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GEOGRAPHICAL VARIATION IN THE GROWTH RATE OF THE HERMATYPIC CORAL *PORITES* IN THE GREAT BARRIER REEF PROVINCE, AUSTRALIA

Thesis submitted by

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in December 1981

for the Degree of Doctor of Philosophy in the

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James Cook University of North Queensland

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ABSTRACT

This thesis examines the growth rate of 452 colonies of the massive reef-building coral *Porites* from the Great Barrier Reef Province, Australia. The corals were collected from thirty-four different reefs, and from different zones within those reefs.

Five species of the genus were used in the project, each being a massive, hemispherical form, with a relatively smooth surface, small corallites, and a readily-identifiable point of origin of colonial growth.

The mean annual growth rate for each colony was measured using X-radiography of coral sections, and densitometry on the X-ray plates. The density variations found within the coral skeleton were used to identify periods of lunar and seasonal extension. Growth was measured radially, along maximum colony diameter.

The time of deposition of maximum density skeleton was found to differ with latitude, occurring in October/November in the south of the Province, but later, in April, north of Cooktown.

Colony growth rate was found to vary by a factor of two on a year to year basis, and that of similar colonies varied, even under "uniform" conditions. Despite this, broader patterns of growth rate variation were found within the Province. Colony growth varied according to location on reef platforms, with maximum rates on the leeward reef flat and slowest growth on the more exposed central reef flat and windward crest areas. Growth was faster and more variable on the fringing reefs of the inner continental shelf than at the outer barrier, where rates were depressed and stable. Annual growth also varied with depth and according to species.

Examination of the spatial patterns of growth variability at each of the scales employed provides a background to the discussion

of the relationships between scleractinian skeletogenesis and environmental and genetic factors. These findings are discussed in the context of modern reef investigations, in the light of their contribution to the study of reef development within the Province.

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CHAPTER ONE

INTRODUCTION TO CORAL GROWTH RATE STUDIES

The marine ecosystems known as coral reefs have fascinated naturalists and scientists for centuries. Inquiry into the structures, the largest biogenic features of the earth's surface, have centred around three principal questions: Where do they exist, what is their physical/chemical/biological makeup, and how do they grow and decay?

The early geological work of scientists such as Darwin (1842) and later Daly (1910 onwards) concentrated on the historical sequence of reef development, treating the origins and growth of reefs as exercises in deduction based on limited data. Biological studies on the growth and form of individual corals were based more on the intrinsic curiosity of the systematists. The rapid expansion of coral reef studies since the 1928-29 Great Barrier Reef Expedition has seen the life histories of individual colonies become more important in general reef studies. Corals are seen in the context of their relative contribution to the growth of coral reefs with each of the other major taxa of the calcareous organisms.

The importance of the study of the growth of individual colonies at present lies in two areas: contribution to the development of individual reefs, which in turn form the basis of reef complexes, and the ecological significance of differences or patterns of growth rates, in time and space.

Earlier ideas about the dominance of the role of coral colonies have been somewhat modified. The present broad model for coral reef development, as hypothesised by Chave *et al.* (1972) shows a single coral reef as being a function of the net production of calcium carbonate at that location over a period of time. The relative contributions of corals and other major calcareous taxa in given locations within the reef area determine what kind of reef is built and retained over time. Coral growth rate values are essential in determining the calcium carbonate contributions for each location. Buddemeier and Kinzie (1976) point out, however, that reef development studies at present require little, if any, additional information from coral growth studies for the following reasons. Physical events such as storms can destroy centuries of structured coral growth. Other processes such as sea level changes, coral mortality or over-crowding may intervene. Furthermore, the present state of the art of growth measurement, being so relatively precise compared with methods used in determining the growth rates of other contributing organisms, is perhaps too refined to use in conjunction with them.

The major need in studies of coral growth rates (and growth forms) certainly lies with the biological, ecological and environmental questions which are and will be posed in the framework of coral reef studies. The variability of growth rate and form which has been demonstrated remains of more than passing interest to the biologist. While the greatest diversity of growth form lies in species difference, the variability in rate can be accounted for by a combination of factors, both endogenous and exogenous, with the major influence probably lying with the latter. These exogenous factors are themselves spatially and temporally variable, thus posing the question of correlation between observed environments and growth rates. The historical correlation of growth rate parameters such as density band patterns may provide information on past environments, though as Buddemeier and Kinzie (1976) have pointed out, inorganic chemical models alone do not equate skeletal chemistry with conditions at the time of growth, but rather await the refinement of biochemical techniques and findings to describe the complete effect of environment on growth.

This thesis contributes to the body of data on growth and skeletal characteristics of a widely distributed genus of coral from the Great Barrier Reef Province. It analyses geographic patterns in rates of growth, and suggests some models of environmental causation in these distributions.

Definitions

The discussion of the history of coral growth rate measurement must be prefaced by some discussion of the definition of growth, and of the limitations of the types of corals under discussion.

The first definition, that of growth, is based on the form of the colony, and the processes involved in creating that form. For example, the growth of the plate-like corals is suited to measurement on a horizontal expansion basis. The growth of the corymbose or antler-type species may be measured in terms of tip extension, or weight increment converted to volumetric parameters if necessary. Growth in scleractinians is a function of skeletal framework extension. Calcification is the rate of deposition of skeleton, irrespective of extension rate. The relationship of calcification to extension rate is thus a measure of skeletal density.

Since this study is based on the use of X-radiography, it uses only those corals which are suited to the method, namely the fine-grained massive, spheroidal types, and derives measures of linear radial expansion in cm/year. Many other methods of growth rate measurement have been employed in the past, ranging from direct sequential field measurement of dimensional increment, such as that of Mayer (1918), Edmondson (1929), and Shinn (1966), to the radio-isotopic uptake methods of Goreau (1959). These have, of necessity, been expressed in differing units in many cases. The consequences of this lack of conformity have been discussed by Buddemeier and Kinzie (1976).

The definition of a scleractinian coral, for the purposes of this study, is that of a true "reef builder," or heratypic coral.

History of Growth Rate Measurement

This subject has been very comprehensively reviewed by Buddemeier and Kinzie (1976). The earliest estimates of colony growth rates were made by direct measurement of the colony over an established period of time. In 1913, Mayer remeasured several large colonies of *Symphyllia, Porites* and *Goniastrea* lying off Vivien Point, Thursday Island, and derived growth rates for the colonies for the interval since the colonies were photographed and measured by Saville-Kent in 1890. Previous to this, such workers as Gardiner (Maldives), Guppy (Cocos-Keeling), Sluiter (Krakatoa) and Wood-Jones (Cocos-Keeling) had all published dimensional growth increments for individually measured coral colonies. Vaughan (1915) measured a large number of corals in terms of colony height and diameter on Dry Tortugas in the Caribbean, finding variability in growth rate both intraspecifically and over time. He noted, along with later researchers (Mayor 1924; Edmondson 1929; Stephenson and Stephenson 1933), the differences in growth rates between the faster-growing branching forms and the heavier, more robust massive types. Of the more recent direct linear colony measurement workers, Shinn (1966) measured *Acropora* extension rates in an attempt to correlate growth with environmental conditions, while Woodhead (1971) established the annual growth increment for 1968-69 of 171 colonies representing more than a dozen species of corals from the Heron Island reef area, by measuring weight increase and height increase, as well as two different diametric dimensions for each colony. The ultimate refinement of the linear extension measurement method is probably that of Barnes and Crossland (1980), who used high resolution photographic methods in conjunction with an intervalometer to record six-hourly growth increments in the tips of *Acropora acuminata* (Verill) taken from the Great Barrier Reef. Most of the more recent weight-type growth measurement methodology has been used in conjunction with investigations of changing environmental conditions in laboratory studies on colony growth, e.g. Jokiel and Coles (1977) and Coles and Jokiel (1978).

Barnes (1972) showed the applicability of vital staining of the coral skeleton to growth studies. He used alizarin sodium sulphonate (Alizarin Red S) to stain a time marker in the living colony, allowing growth after this event to be measured at a later date. Jell (1974) applied this method to investigations of the microstructure of several species of coral from Heron Island (Great Barrier Reef). This method was also used by Dustan (1975) in field studies of growth characteristics in *Montastrea annularis* in Jamaica. Glynn (1977) derived the growth rates of colonies of *Pocillopora damicornis* in the Gulf of Panama and the Gulf of Chiriqui using Alizarin staining. Jokiel (1978) noted the effect of water motion on growth of three species of Hawaiian corals using the method to assess growth parameters.

Two methods of coral growth measurement which have been applied in a large number of recent investigations are the radiometric method of calcification measurement and the X-radiographic technique of density band analysis within the skeletal structure of colonies. The first method involves the estimation of calcification rates as an index of skeletal accretion. This is usually done either by direct measurement of calcium carbonate deposition or by using a "tracer" chemical which mimics the activity of the skeletal material being deposited. The measurement of isotopic ratios which are found naturally in the skeleton also form part of this approach. The many workers in this field have been reviewed at some length by Buddemeier and Kinzie (1976). Perhaps the principal value of these approaches is in the field of tissue/skeleton interaction, in conjunction with the algal symbionts present in hermatypic corals, with the ramification for coral growth studies in the growth *rate* sense being largely a by-product of the research. Certainly, they have led to a greater understanding of the interactive effect of environmental parameters with individual corallite chemistry.

The application of annual density band analysis in certain hermatypic corals by Knutson *et al.* (1972) has led to a widespread usage of X-radiography of coral skeletal structure as a tool for investigating coral growth rates. The density band patterns form a record of colonial growth in each coral, allowing historical assessments of growth response to environmental change, both in terms of linear extension variation and density fluctuation (daily, lunar, or seasonal). A summary of the applications of this technique to the field of coral growth rate studies is provided by Buddemeier and Kinzie (1976) who conclude:

> The development of the radiographic technique has rendered almost trivial the previously unsolved problem of measuring long-term growth rates and growth histories retrospectively. . . .

The standard reference to the procedure may be that of Buddemeier (1978).

Biology of Hermatypic Corals

The hermatypic or reef-building corals are characterised by the presence of large numbers of unicellular dinoflagellate algae in their endodermal tissues. These algae perform special functions relating to the skeletogenesis in the coral colony, and in return derive some special benefits themselves from the metabolic activities of the coral polyps (see Goreau *et al.* 1979).

The initial stage in the development of a sessile hermatypic colony is the settling of the planula, or fertilised ovum on a suitable, hard substrate. This planula then secretes a basal calcareous disc, upon which it builds a column of aragonite, or thecal wall. Finally, it secretes the internal skeletal elements distinctive to the species (septa, synapticulae, pali, dissepiments, etc.), and the colony grows by polypal replication either through intra- or extra-tentracular budding.

The simplistic model of growth above does not explain the chemico-physical nature of tissue growth and skeletal development in its complicated detail. While much is known about the algal/animal and tissue/skeleton relationships, the complete story is as yet unavailable. In simple terms, the tissue lays down aragonite at the sites of calcification as a result of the creation of a suitable chemical "climate" by both the polypal tissues and their algal symbionts. The dependence of skeleton formation on the zooxanthellae is the principal focus of interest in coral calcification, and is well reviewed by Johnston (1981). The relevance of this relationship to skeletal growth studies lies in the response of the alga to varying environmental conditions. In particular, the photosynthetic requirements of the zooxanthellae are light dependent, making that variable a controlling factor on the growth of the coral symbiont.

