both natural and experimental isolates at the first site. A suggested explanation was that at the second site, the parent colonies already consisted of a collection of "more or less" isolated nodules, and that this might have predisposed the colony to being able to reproduce at a smaller size. It was not determined whether this disposition was genetically or phenotypically based. However, it is interesting that the isolated remnant branches of A. formosa used in the present study showed a similar lack of size/reproduction relationship. Although it is not known how long these branches had been isolated from a larger colony, fragmentation, and subsequent regeneration of small pieces is a very common occurrence in branching Acropora species (Tunnicliffe; 1981; Collins, 1978; Highsmith, 1982) and it is possible that A. formosa has developed the ability to maintain its reproductive output even when its size is drastically reduced.

In the present study there was no obvious linear relationship between size and reproduction of isolated fragments. Instead there was a tendency for branches to have either no gonads, or to be fully reproductive.

Transplant Experiments

This experiment differs from those of Kojis & Quinn (1985) and Szmant-Froelich (1985) in that fragments were broken off the parent colony after gametogenesis had already begun. Thus the question addressed was not whether smaller sized colonies would develop gonads, but rather if the trauma associated with breakage, and the subsequent demands of basal repair in addition to growth would cause a disruption of the normal gametogenic cycle. The data clearly indicate that, except for very small branches, the experimental procedure did not noticeably affect reproductive output of the branch. Again there was no obvious relationship between size and reproduction among those branches which developed gonads. Although formal growth measurements were not taken, it was apparent from the size of main branches, and the number of new lateral branches, and the new growth around the base of the corals that skeletal growth had not stopped during the experimental period. If anything the branches appeared to have grown more than would normally have been expected.

Since this experiment was conducted about half way through the gametogenic cycle, it would be interesting to determine whether a similar pattern occurred if breakage and transplantation occurred just after spawning, and prior to the onset of the next gametogenic cycle. Possibly, gametogenesis, can be postponed or inhibited during periods of stress if it has not already begun, but that once it has commenced it must proceed to completion.

The results of Rinkevich & Loya (1985) suggest that in S. pistillata there may be a different response to physiological trauma and repair activity, since they found a significant reduction in reproduction in transplants, especially near edge zones which were contact with a conspecific. However their results are not strictly comparable since corals were responding to competitive interaction along the contact zone, rather than just initiating repair. In addition, calcification was significantly inhibited, indicating that the corals were much more stressed than in the present experiment.

The lack of difference between experimental branches with gonads present, and the lack of a significant trend between branch size and reproductive effort suggest that reproduction in A. formosa is an all or nothing process with no (or very few) intermediate stages. i.e. if a branch initiates gametogenesis then it develops a full complement of eggs which develop to full size.

A. formosa seems to be able to maintain its reproductive output at nearly normal levels even when isolated as small fragments after the onset of the annual gametogenic cycle. This may be an adaptation to fragmentation, which is an integral part of its life history. It is possible that reproduction in Acropora and other largely autotrophic corals is not a process which diverts energy away from other essential processes. Crossland (1980) has found that in A. cf acuminata (probably A. formosa) some 80% of the mucus released into the water is lipid, and that this mucus release represents 40% of the net carbon fixed by the coral per day. Thus it appears that there is considerable surplus energy in the form of lipid which is not used by the coral. The purpose of this "wastage" has not been satisfactorily explained. Crossland (1980) has suggested that it is an alternative to photorespiration in saturating light regimes. Since coral eggs are largely composed of lipid, reproduction may simply draw on this unused, and otherwise discarded energy source.

Conclusions

1) The energetic investment into gonad material is not constant throughout the year, but exhibits a pronounced peak in early spring just before an annual spawning event.

2) There does not appear to be a negative correlation between growth and gonad buildup. Rather, the two processes appear to exhibit maximums at approximately the same time, possibly in response to seasonally optimum conditions.

3) There can be significant differences between colonies in terms of both the timing of gonad buildup and spawning, and in the total volume of gonad material produced. These differences can be found within a single relatively homogeneous environment, although the most dramatic differences were found to occur in colonies at different depths.

4) Small juvenile colonies go through a non-reproductive stage. The size at first reproduction was not determined but the data obtained suggest it is over 14cm mean diameter

5) Isolated remnants of older colonies are, except for very small fragments, reproductively active at sizes much smaller than found in juveniles.

6) Fragments removed from a large colony and transplanted onto racks after the initiation of gametogenesis did not, except for very small individuals, show a significant reduction in reproductive status.