This study concentrates on *Porites*, a wide-ranging genus found in both the Atlantic and Indo-Pacific regions. It should be noted that no species of *Porites* is common to both areas. In the Great Barrier Reef Province it is found from the Solitary Islands in the south to the northern limit of the area, while on the west coast of Australia it is found as far south as Abrolhos Island (Veron *et al.* 1974). The colonies found at the extreme southern limits of the range are not as rounded or hemispherical as those further to the north, but tend to assume a flattened, encrusting layer on the substrate. As a genus, it shows two predominant growth forms, massive and branching (ramose), if the encrusting form is taken to be an aberration of the massive form. It possesses very small corallites (max. 2mm diam.), which divide extra-tentacularly. Highsmith (1980) also reports that heads of *P. lutea* may disperse and resettle on new substrates as a result of dislocation due to storms, etc. Glynn (1974) noted the existence of mobile *Porites* in the Gulf of Panama. (A few of these were collected from Heron Island for the purposes of this research.) Wells (1956) described *Porites* as one of the most important hermatypic coral genera, being second only to *Acropora*.

Influences on Coral Growth Rate

Coral growth rates can be said to be dependent on two broad groups of influences, environmental (exogenous) and systematic (endogenous). The first group includes such variables as depth, temperature, salinity, nutrient supply and other water qualities, sedimentation and turbidity. The second group encompasses species, size, colony age, and entrained biological rhythms.

It is the first group, the exogenous controls on growth, which determine the *limits* of the geographical range of the corals, and within these limits it is both the internal and external influences which determine growth rates. True scleractinian corals do not grow outside these environmentally imposed thresholds.

Environmental controls over coral growth have been well documented, and are summarised by Wells (1957), Stoddart (1969), and Buddemeier and Kinzie (1976). The application of the consequences of these factors to this study lies not so much in the environmental limits within which corals *will* grow, but how they respond to change within those limits. In this context the following physical factors will be discussed: temperature, depth, water chemistry, emersion, light availability, turbulence and sedimentation.

Temperature

The lower limit of temperature that hermatypic corals can survive for long periods is about 9°C (Macintyre and Pilkey 1969), with the upper limit at over 37°C (Orr and Moorhouse 1933). The limits vary with the species involved, some being more responsive to extremes than others. The mechanics of temperature control over coral growth are reviewed by Stoddart (1969) as being perhaps more concerned with control of reproductive ability rather than feeding or physiological death.

Early work showed that corals lost their ability to feed at certain upper and lower temperatures (Mayer 1915 and Edmondson 1929, respectively). The relative importance of each of these mechanisms (reproductive or feeding inhibition, or physical damage) is of less interest between the temperatures of 25°C and 29°C, the range of optimum growth conditions. In this range, the proportional effect of temperature on growth rate values is important. Weber and White (1974) found a growth/temperature coefficient of 0.9mm/yr/°C for *Platygyra* from various Indo-Pacific regions, using radiographic techniques. Weber *et al.* (1975) found that greater skeletal density was associated with lower ^{18}O content in annual coral bands, thus relating higher water temperature to an increase in calcification rate. An earlier paper by Weber on the incorporation of strontium into reef coral skeletal carbonate discussed the relationship between "growth" in the calcification sense and temperature, finding that, within the range of 20°C-30°C, calcification rates increased with temperature (Weber 1973). However, Clausen and Roth (1975a) showed that calcification in *Pocillopora* peaks at 27°C, and again at 31°C. Highsmith (1979) reviewed this point in relation to his own findings on Enewetak corals, and postulated that the preferred optimal temperature of zooxanthellar photosynthesis lies at about 27°C-28°C, and the rate decreases progressively at higher temperatures, with consequent results for coral growth. This may explain high density band formation in warmer water, an event he states is simultaneous with a low growth period in corals.

Many of the problems that have occurred in the investigation of coral growth rates and water temperature have arisen from the fact that all large-scale ecological studies encounter the dilemma of which temperature indicator to use. For example, average annual water temperatures, when used against measured growth rates, may not sufficiently account for variability and seasonality, nor even extreme temperature effects, to make valid conclusions. Some mention should be made of the different responses of unlike species to changes in temperature. Mayor (1924) subjected several different species of reef flat corals from Murray Island and Aua Reef to artificially produced high temperatures for various time intervals, and concluded that some corals were more resistant than others to upper temperature extremes. Among the more pertinent of his findings for this thesis was his conclusion that the larger massive *Porites* ("aff. *lutea*") were the most resistant Samoan coral to asphyxiation, dilution by fresh water and temperature rises of an extreme order. Salvat *et al.* (1977) reported that the only scleractinian extant in the isolated lagoon in Taiaro Atoll, Tuamotus, in fairly extreme physical and chemical conditions was *Porites lobata*.

Salinity

Many studies have investigated the effects of high and low salinities on coral survival, but few workers have tried to determine the effect of altering salinities on the growth *rate* of coral colonies. The literature to date has established that most hermatypic corals survive between 25 and 48 parts per thousand (extreme values).

Lowered salinities due to extremely heavy rain falling on wide shallow reefal areas has been documented many times as having severe physiological effects on corals. Mayor (1924) tells of the large areas of coral killed in Pago Pago harbour in June 1920, following heavy rains, although he makes no distinction as to the contributory effect of increased sedimentation. In the Great Barrier Reef area, Hedley (1925) reported the destruction of the Stone Island fringing reef near Bowen, Queensland, in a cyclonic episode in 1918, when almost 1400mm of rain fell in three days in Mackay, just to the south of the area. The tremendous dilution of the reef flat waters proved fatal to almost all the corals present. The results of this downpour are still to be seen today in the form of dead, high-standing microatoll formations on Holbourne Island, just to the north of Bowen (Hopley and Isdale 1977). Peel Island, in Moreton Bay, near Brisbane, was the scene of extensive coral damage when the bay was inundated with fresh water following heavy rainfall in 1956 (Slack-Smith 1960). Banner (1968) reported a similar event in Hawaii at Kaneohe Bay in May 1965. Lowered salinities and sedimentation were blamed for coral mortality.

Upper salinity limits are discussed by Kinsman (1964) from the Persian Gulf. He records that *Porites* can tolerate salinity levels in lagoonal areas along the Trucial Coast of up to 48 parts per thousand. Coles and Jokiel (1978) examined the effect of altered salinity on growth in *Montipora* in conjunction with temperature variation. They showed that the temperature tolerance of the coral is lowered as salinity drops, and postulated that the reverse is true, since Kinsman (1964) described Persian Gulf corals living in temperatures of 49^{o}C at up to 48 parts per thousand salinities. These findings do not, however, show the relativity of salinity alone to growth rate, and this relationship remains obscure.

Depth

The physical parameter of depth is a compound variable, representing the effects of light penetration, water movement, food availability and other factors. The lower limits at which hermatypic corals grow and survive are generally agreed to be those at which the availability of light does not attain the threshold requirements of the symbiotic zooxanthellae for photosynthesis. The variability of growth rate and form in the surface layers of the ocean (down to 15m) is thought to be influenced by variables other than light levels. Below this depth, most corals show a decrease in growth with depth. Wells (1957) gives the maximum survival depth of hermatypic corals as about 90m, with most corals growing above 50m, and the most luxuriant growth being above 20 metres.

While most of the early work on the relationship of coral growth to depth was concerned with the variation in form of the corals, later efforts have concentrated on determining the relativity of depth to such factors as linear growth, calcification rate, density variations within the coral skeleton, and rates of photosynthesis. Within the context of this thesis, which is mainly concerned with skeletal extension rate, the results of various workers have shown that growth is species dependent or dependent on local environmental factors above about 15 metres (Buddemeier and Kinzie 1976). More specifically, Buddemeier *et al.* (1974) suggested that the growth rate of *P. lutea* from Enewetak Atoll was less than half the rate at 30 metres than it was at 4 metres. At depth 18m, they found that the same species grew almost twice as slowly as it did at 7 metres. Baker and Weber (1975) reported that the rapid fall-off in growth rate at 18m of *M. annularis* in the Virgin Islands was accompanied by a significant reduction in growth rate variance. Other researchers have found that some species do not show a significant decline in growth rate below any specified depth. Weber and White (1977) showed that *M. cavernosa* does not respond to depth increase, while *M. annularis*, which is a faster growing species, does. Buddemeier *et al.* (1974) reported that *Favia speciosa* from Enewetak showed no systematic variation with depth. Highsmith (1979) suggested the reason that different species are affected differently by depth may be a function of the corals possessing different zooxanthellar strains, which have unlike responses to the depth-dependent decrease in light levels.

Other Controls

Water turbulence is considered to be an important influence on coral growth. Rapid movement at the air-water interface results in oxygenation of surface waters, such an effect being demonstrated by the higher oxygen supply available in surf zones. In some species, however, heavy turbulence may have an inhibiting effect on growth through disruption of feeding activity. The corals most affected would be those with small corallites, such as *Porites*. Turbulence was considered by Milliman (1974) to prevent siltation, a function which aids the deeper-polyped corals such as the Favids. The distribution of the *Porites* biotype in Rosen's (1975) model for Indo-Pacific corals seems to support this suggestion.

Turbidity affects coral growth rate principally through reduction of available light to the algal symbionts of the coral. Dodge *et al.* (1974) and Aller and Dodge (1974) found an inverse correlation between growth rate of *Montastrea annularis* from Discovery Bay and the resuspension of bottom sediments. Heavy siltation has a species-dependent effect on growth. Some genera (e.g. *Porites* and *Fungia*) have very effective sediment removal capacities, while others such as *Pocillopora* do not. The death of the latter species on Middle Reef in Cleveland Bay (North Queensland) due to the effects of sedimentation from the dumping of dredge spoil to windward of the reef, and the continuing vitality of *Porites* microatolls in a similarly affected area on Magnetic Island bears this out.

Many of the above environmental controls act synergistically, with consequent problems for the researcher interested in assigning levels of responsibility for growth rate influence to each. For example, available light may be a function of depth and turbidity, while turbidity in turn may be related to water turbulence. The breakdown of environmental causation is thus often difficult to ascertain with accuracy.

Systematic Controls on Coral Growth

Endogenous (internal) controls on growth rate have not been studied extensively to date. Among the earliest references to the subject of determinacy in coral growth, Wood-Jones (1910) regarded growth as being indeterminate, while Vaughan (1915) and Mayor (1924) thought that corals reached growth limits. More recent workers have postulated that certain species exhibit genetic limitations on colony size (Goreau and Goreau 1960; Maragos 1972). Size-growth relationships have been noted (Motoda 1940) in terms of polyp multiplication rate, and geometric constraints (Barnes 1973), while Grigg and Maragos (1974) noted determinate growth in *Pocillopora*. Buddemeier and Kinzie (1976) summarise the topic, pointing out that the new retrospective methods of growth rate analysis (such as X-radiography) show that there is no decrease in rate with age in the massive corals. They illustrate the difficulty of verifying the existence of size/growth rate relationships by noting that conventional laws of growth based on volumetric reasoning do not apply to corals, whose growth vector, the coral tissue, is largely two-dimensional, being a flattened layer of material arranged on a skeletal surface. Thus they state:

> . . .corals may exhibit determinate growth, but it is unlikely to be predictable or rationalizable on the basis of conventional growth laws. Secondly, the problems of inherent variability and environmental effects on coral growth greatly complicate observations and interpretations.

Aims of The Study

This study examines the geographical distribution of the mean annual growth rates of 452 coral colonies from the Great Barrier Reef Province. It seeks to answer questions on the distribution of those rates at a number of scales: provincial, regional, single reef scale, and microhabitat within the single reef area. It also attempts to use year-to-year variances in growth rate in conjunction with historical environmental data to investigate external controls on growth.

The importance of the problem of scale is emphasised. The variability of annual skeletal extension rate is analysed, from the smallest to the largest scale, since this statistic usefully delineates geographical/ecological boundaries within the ecosystem.

The thesis examines the growth rates of colonies from the entire length of the Great Barrier Reef Province. Several benefits accrue from having such a large sampling area. One of these is that the Province covers a large latitudinal range, from the Torres Strait, at about 10^{o}S, to the Capricorn-Bunker Group, around 24^{o}S. This range encompasses several different climatic types and is within the ambit of movement of several discrete bodies of water from oceanic sources. These factors provide a range of environments within which to examine the response of coral growth rates to changing external influences.

Another feature of the Great Barrier Reef Province which makes it ideal for an extensive geographical/ecological sampling programme is the varying width of the continental shelf along the north-south axis. Thus, the effects of such factors as distance from landward influences and oceanic waters may be weighed in relation to each other, as well as in absolute terms. Sincethe shelf width ranges from about 24 kilometres in the north, at its minimum extent, near Cape Melville ($14^{o}10'S$), to 200 kilometres wide, east of Mackay, in the region of $22^{o}S$, the degree of influence of each factor can be judged with relative ease.

The range of climatic variables, and water quality and properties over the whole extent of the Province is quite large. For example, the northern region around Cape York has a monsoonal wet-dry (Koppen's Awg,Aw,Am) climate, while the the Capricorn-Bunker Group in the south has a subtropical (Koppen type Cw) climate.

The range of monthly mean minimum temperatures is more than $5^{o}C$ for the Province, that of monthly mean maxima more than $12^{o}C$ (see Pickard 1977, Figure 6). Mean annual rainfall is between 600-1800mm/yr in the Cape York area ($10^{o}S$), peaks at about 4000mm/yr on the Innisfail coast ($17\frac{1}{2}^{o}S$), and drops to around 1000mm/yr at the southern extremity of the Province (Pickard 1977, from Figure 7). Sea surface temperatures of $29^{o}C$-$30^{o}C$ occur around Cape York in January, dropping to just above $24^{o}C$ in August (ten year average temperature field for each month—CSIRO 1979), while the same figures for the Heron Island area are $27^{o}C$-$28^{o}C$ in January and $21^{o}C$ in September (CSIRO 1979). The ten year average salinity fields for Cape York show a range of from 35.6 parts per thousand (October-November) to 33.6 parts per thousand (March-April) The equivalent figures for the Capricorn-Bunker Group are 35.5 parts per thousand (August-September) and 35.2 parts per thousand (April, October) (CSIRO 1979).

This wide range of environments allows systematic conclusions to be made from correlative studies between growth and growing conditions. The problem of comparing growth data from global scale differences in location (e.g. high rainfall period in Florida with the monsoon season in the Indian Ocean) is avoided, since the environmental "zones" of the Great Barrier Reef Province are contiguous.

The colonies used in this research were all of the genus *Porites* Link, 1807. Of this genus only eight species were collected, those which formed hemispherical, massive colonies. The genus is widespread throughout the Province, and this allowed comparisons to be made between growth rate values of colonies in the certain knowledge that the conditions for growth are well within the environmental range for the whole genus.

Porites is a finely structured, relatively porous coral in its massive growth form. It is also fairly slow growing when compared with the branching forms, such as *Acropora*, although its growth rate (linear extension) is greater than some of the Favid corals, which are denser. It is the fine structure of the genus which makes *Porites* ideal for X-radiographic studies, since the analysis of the X-ray plates is not confused by the intrusion of skeletal element images, as would be the case with some of the larger-structured Favid corals.

The regular hemispherical or semi-hemispherical shape of the selected species proved a definite asset in colony preparation for X-radiography. The objective of X-raying the colonies was to determine the full spectrum of annual density bands (see Chapter Two, Densitometry). Cutting of each colony required that the finished slab contain all the density bands, from origin to edge. This was facilitated by the rounded, symmetrical shape of the coralla, clearly identifying the point of origin of growth. Irregularly shaped colonies were not used, nor were those that had been severely bored by bioeroders (see Chapter Two).

In summary, the genus *Porites* was used exclusively in the programme because of its ubiquity, structure, and suitability of shape for dissection and X-raying.

CHAPTER TWO

METHODOLOGY

Introduction

In this study, the methods of investigation employed comprised three main components. These were:

(a) fieldwork;

(b) laboratory analyses; and

(c) statistical analysis.

The relative timespans allocated to each of the above were dictated by the immensity of the study area, and its inaccessibility, and reflect the large period of time needed to assemble the corals, and the handling of the colonies in sectioning and screening them. The high cost of transport to the areas of collection required that a certain degree of opportunism appear in the sampling procedure, entailing the availing of ship-time on the expeditions of other scientists.

Fieldwork

The study of geographical variation in growth rates of corals necessitated the sampling of colonies over as wide an area as possible, in order to be able to investigate patterns in as large a range of differing environments as was essential to show up the main external factors influencing that growth. Therefore, at various scales of intensity, sampling was undertaken over the complete latitudinal extent of the Great Barrier Reef Province, from Port Moresby in the north to Heron Island in the south (see Location Map,

Figure 2.1). Several colonies were kindly supplied from Noumea (see Acknowledgements), enabling growth pattern comparisons from a different seasonal regime to be made with Great Barrier Reef corals.

At the next smaller scale of sampling, the study required comprehensive samplings along lines or transects across the Province in an east-west orientation, over the continental shelf. This was intended to ascertain the relative effects of distance from oceanic and terrestrial influences on growth patterns. On a smaller scale, collections were made from single reef units on an intensive basis, with the reefs chosen to represent the greatest diversity of geomorphological types. Three reefs in this category were sampled, these being Three Isles (a low, wooded island reef), Wheeler Reef (a small platform reef), and Barnett Patches (a dispersed pattern of resorbed reefs). The intention of the examination of these reefs was to find if colony growth was in any measure affected by the type of reef on which it grew. Different reef types in both plan and profile cause different micro-environments to occur within their boundaries, as exampled by the fact that the height of a reef flat relative to mean sea level (MSL) influences the direction and intensity of the current regimes about it. At the smallest scale of all, collections were made from a small (15m diameter) reef crest pool on Fairey Reef, all of the same species. The rationale behind this activity was the investigation of the assumption that similar corals in a uniform environment should show similar patterns of growth in time, having negated the effect of space.

In each location, colonies were taken by hand using scuba or shallow diving, or were collected at low tide (Figure 2.2). With the exception of the collection on Fairey Reef, sampling was generally