Chapter 7
General Discussion

7.1 Discussion

This thesis has shown that branch extension can vary over a range of spatial and temporal scales. In addition, indirect evidence suggests that a similar pattern of variation also exists in area or tissue specific calcification rate.

Small scale (1-100cm) spatial variation in extension has been shown to occur between different tips within a colony (Chapter 3). This variation is probably related to changes in the micro-environment in different parts of a colony.

Medium scale (10-100m) spatial variation is seen in the different mean extension rates of colonies growing within a single location on a reef (Chapters 4 & 5). The causal parameters involved in this variation have not been unambiguously identified. At Davies reef, the three colonies investigated were at different depths, and the results of the reciprocal transplant experiment (Chapter 4) suggest that some exogenous environmental parameter (probably depth related) was responsible. Light and water motion are the two most likely parameters. Significant inter-colony variations were also found in a single relatively uniform habitat at Nelly Bay (Chapter 5). In this case no environmental parameters were obviously responsible, and it is concluded that either subtle changes in the environment between colonies was responsible, or that the colonies have inherent, genetically based differences in their rates of branch extension.

Large scale (1-1000km) spatial variation in extension rates was not directly investigated in this thesis. Although concurrent measurements were taken at two different reefs (Nelly Bay and Davies Reef) the within reef variability was too great to warrant analysis of any between reef variation. The results of the studies carried out at a smaller spatial scale, however have laid the necessary ground work for an investigation of large scale geographic growth variations. The degree of small and medium scale variation which

has been described here clearly indicates that such a study would need to involve careful stratified sampling and/or a high degree of replication. In addition reciprocal transplantation, if feasible, would be required to distinguish between genetic and phenotypic responses in such a study. Work on the massive coral Porites spp shows that extension exhibits significant variation across the continental shelf in the Townsville region, with highest extension occurring on turbid nearshore reefs, and lowest rates occurring on the reefs at the edge of the continental shelf in clear water (Isdale, 1983). In addition corals in the northern GBR also showed a similar cross-shelf variation, but extended significantly faster at all locations than the southern corals (Isdale, 1983). It would clearly be of interest to determine whether the branching coral A. formosa shows similar trends.

Branch extension has also been shown to vary over a range of temporal scales. Within a colony, some tips can change their growth status from active growth to virtually nil extension in a period of a month or less (Chapter 3). Over a period of a year, extension rates can also change on a seasonal basis (Chapter 5). These variations would be important to consider when planning any large scale study of coral growth.

In addition to describing the range of temporal and spatial variations which can be observed in A. formosa, this thesis has also attempted to clarify some of the theoretical and methodological issues involved in growth studies on perforate arborescent corals. In Chapter 1 it was shown that linear branch extension is a better indicator of both total skeletal deposition and tissue specific calcification than the weight of newly extended skeleton. Although the data presented in Chapter 1 suggest that linear extension can explain a large proportion of the variability in total skeletal deposition, certain aspects of the calcification process in a growing branch are not taken into account, and are thus a potentially significant source of error. The principal sources of error are changes in the density structure of a growing tip over time (infilling), and continued thickening of the basal regions of a branch (radial growth). It is evident from the preliminary data on these two processes (Chapters 3 & 4) that further, more detailed

work is required if accurate predictive models of growth in branching Acropora species are to constructed. For instance small changes in the rates of radial growth, or in the final density attained by a branch, could lead to large errors in estimates of total carbonate productivity for a colony if the estimates were based on linear extension alone. Direct measurements of radial growth under different conditions and experimental work aimed at determining the principal factors controlling rates of radial growth and infilling should therefore be carried out. One possible parameter which might affect both branch density and radial growth is water motion. The resistance of branches to breakage during periods of high wave energy is an important ecological parameter (Tunnicliffe, 1981) and is a function of both density, and branch width (Vosberg, 1982; Chamberlain, 1976), and it is possible that these properties respond to increased water motion in a manner which increases their resistance to breakage.

One further source of error in the use of linear extension data to measure total skeletal deposition is branch initiation. Although this factor was taken into account in some the experiments performed in this thesis, it was not measured in the analysis of seasonal variations (Chapter 5), and this may have contributed to the poor explanatory power of multiple regression model. Branching has similarly been ignored in virtually all other studies of linear extension in branching corals. Consequently there is almost nothing known about the branch initiation process and what factors control it. Shinn (1972), reports that branching occurred annually over a short period of the year at his study sites. This striking phenomenon has been reported by almost no other workers (but see Tunnicliffe, 1983), and was not evident at either Nelly Bay or Davies Reef. One environmental parameter which may influence branch initiation is water motion. Taxonomic and growth form studies such as those of Wood-Jones (1910) and Veron & Pichon (1976) and Bottjer (1980) have correlated the degree of branching with the turbulence of the environment, but so far, no experimental work has been carried out.

One final aspect of growth which requires further study if measurements of total skeletal deposition are to be reliably

converted into rates of tissue specific calcification is the effect of translocation of metabolites on growth at the branch tip. The work of Pearse & Muscatine (1971) and Taylor (1977) has clearly demonstrated that translocation enhances calcification at a branch tip, and that translocation can occur over distances of at least 10cm. Gladfleter (1983) has investigated the rates and mechanism of fluid movement in gastrovascular canals, but little is known about the maximum distance over which translocation can occur within a colony, and whether this distance varies under different conditions. The results of Chapter 4, suggest that high extension rates may be achieved in some colonies by drawing on translocated material from a greater area of tissue than other colonies, but again direct experimental data are lacking. Obtaining data on this phenomenon may prove to be logistically difficult, since not only is it necessary to determine the area over which a growing tip obtains translocated material, but also to determine the quantity translocated from different locations, and the effectiveness of the translocated material in enhancing calcification and subsequent skeletal growth. The importance of translocation within a colony extends well beyond extension of branches and the physiology of calcification. Translocation may play an important role in the coordination of many different physiological processes so that a colony can respond as an integrated entity to different circumstances. Thus translocation may be important in maintenance, or adaptive alteration of overall growth form, and in the rapid repair of damage to portions of a colony.

While more detailed studies are required on the mechanisms of calcification and skeletal growth, there is also a need for more data on some parameters which influence growth. Three parameters which are at present poorly studied but potentially very important are food, water motion and reproduction.

The nutritional requirements and feeding ecology of A. formosa have not been comprehensively studied. As for other coral species, there is the potential for all of the coral's energetic requirements to be met by its endosymbiotic zooxanthellae. Porter (1976) has suggested that small-polyped branching corals with a high surface area to volume ratio are adapted to a more autotrophic status than

massive corals. The results of Chalker and Dunlap (1983) for Acropora spp support this view since they calculated that photosynthesis will exceed daily respiration down to depths of 60m at Davies Reef. In addition, Oliver (1979) found that linear extension rates of A. formosa in laboratory aquaria remained at normal levels during a one month period when all particulate matter above 5μm was excluded. However the in vitro observations of Lewis and Price (1975) indicate that A. cervicornis exhibits effective particle catching behaviour under certain conditions. It is possible that A. formosa and other Acropora species are facultative, opportunistic heterotrophs. If this is the case, then determination of the importance of food to the in situ growth of A. formosa may prove exceedingly difficult, and will require careful experimental work coupled with detailed in situ measurements of food availability. The role of heterotrophic nutrition in satisfying micronutrient and nitrogen requirements as well as calorific needs, should also be investigated.

Although water motion is considered one of the most important factors governing both the growth form of coral colonies (Wood Jones, 1910; Veron & Pichon, 1976) and the composition of entire communities (Rosen, 1975; Pichon, 1978; Done, 1983), only one experimental study on the effects of water motion on coral growth has been carried out (Jokiel, 1978). This study on three Hawaiian corals indicated that growth (weight increment) was indeed influenced by changes in turbulence, but the study needs to be repeated on different species (e.g. Acropora), and extended to measure a variety of growth responses.

Reproduction is the third potentially major factor about which very little is known. In Chapter 6 the season reproductive cycle was described, and the effects of fragmentation and fragment size on reproductive condition was investigated. The results did not show any obvious tendency for reproduction to be adversely affected by periods of high growth or repair. These results differ from those of Rinkevich & Loya (1985) and Loya (1985) who found evidence for an inverse correlation between reproduction and colony growth rates or zones of enhanced calcification. More detailed experimental work on A. formosa involving simultaneous measurement of reproductive

condition and calcification are required. In addition, if the role of reproduction in controlling growth rates is to be unambiguously determined, correlative studies must be coupled to studies on the overall energy budget of corals, in which the actual calorific demands of growth and reproduction are determined.