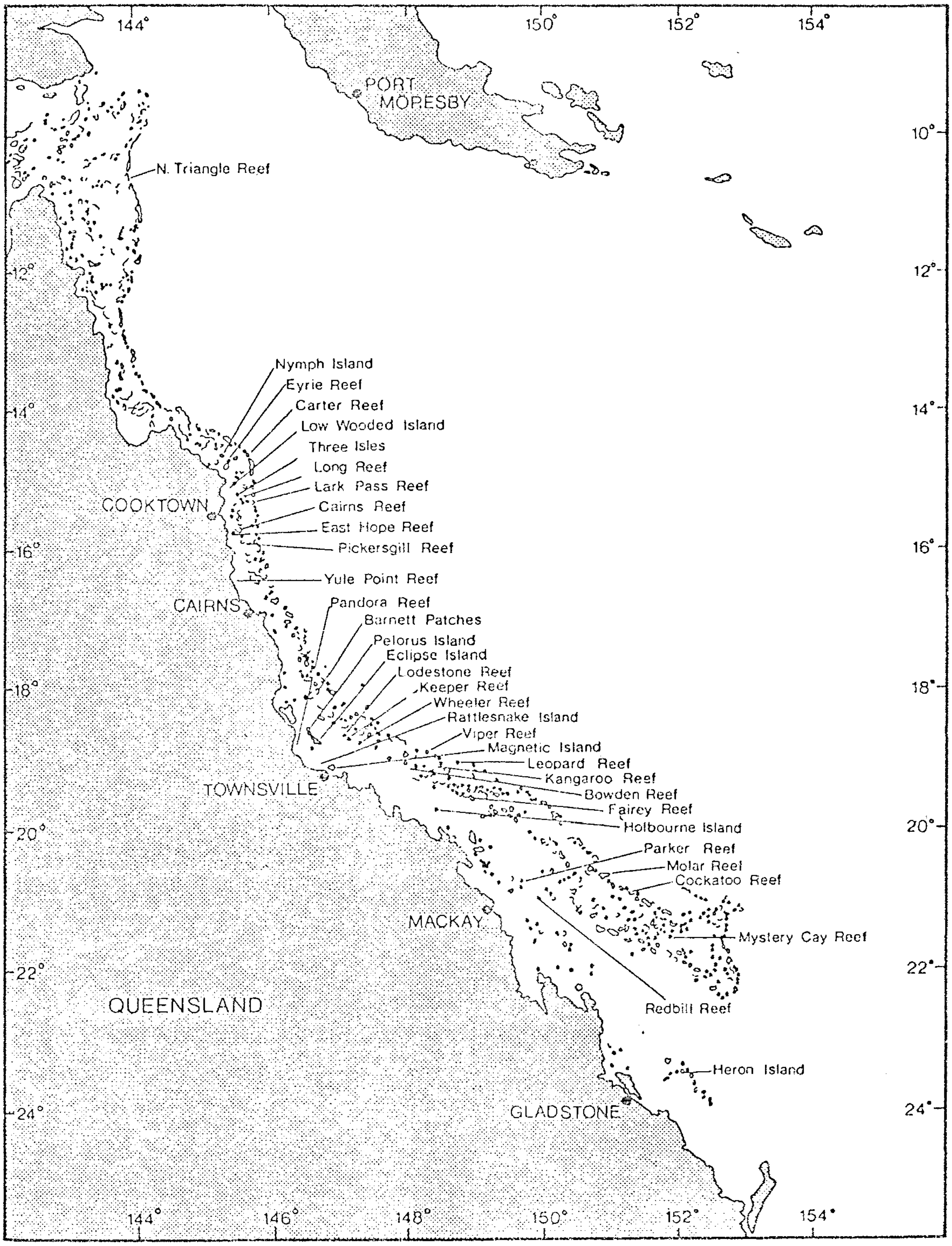
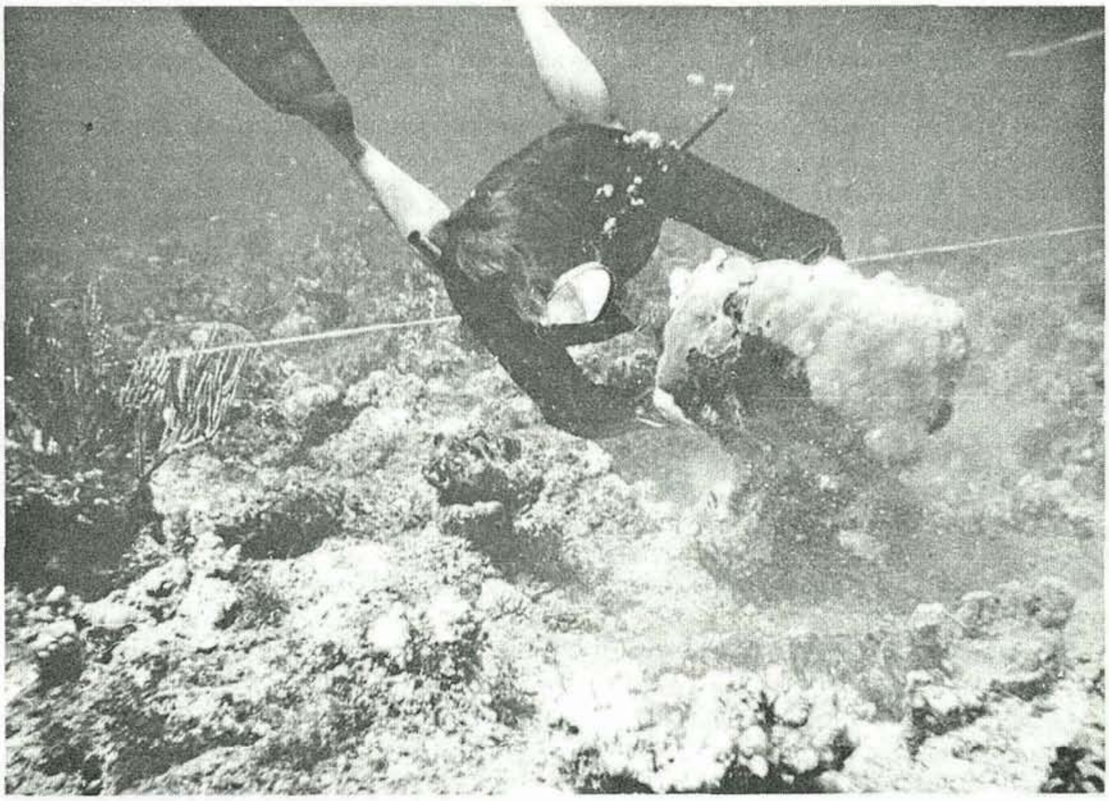
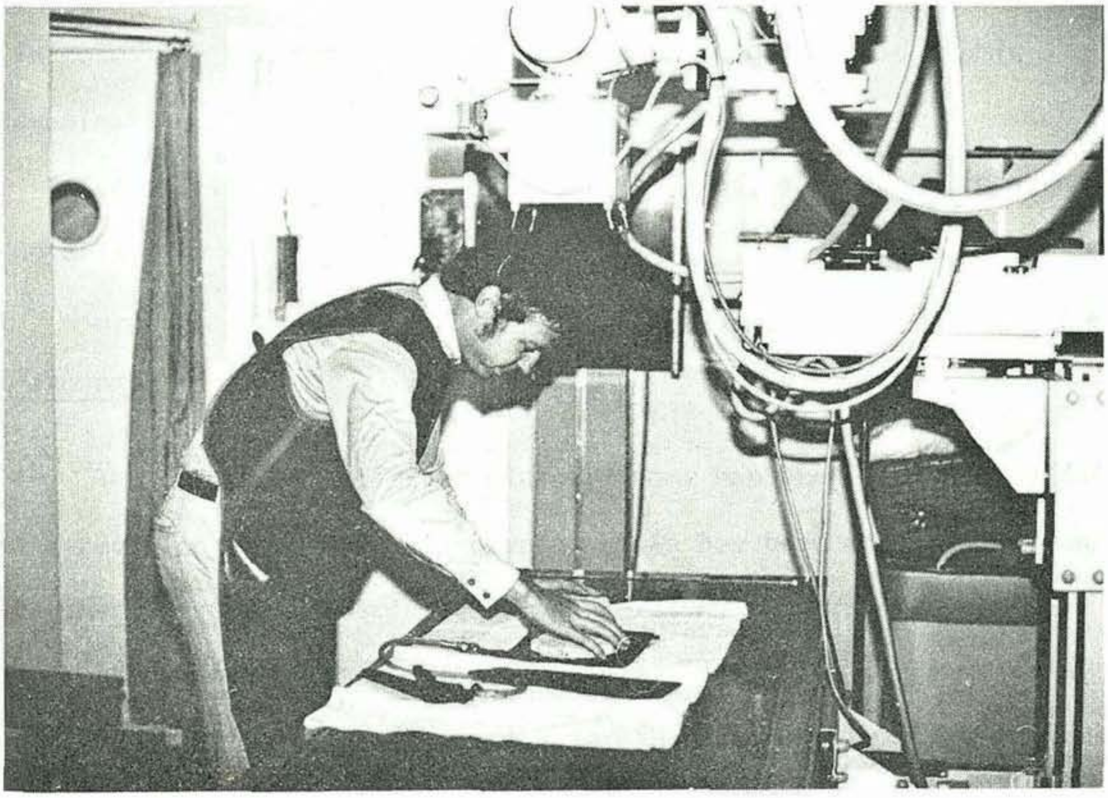


Figure 2.1 Location Map—Collection Sites from the Great Barrier Reef Province

Figure 2.2 SCUBA Collection of Massive *Porites* from Reef Top.

Figure 2.3 X-raying Coral Sections with Medical Radiography Machine





confined to areas of about 50 square metres. The selection of individual colonies was opportunistic since no field identification of *Porites* could be done at the specific level (see Taxonomy section). The main limitation on taking a colony was that of size and shape. Colonies more than about 35cm in diameter were too big to section using the available equipment, while colonies which were exceedingly asymmetrical provided growth interpretation problems. This latter point is discussed in detail below. Initially, some Favid corals were taken, but this practice was discontinued as it became obvious that the skeletal "grain" of the family was too coarse for the densitometric technique. This was because of the minute size of the maximum beam width obtainable on the machine, it being several millimetres smaller in diameter than that of the corallites in the Favid family. The finer structure of the Poritidae proved superior in resolving the density banding patterns under X-radiographic examination.

Descriptions of every field site sampled, along with relevant details, are given in Appendix A.

Taxonomy

The history of scleractinian taxonomy has been attended by debate and revision throughout its course. This has been principally due to the nature of the scleractinian skeleton, which shows an extraordinary degree of structural variation. It is the range of this variation that creates difficulty for the taxonomist, since the specific "boundaries" are often hard to define due to the overlapping of principal skeletal characteristics. Veron and Pichon (1976) have reviewed the history of the species problem, and Veron (1981) the present state of thinking on variation within species boundaries.

Their use of the "ecomorph" approach to taxonomic differentiation has led to the divisions used in the present study. Although the genus was first described as such by Link in 1807, the first references to the group may have been those of Pallas (1766), in which an assortment of corals from a now lost collection were called *Madrepora porites*. Link described two species, *Porites polymorphus* and *Porites damicornis* (the latter is now known to be a *Pocillopora*), but since then over 100 nominal species have been added to the list. Bernard (1905) provided the first world-wide comprehensive study of the genus, but was unable to distinguish species, and abandoned the binomial system of classification in favour of a numerical one based on geographical location. The difficulty of classification of the genus is well described by him:

> So great, indeed, is its apparent complexity, showing so many subtle differences which baffle all attempts to define or describe them, that the student stands long before the task in despair.

Vaughan (1918) reverted to the binomial system in his revision of the genus, and his published work remained the best of its kind for many decades. The last revision of the taxonomy of the genus has been that by Veron and Pichon (in press). The results of this revision show that in Eastern Australia there are four groups within the genus, based on the structural similarities of their corallites and their colonial formations. Within the Great Barrier Reef Province there are 13 species of the subgenus *Porites*. Of these six form massive, generally hemispherical colonies of large dimensions, four form small hemispherical colonies, two are branching species, and two form flat plates or columns. These are widely distributed in the Province in the northern and central regions, but the number of species represented falls off south of the Great Barrier Reef, so that Moreton Bay has two species and Solitary Island and Lord Howe Island (both in New South Wales) have only one each.

For this study, eight species were used. They were:

P. lobata Dana 1846

P. australiensis Vaughan 1918

P. lutea Edwards & Haime 1860

P. mayeri Vaughan 1918

P. densa Vaughan 1918

P. murrayensis Vaughan 1918

P. solida (Forskal 1775)

P. lichen Dana 1846

Porites lobata is massive, hemispherical and generally forms large colonies. It has a very porous theca and each corallite possesses three discrete paliform lobes per trident or triplet.

Porites australiensis is another massive species, similar to *P. lobata*, although the colonies may be "ribbed" or angular in a jelly-mould formation. It has angular calices and thin razor-edged theca, with deep, fused triplets and a single paliform lobe. The columella points to the trident and the directive.

Porites lutea is another large hemispherical species with a much denser theca than the above. It has one high paliform lobe per triplet (which is fully fused), and a deep conspicuous synapticular ring. It lacks a columella.

Porites mayeri is similar to *P. australiensis* except that it has smaller columellae, thicker thecae and larger paliform lobes. *Porites densa* usually forms smaller hemispherical colonies and possesses very thick thecal walls, with small, rounded corallites.

Porites murrayensis is another small massive species, with deep, hollow calices, inconspicuous columellae and very tall pali. *Porites solida* is one of the larger massive species of the genus, and is distinguished by its large corallites, absence of paliform lobes, and free-ended triplets. *Porites lichen* is a massive, submassive or encrusting species. It is also distinguishable from the other massive species by its corallites sometimes being arranged in rows or valleys.

There were several colonies collected which did not fit any of the above descriptions, and these were not used in the study.

Corals were not collected in order to define the range of any particular species, but collections were opportunistic, with only those species noted above being used. The identity of these species was determined using the criteria established by Veron and Pichon. One of the major difficulties encountered in identifying each colony was the fact that all colonies had to be examined under a stereo-microscope. Owing to the small size of the corallites (0.5-2.0mm), no field method of identification was found to be sufficiently reliable.

Specimen Cutting

Using a very large diamond saw (50cm diameter), each coral colony was sectioned so that a vertical slab about 10mm thick remained, from the centre of the colony. The slab was taken from the vertical axis of greatest dimension, and incorporated the nodal point of growth on the underside of the colony. It was then presumed to contain every radial growth feature in the life history of the corallum. In cases where the exact origin of growth on the colony could not be identified due to boring or encrusting organisms, the base of each colony was carefully shaved away until the concentric circles of banding (algal and depositional) could be identified. After the sections were cut, they were rinsed and scrubbed in fresh water to remove the fine products of abrasion during cutting, and allowed to dry.