A final consideration in the design of future growth studies is the need for more detailed information on the fine scale spatial distribution of environmental parameters which affect growth. The principal factors which exhibit such variability are light, water motion and particulate food material. Little data exists on the degree of variation in light and water motion which can occur within a branching colony. Chamberlain & Graus (1975) have shown that zones of low water motion exist in the middle of real and model corals under conditions of constant laminar flow, but measurements under in situ conditions of variable, turbulent flow have not been carried out. Stagnant zones within a colony could also create zones of depleted food material. The internal areas of branching colonies also experience, through self-shading, less light than the periphery of a colony, and this pattern need to be documented in more detail.

In addition to the variations within a colony, the topographic complexity of most reef zones means that similar micro-scale variations may be caused by adjacent features (large boulders or colonies, outcrops, overhangs etc).

It is only through a comprehensive characterization of the environmental conditions in which a colony grows that the results of experiments on the effects of specific parameters can be put to effective use. Similarly, in situ correlative studies such as those of Chapter 5 cannot be expected to adequately explain growth variations if the environment of the colony has not been accurately measured.

Chapter 8

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APPENDIX

Table 1

Descriptive Statistics for Extension Rates (cm/30 days) of Colony 1 at Nelly Bay

Sample	Count	Mean	St'd Dev'n	St'd Error	Minimum	Maximum
DECJAN	34	.3733	.1939	.0333	.0671	.7393
FEB	35	.4556	.1665	.0281	.1776	.8256
MARCH	18	.4819	.1929	.0455	.0236	.8036
APRIL	43	.5342	.2864	.0437	.0650	1.1050
MAY	46	.3980	.2063	.0304	.0236	.8627
JUNE	61	.4683	.1846	.0236	0.0	.6993
JULY	28	.3602	.1284	.0243	.1076	.6186
AUG	43	.2688	.1550	.0236	.0709	.6500
SEPT	29	.3954	.1895	.0352	.0910	.7410
OCT	46	.4018	.1858	.0274	.1182	.8745
NOV	48	.4631	.1847	.0267	.1147	.8029
DEC	58	.3922	.2228	.0293	.0144	.8378
JAN80	38	.4522	.1964	.0319	.0118	.8509
FEB80	56	.2332	.2149	.0287	0.0	.8741
MAR80	53	.2603	.1486	.0204	.0211	.6008
APR80	43	.3286	.2011	.0307	0.0	.8250
MAY80	52	.4989	.2402	.0333	.1006	1.0568
JUN80	36	.3911	.2017	.0336	.0538	.9145
JUL80	44	.3072	.1179	.0178	0.0	.5119
AUG80	8	.3944	.0753	.0266	.2364	.4609
SEPT80	15	.3605	.2024	.0523	.0260	.7150
OCT80	40	.4899	.2544	.0402	0.0	.9100
NOV80	20	.5868	.1918	.0429	.2305	.9750
DEC80	19	.3371	.1808	.0415	0.0	.6618
JAN81	19	.2645	.1355	.0311	0.0	.5100
FEB81	30	.4749	.2017	.0368	.0650	.8580
MAR81	30	.5638	.1861	.0340	.0650	.8840
APR81	24	.3664	.2176	.0444	.0780	.7897
MAY81	21	.5001	.1086	.0237	.2167	.6356
JUN81	20	.3398	.1585	.0354	.0118	.5909
Total	1057	.4011	.2133	.0066	0.0	1.1050

Table 2

Descriptive Statistics for Extension Rates (cm/30 days) of Colony 2 at Nelly Bay

Sample	Count	Mean	St'd Dev'n	St'd Error	Minimum	Maximum
SEPT80	16	.4834	.18 5	.0459	.2470	.9100
OCT80	23	.8157	.2010	.0419	.4100	1.2800
NOV80	16	.9928	.2329	.0582	.3550	1.3300
DEC80	14	.6864	.2015	.0539	.2720	1.0990
JAN81	14	.4564	.1549	.0414	.1800	.7500
FEB81	11	.5342	.1662	.0501	.3120	.8450
MAR81	1	.6630				
APR81	22	.6141	.1928	.0411	.1460	.9940
MAY81	17	.5777	.2156	.0523	.2460	.9530
JUN81	20	.4308	.2182	.0488	.0830	1.0640
Total	15	.629	.2608	.0210	.0830	1.3300