X-Radiography

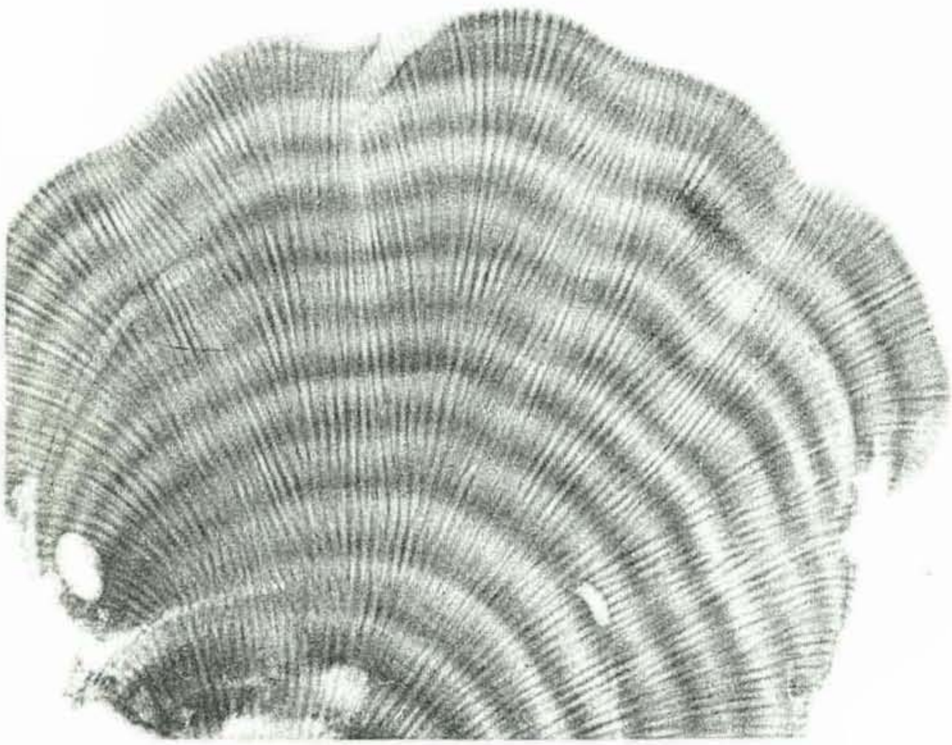
X-radiographic images of the specimens were made on a Konrad 600, 3-phase, 6 valve, medical radiography machine (Figure 2.3). Following experimentation to establish the optimum technique which showed the skeletal banding and fine structure at its best, the exposures were made with fine focal spot, with the beam coned to object size, at an object-to-filament distance of 100cm. This large distance allowed the incident beams to be as parallel as practicable on striking the film. The film type used was DuPont Cronex "LoDose" Mammography film. Exposures were made at 52KvP/150mAs. The films were then developed at 35°C in a Kodak MN6, 90 second automatic developer. The resultant plates were thus in negative format, and showed regions of high density as light bands, and low density areas as dark bands (Figures 2.4a, b, c).

Densitometry

Since the aim of the study was to measure only the annual growth increments of each colony, it was not considered necessary to undertake quantitative density measurements on each band of each colony. These would have been desirable in calcification determinations, rather than linear growth measurements. The density of a particular band is essentially a function of calcification and

Figure 2.4(a) X-radiographic Positive of *Porites* Section from Viper Reef Showing Annual Density Banding. (X 0.8)

Figure 2.4(b) X-radiographic Positive of *Porites* Section from Leopard Reef. (X 0.6)



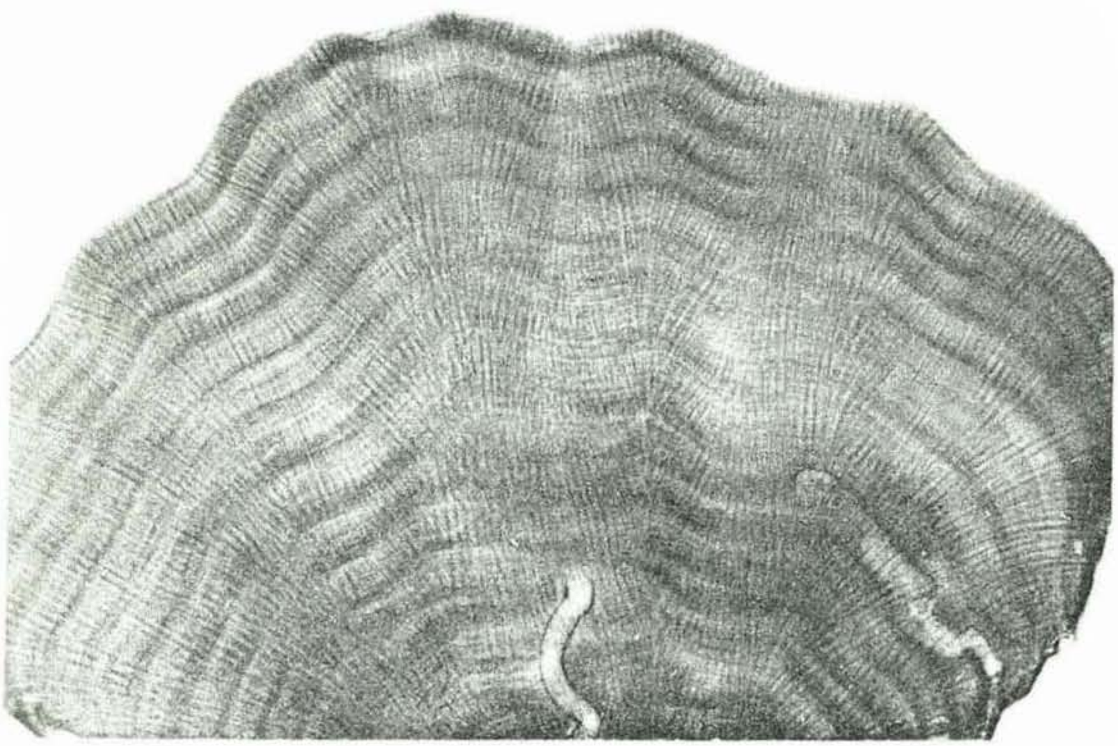
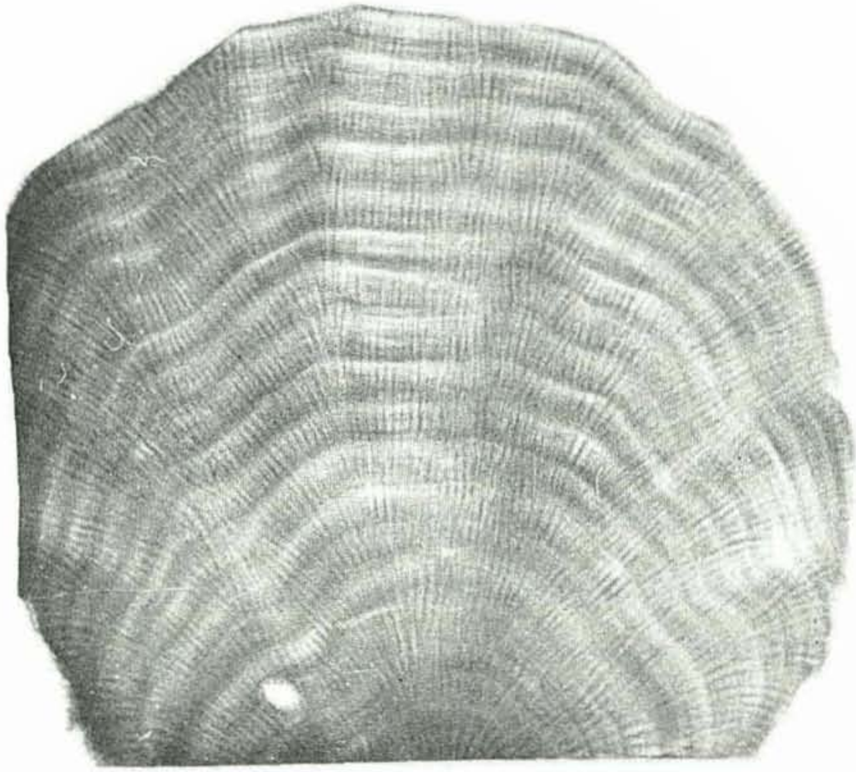
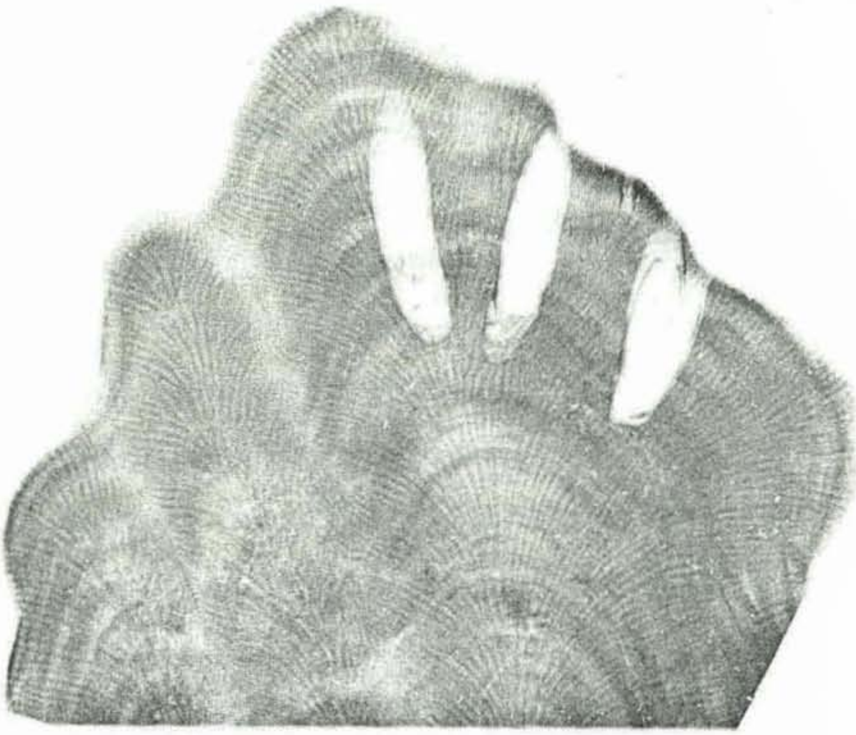


Figure 2.4(c) X-radiographic Positive of *Porites* Section from Lark Pass Reef. (X 0.6)

Figure 2.7 X-radiographic Positive of Poorly Banded *Porites* from Parker Reef. (X 0.6)





and skeletal extension, although it must be realised that high density is not only the product of rapid calcification and low extension rate. It can readily occur where calcification is carried out at particular sites in the skeletal matrix (as in the case of very dense crystal packing) at normal rates of deposition and extension. This phenomenon is examined in greater detail later in this chapter.