Table 3

Descriptive Statistics for Extension Rates (cm/30 days) of Colony 3 at Nelly Bay

Sample	Count	Mean	St'd Dev'n	St'd Error	Minimum	Maximum
SEPT80	15	.5451	.2247	.0580	.2730	.9230
OCT80	17	.7679	.3829	.0929	.1540	1.4230
NOV80	21	.7810	.2094	.0457	.4610	1.0810
DEC80	16	.7238	.2655	.0664	.0710	1.1700
JAN81	14	.2818	.1673	.0447	.0450	.5550
FEB81	11	.6382	.2111	.0636	.3640	1.0790
MAR81	19	.5501	.2811	.0645	.0520	.8970
APR81	15	.3569	.2222	.0574	.0580	.6340
MAY81	15	.5603	.2920	.0754	.1440	1.0400
JUN81	19	.3036	.1713	.0393	.0830	.7560
Total	162	.5565	.3036	.0239	.0450	1.4230

Table 4

Descriptive Statistics for Extension Rates (cm/30 days)
of Colony 4 at Nelly Bay

Sample	Count	Mean	St'd Dev'n	St'd Error	Minimum	Maximum
SEPT80	12	.6500	.2086	.0602	.2730	.9230
OCT80	10	.7650	.2556	.0808	.3100	1.0000
NOV80	7	.8787	.0851	.0322	.8150	1.0640
DEC80	14	.8779	.2534	.0677	.3900	1.3000
JAN81	9	.5383	.1002	.0334	.4050	.6450
FEB81	8	.6825	.1024	.0362	.4810	.7800
MAR81	15	.8259	.2259	.0583	.3640	1.1440
APR81	14	.6400	.2114	.0565	.1750	.9460
MAY81	8	.7817	.0836	.0296	.6360	.8670
JUN81	9	.6762	.2095	.0698	.3310	.9100
Total	106	.7348	.2180	.0212	.1750	1.3000

Table 5

Descriptive Statistics for Extension Rates (cm/30 days)
of Shallow Colony at Davies Reef

Sample	Count	Mean	St'd Dev'n	St'd Error	Minimum	Maximum
1	56	.5957	.3542	.0473	0.0	1.2171
2	56	.5381	.2807	.0375	0.0	.9512
3	33	.2479	.1826	.0318	0.0	.6240
4	53	.6318	.2468	.0339	.065	1.0864
5	43	.6761	.3256	.0497	0.0	1.2371
6	39	.8036	.3573	.0572	0.0	1.6424
7	39	.9518	.3940	.0631	.073	1.5523
8	36	.8212	.3647	.0608	.063	1.3858
9	36	.7863	.2283	.0380	.333	1.2717
10	32	.6503	.2322	.0411	.183	.9667
11	26	.8248	.3269	.0641	.084	1.4745
Total	44	.6744	.3487	.016	0.0	1.6424

Table 6

Descriptive Statistics for Extension Rates (cm/30 days) of Middle Colony at Davies Reef

Sample	Count	Mean	St'd Dev'n	St'd Error	Minimum	Maximum
1	46	1.214	.2253	.0332	.6496	1.5818
2	49	.948	.3187	.0455	.1743	1.4629
3	32	.843	.2771	.0490	.1286	1.1633
4	75	1.045	.3127	.0361	.2107	1.5698
5	35	1.135	.3222	.0545	.3067	1.6989
6	32	.543	.4864	.0860	.0234	1.4420
7	31	1.341	.3402	.0611	.0809	1.9965
8	53	1.200	.2971	.0408	.4257	1.6403
9	44	1.124	.2609	.0393	.5346	1.5969
10	37	1.040	.2526	.0415	.4900	1.4717
11	34	.861	.3549	.0609	.1042	1.3942
Total	468	1.0	.3642	.016	.02	1.9965

Table 7

Descriptive Statistics for Extension Rates (cm/30 days) of Deep Colony at Davies Reef

Sample	Count	Mean	St'd Dev'n	St'd Error	Minimum	Maximum
1	39	1.541	.3946	.0632	.3739	2.1054
2	45	1.389	.3736	.0557	.3781	1.9465
3	55	1.165	.3438	.0464	.1861	1.7192
4	60	1.332	.4508	.0582	0.0	1.8670
5	36	1.505	.4838	.0806	.1276	2.0945
6	36	1.173	.6079	.1013	0.0	2.1498
7	33	1.360	.4565	.0795	.0617	1.9363
8	40	1.206	.6182	.0977	.0411	1.9085
9	35	1.050	.6487	.1097	.0144	1.9238
10	32	1.246	.3419	.0604	.3667	1.9750
11	29	.899	.6735	.1251	0.0	2.0626
Total	440	1.27	.515	.0246	0.0	2.1498