The dimensions of each annual increment were measured using only qualitative density pattern analysis. To do this, each X-radiograph was scanned with a Joyce-Loebl MK 111 CS double-beam recording microdensitometer. On this machine the beam slit-width was set at 2.0-3.0mm. The greatest possible movement ratio between the beam and the recording carriage was used, so that while linear exaggeration was usually X2, a ratio of X5 was sometimes possible with smaller specimens. Each plate was scanned along the axis of maximal growth, from the outer surface of the corallum to the point of origin of growth. It was felt that the use of several scan lines per colony was unnecessary, as the parameter of most importance to the exercise was maximum growth possible for the colony in any year. To avoid the problem of spuriously high growth rates being taken as representative of colony growth as a whole due to exaggerated asymmetry, those colonies with extremely elongated profiles were not used. In all cases then, the maximum growth axis remained relatively similar in dimension to the "average" growth axis. Where extreme lenticular development was found on the surface of a colony, the axis of maximum extension was taken to finish at a point on an estimated smoothed surface, and this fact noted on the graph output from the densitometer. Most densitometer traces showed a series of distinct peaks and troughs (Figures 2.5a, b). Some

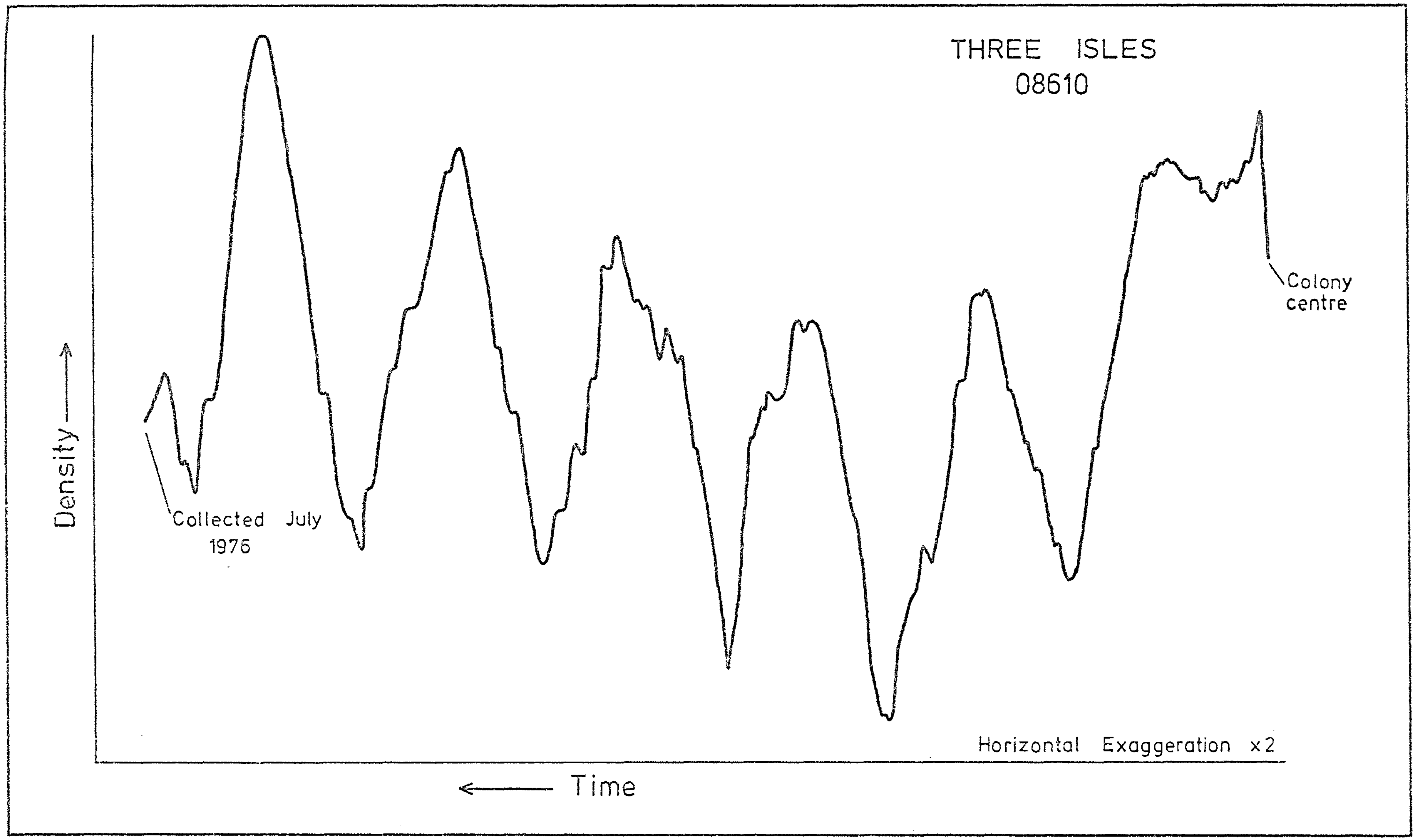


Figure 2.5(a) Microdensitometer Trace of *Porites* X-radiograph from Three Isles

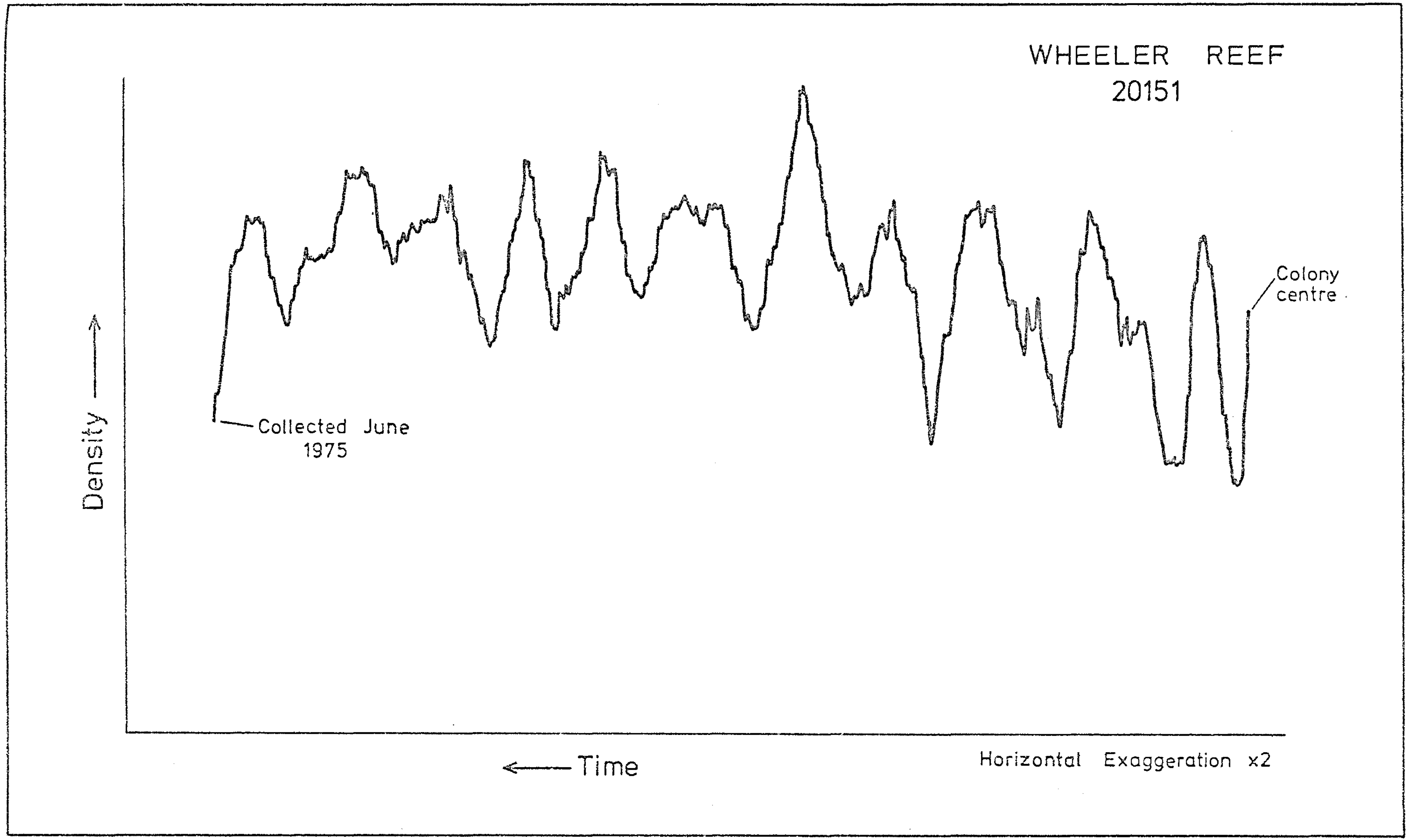


Figure 2.5(b) Microdensitometer Trace of *Porites* X-radiograph from Wheeler Reef

showed small scale serrations corresponding to fine structural features of the skeleton (Figure 2.6). These were in no case large enough to mask the large density variations in the skeleton indicated by the traces. Minimisation of the prominence of these small irregularities was facilitated by using the maximum slit-width possible on the densitometer, in order to average the scan path over several corallite diameters. Some traces did not show readily recognisable sequences of high and low density banding, reflecting a lack of density contrast in the original corals (Figure 2.7). The reasons for this lack of contrast could not be determined. These corals were of no use to the study and were discarded. The traces were unreliable at the very edge of the specimen image. When the slabs were X-rayed, the outer growth surface of the slices was seldom parallel with the incident X-ray beam. Thus, only where the beam passed through the full thickness of the slice was the image truly representative of skeletal density. This error was compounded during densitometry, as the entire beam had to pass through the image at a point representative of the full thickness of the coral slice before a valid reading was obtained. The absolute dating of the density features within the skeleton depended on the date of collection, represented by the growth surface at the edge of the colony. Thus, although for most of its length each trace gave sharp indication of the points of maximum and minimum skeletal density, it was often difficult to relate directly those features to the beginning of the trace.

Interpretation of Measurements

In all the X-radiographs, the last obvious feature before the growth surface was related to the recorded date of collection. From

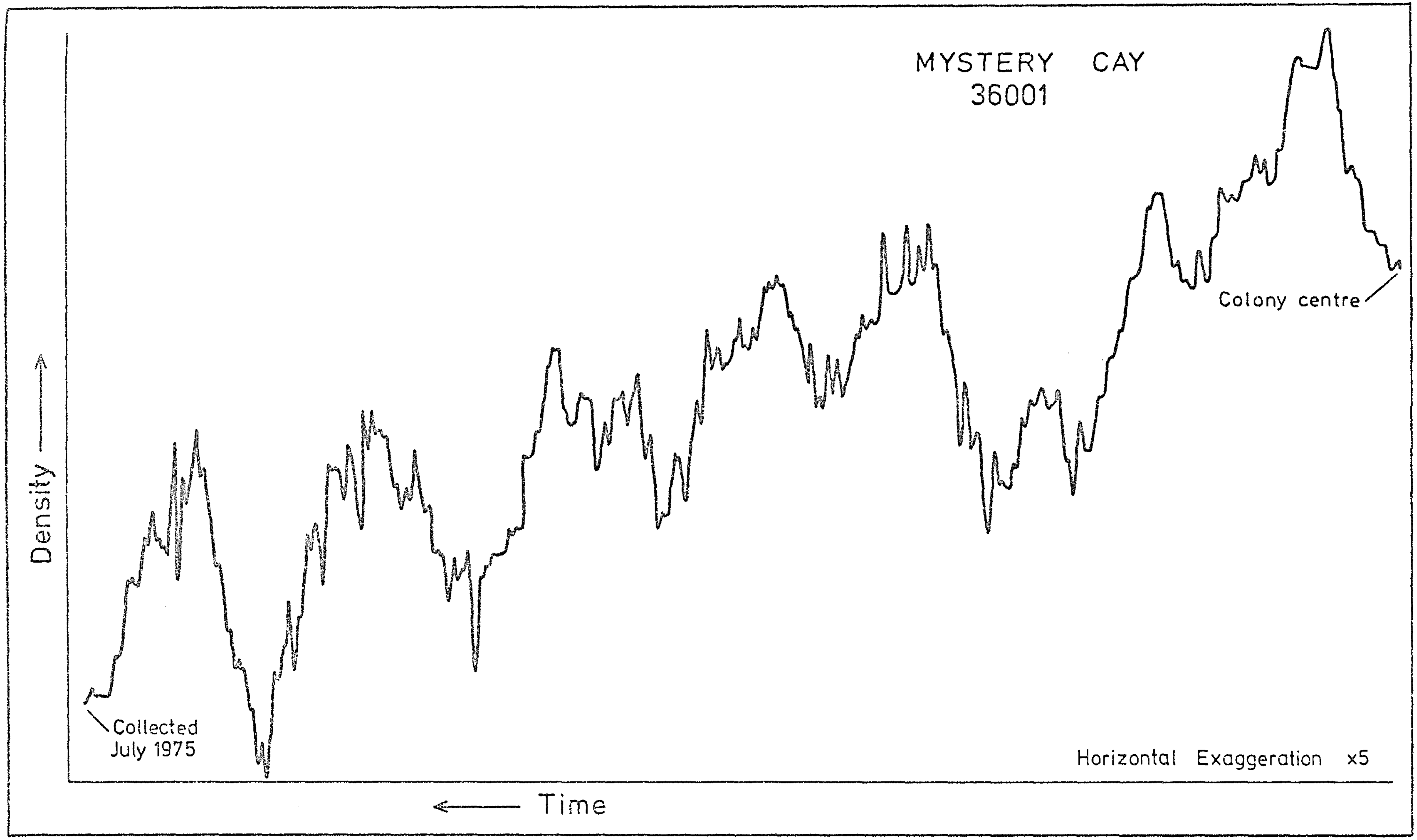


Figure 2.6 Microdensitometer Trace of *Porites* X-radiograph from Mystery Cay Reef, Showing Fine Scale Skeletal Structures as Serrations

interpolated analyses, allied with results obtained from vital staining experiments, it was found that in almost every case the density peaks occurred in the later summer months, and the lows in late winter. Some minor departures were noted, arising perhaps from an inability to read the exact nature of the density band at the colony growth surface. A gradual shift in the time of deposition of density bands was also noticed as the latitude from which the coral was collected changed. This feature is discussed in Chapter Five. All the traces were analysed using the last detected low density (LD) band as a marker to represent the winter months prior to collection. In this fashion, all the skeletal features of the colonies could be dated.

Annual growth increments were determined by measuring the real distance between the LD extremes (winter minima). It will be remembered that the densitometry techniques employed ensured that these values represented the optimal annual radial extension rate of the colonies.

Staining Experiments

When the investigation was started in 1975, it was felt that some verification of seasonality in density banding was necessary. Accordingly, following the method used by Barnes (1972), several large colonies of *Porites lutea* in a large shallow pool at Geoffrey Bay, Magnetic Island, were selected for staining. The programme entailed 24-hour Alizarin incubation periods at the extreme spring tide range during the months of April, August, and December in each year of a three-year period. Unfortunately the stains could only be laid in April 1975, April 1976, August 1976, December 1976, and April 1977. This spread of dates was sufficient, however, to allow the correlation of density band types with time of year. The results of the experiment are shown in Table 2.1 (including real growth increments for the largest colony).

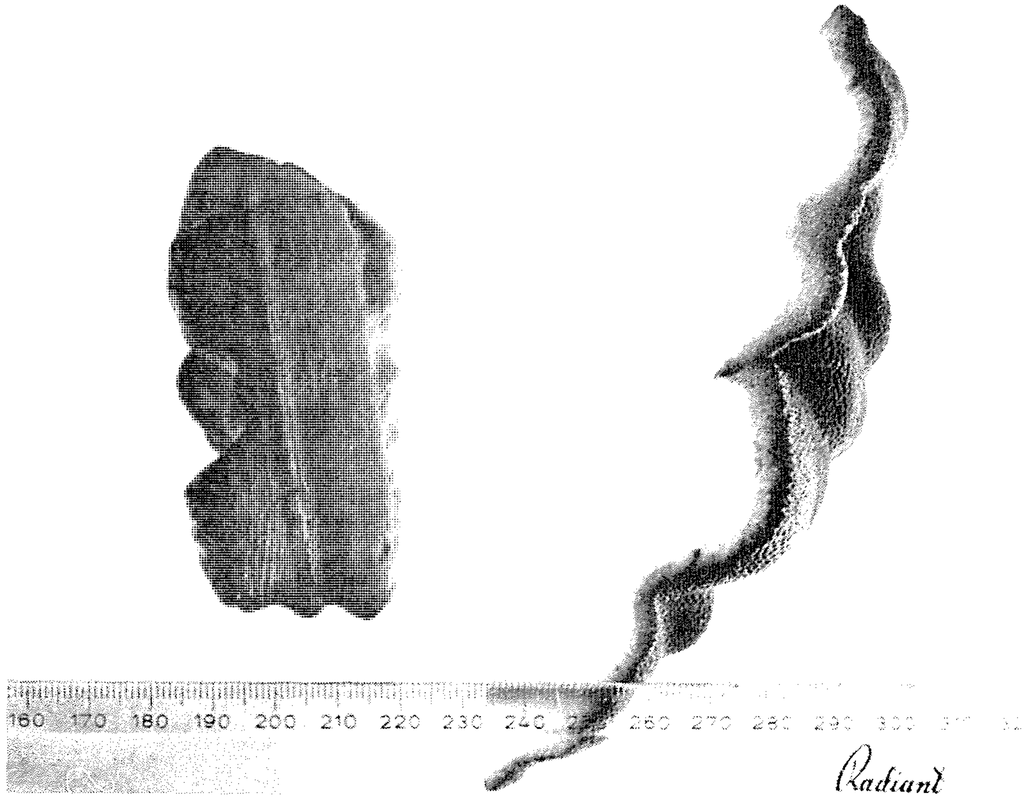
The technique used in the Alizarin experiment is described in Barnes (1971, 1972) and in Lamberts (1974). Alizarin is a substance (sodium alizarin sulphonate) which can be incorporated into the coral's skeleton during calcification. It is deposited at the site of calcification and is an accurate measure of calcification activity in the skeleton (Lamberts 1974). The present use of the Alizarin dye method was not to measure calcification, but to insert skeletal time markers in the coralla, to correlate afterwards with X-radiographically determined density bands. The intertidal colonies of *Porites* were bagged *in situ* at low water spring tide, and about 5 grams of Alizarin powder introduced into each bag (estimated volume = 4-$5m^3$), and well mixed by agitation. The bags were left on the colonies through two full tidal cycles, then removed.

The colonies were sectioned and X-rayed in April 1979, and showed five very distinct red bands in their skeletons. Figure 2.8 shows band after one year from a colony. Two staining periods showed as very heavy red bands, while the remaining three were lighter in colour. No reasons could be given for this difference. The finest line (April 1976) was less than 0.5mm in width, while the heaviest (April 1975) was more than 1mm wide. The correlation between the position of these red bands and the type of density band in proximity to each of them allowed accurate determination of the month of density band deposition. The mean annual growth rate of this colony during the experiment was .83cm/yr.

The experiment at Magnetic Island confirmed the seasonal nature of density banding in the corals. High density (HD) bands were

Figure 2.8 Wedges from *P. lutea* Colony, Geoffrey Bay, Magnetic Island, Showing Skeletal Increment During One Year Following Alizarin Staining.

Figure 2.9 X-radiographic Positive of *Porites* Section from Moated Reef Flat, Holbourne Island, Showing Sub-Annual Fine HD Bands. (X 0.5)


160 170 180 190 200 210 220 230 240
260 270 280 290 300
Radiant

formed between October and March, while low density (LD) bands were laid down from April to September. The importance of this is discussed in later chapters. It is essential here to differentiate between growth (volumetric and linear), and gross calcium carbonate deposition. In almost every colony used in this investigation, the LD band occupied the major proportion of the width of each density pair-band. A very few colonies excepted to this rule, and these showed extremely slow and consistent growth overall. The average proportion of HD to LD skeleton in the colonies was 1:3. This would seem to indicate that the greater part of the annual linear expansion of a colony took place in the winter half of the year, but it says little about the seasonality of calcification, since the relationship between the two variables is not clearly understood.

It proved possible, however, to make some statements on this problem, based on observations made on some intertidal *Porites* micro-atolls from Holbourne Island, north of Bowen, in North Queensland. These colonies have been described in the literature in relation to their function as indicators of changes in reef flat morphology (Hopley and Isdale 1977). When sectioned and X-rayed, these showed very fine pair bands within the larger annual scheme of density pair-bands (Figure 2.9). There are 13 or so fine pair bands in every annual pair-band, indicating a lunar periodicity. These fine bands may approximate the periodicity reported by Buddemeier and Kinzie (1975), although they found that fine structure variation was closely associated with fine LD bands, in a lunar cycle.

Interpolation of the spacing of these fine bands reveals that only about one third of the total linear growth in a year is comprised of the major HD band, this being laid down from October-November to about March. The remaining months of the year show LD

TABLE 2.1: RESULTS OF STAINING—MAGNETIC ISLAND CORAL

Date of Staining	Growth Increment	Density Characteristics
April 1975		slightly before minimum density
	9mm	
April 1976		almost at minimum density
	1.5mm	
August 1976		between maximum and minimum density
	2.5mm	
December 1976		at maximum density
	5mm	
April 1977		between maximum and minimum density
	7mm	
April 1978 (colony surface)		difficult to read, but close to minimum density

banding. Since the relative HD-LD absolute density figures were not measured, it was not possible to ascertain the period during the year when the highest gross amount of skeletal material is laid down. However, results from elsewhere (Highsmith 1979) suggest about equal deposition of calcium carbonate in each period.

In summary, the staining experiments relied on existing techniques to verify the seasonality of density banding. These methods were quite suitable for time marker inclusions several months apart in the field, but would not have suited monthly stainings in fieldwork, chiefly due to the width of the Alizarin line deposited in the skeleton. The utilisation of the fine lunar pair-bands found in intertidal colonies effectively solves the latter problem.

Statistical Analysis

Of the more than 1000 colonies collected, the majority were rejected for study, for reasons described earlier. In all, only 452 colonies were deemed suitable for analysis. Statistical investigations of the growth data were performed on the James Cook University of North Queensland's DEC-System 10 computer. The growth data recorded on the microdensitometer traces were coded onto cards and read to disk. The following identifiers were placed with each colony data: reef code; latitude; shelf zone; reef zone; depth; date of collection; species.

The *reef code* developed for the analysis consisted of a numerical code containing the elements of both a north-south sequence for each reef, and an identifier for each colony.

Latitude was represented as a decimal value (i.e. 17°30'S became

$17.5^{o}S$), so that the variable was able to be used in interval level calculations.

The relative position of the collection areas on the continental shelf to the shoreline and the open ocean was coded initially into three units, representing three equal divisions of shelf width in each location. The zone closest to shore received the highest value, and the most ocean-ward the lowest. Later, this scheme was found to lack sensitivity, and the real values from shoreline and outer barrier in nautical miles were substituted. This variable was called *shelf zone*.

Reef zone was coded as an ordinal variable from one to five units, in an order which represented the decreasing degree of energy in terms of water motion (windward crest to leeward edge). It was recognised that this ranking was based on assumed conditions rather than on any measurements made in the field, but follows the conventions described in the literature (see Stoddart 1969).

Depth measurements were combined into three classes, those above one metre deep, corals between one and five metres deep, and those deeper than five metres. In the final analysis, it was found that, for the purposes of this study, the latter two groups could be combined to represent "deeper" corals, as distinct from "surface" corals, without affecting the results of the statistical analysis.

The *date of collection* was recorded to provide a time marker for the density band at the colony surface, in month/year format. The *species* of each colony was recorded in nominal form only, each species being assigned a numeral from one to eight. This level of measurement allowed for certain classificatory statistics only.

Specially written computer programmes were used to calculate the following variables:

mean annual growth rate for each colony;

age of the colony;

total diameter;

standard deviation of annual growth rate;

coefficient of variation of annual growth rate.

The values of the mean growth rate for all colonies were tested for normality (approximation to the normal distribution) and the decision was made to use non-parametric statistics in the investigation of relationships between variables. All these analyses were performed using the SPSS system package.

The methodology used in the study ensured that for each colony there existed a complete record of its growth for each year of its life, along with as detailed an array of the environmental factors associated with its location as it was possible to obtain.

CHAPTER THREE

GROWTH RATE VARIATIONS IN A UNIFORM ENVIRONMENT

The multi-scale analysis of growth rate patterns in the Great Barrier Reef Province was initially based on the hypothesis that colonies of the same species from a uniform environment should show a similar response to changes within that environment. In the present case, the delineation of an environmentally uniform area represented no small problem, but it was assumed that the external controls on growth would be similar for all colonies in a small isolated pool on a reef flat set some distance back from the reef crest. Such a small pool was found on Fairey Reef, located in the central part of the Province at 19° 35'S, 148° 52'E. The pool was 15 metres in diameter, having a flat sandy substrate, which remained submerged to about 0.5 metres at M.L.W.S. The area was well represented by *Porites*, with some 80 small colonies between 3.95 and 18cm in diameter residing in the pool. The 28 colonies used in the analysis were taken from this population in October 1976.

Many biological experiments which investigate the reactions of organisms to environmental change employ the principle of using control organisms against which to compare those reactions in the subjects of the experiments. The control organisms must be of the same species as the subject organisms in order to make any valid comparisons. The problem of species definition is fundamental to this exercise. Linnaeus believed that the species was a unit that could be defined on a morphological basis. Since his time, a radical change has occurred in the species concept. Today, most taxonomists agree that geographically representative species are connected in an intergradational scale, in which there are subspecies and even lower orders represented. This study has based its approach on the thesis of Mayr (1976) who summarises the problem by showing that two areas of difficulty exist: delimitation of particular species taxa, and the definition of the word "species." In the first respect, this study accepts the findings of the current literature on the taxonomy of *Porites* based on the morphological characteristics of the skeleton, and attempts to solve the second by defining the species being studied as being those colonies as being indisputably similar to each other in as many other respects as possible. This means that any colonies which were intermediate between definitions based on morphology were rejected, in the absence of any more detailed evidence (such as lack of hybridisation between individuals) to aid placement.

Under the above conditions, a sample of 28 colonies was culled from the original 80 colonies collected. These colonies were defined as *P. lobata*. They ranged from four to 13 centimetres in diameter. It was assumed that this sample population represented the basic, most homogeneous coral population unit that could be found. This population unit was used as a reference group against which to measure the reactions of other, more widely spread populations, such as those on a whole reef scale, or from the total latitudinal range of the Province.

It was surmised that the most basic pattern of growth rate response to environmental change would be reflected in the width of the annual banding in each of the colonies selected from Fairey Reef. The measure of success of the postulate should lie in the isochronous adjustment made to annual band width by each colony. The establishment of this baseline would then lead to the formation of hypotheses about coral growth rate patterns on other scales.

Fairey Reef is a small platform reef sheltered by a complex of larger reefs on its windward side. It consists of two platforms, one about 5km by 2.5km, and the other 3km long by 1km wide. The larger, northernmost platform is separated from the smaller by a 250 metre wide channel some 20 metres in depth. The larger of the two platforms has a 15-20 metre deep, semi-enclosed lagoon in its central portion. The collection point lay in a small pool in the south-west margin of the central lagoon (Figure 3.1).

Following the procedure detailed in Chapter Two, the corals were prepared, sectioned, X-rayed, and the resultant plates scanned with a micro densitometer. The traces obtained showed a series of distinct and alternating peaks and lows. Although they also showed small-scale "serrations" corresponding to structural features of the skeleton, these were too small to mask the larger variations in density indicated by the trace. Shorter-than-annual cycles in density were not apparent in these corals.

The traces were unreliable at the outer edge of the specimen-image. When slices of coral were X-rayed, the outer surface of the slice was seldom exactly parallel with the incident X-ray beam. Thus, only where the beam passed through the full thickness of the slice was the image truly representative of skeletal density. This error was compounded during microdensitometry, as the entire beam had to pass through the specimen-image at a point representing the full thickness of the coral slice before a valid reading was obtained. The dating of the density features within the slices depended upon the date of collection, which was represented by the outer surface of the skeleton. The Fairey Reef corals were

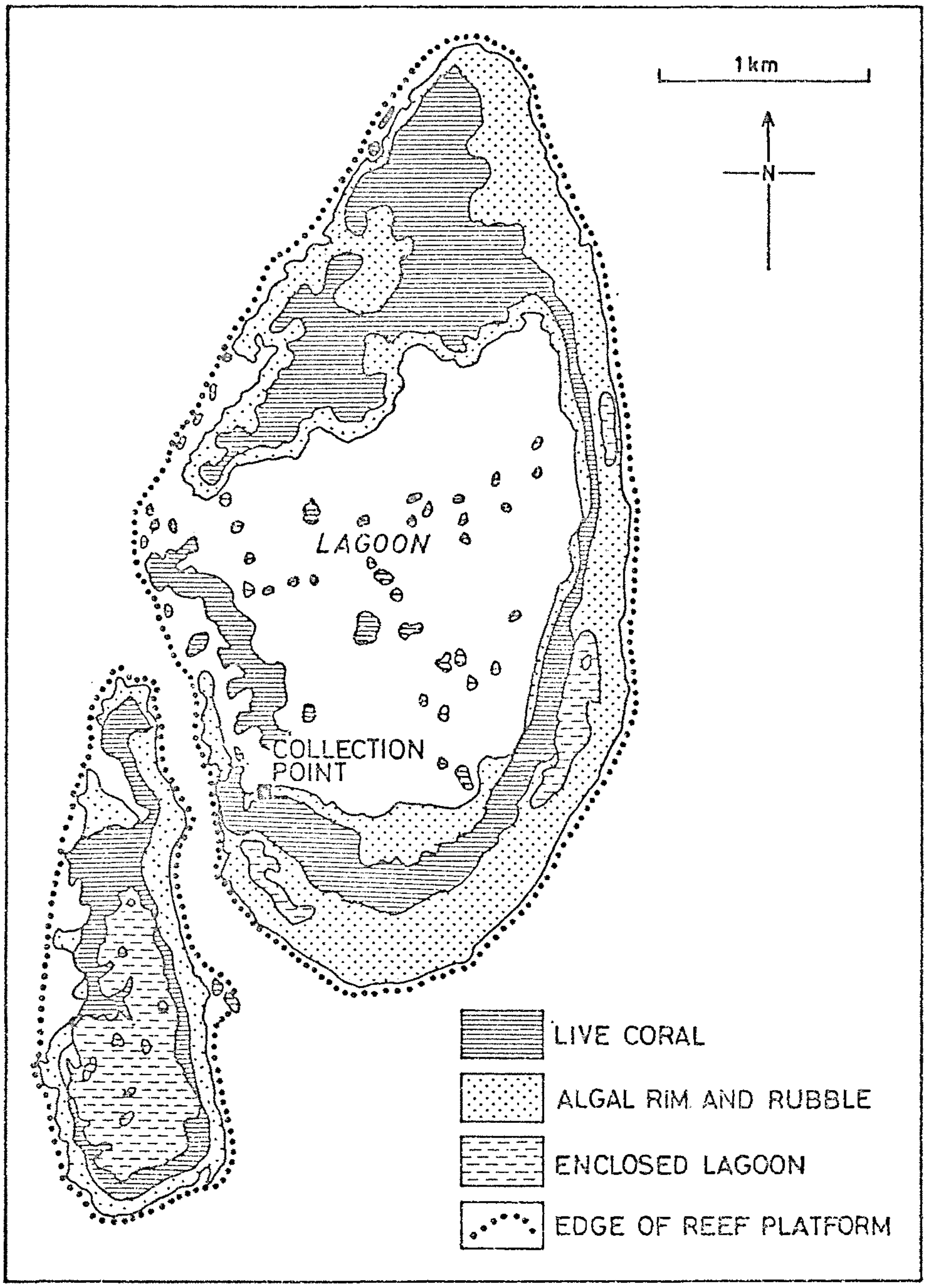


Figure 3.1 Fairey Reef (19°35'S, 148°52'E)—Zonation and Morphology

collected in October. Although for most of its length the trace in each case gave sharp indication of the points of maximum and minimum skeletal density, it was not possible to directly relate these features to the beginning of the trace.

The separation of successive low density points on the traces was measured. Measurements were made up to and including the low point preceding the last obvious light band. The separation of successive low points represented annual growth increments.

The data derived from the traces for the 28 colonies showed the grand mean of the annual growth increments to be 0.64cm/yr, with a standard deviation of 0.114cm/yr. The highest annual growth value was 1.25cm/yr, and the lowest was 0.25cm/yr. The mean growth rate of each colony lay in the range 0.42-0.87cm/yr. The largest colony was 13cm in diameter, and the smallest had a diameter of 3.95cm.

In all the X-radiographs, the last obvious feature towards the growth surface was a light (high density) band. The corals were taken in October when deposition of the subsequent dark band was taking place. The spacing of the dark and light bands in the X-radiographs suggested that much of the outermost light band had been deposited when the corals were collected in October. This indicated that the low density phase of the skeletons occurred during the southern winter.

In the traces from the microdensitometer, this last light band was obvious as a peak. Colony age was determined by the number of dark (low density) bands. The outer band was excluded. The 28 colonies fell into six age groups with ages of 3, 6, 7, 8, 10 and 15 years, with 1, 8, 9, 4, 4 and 2 colonies in each group respectively. For each age class, the respective annual growth

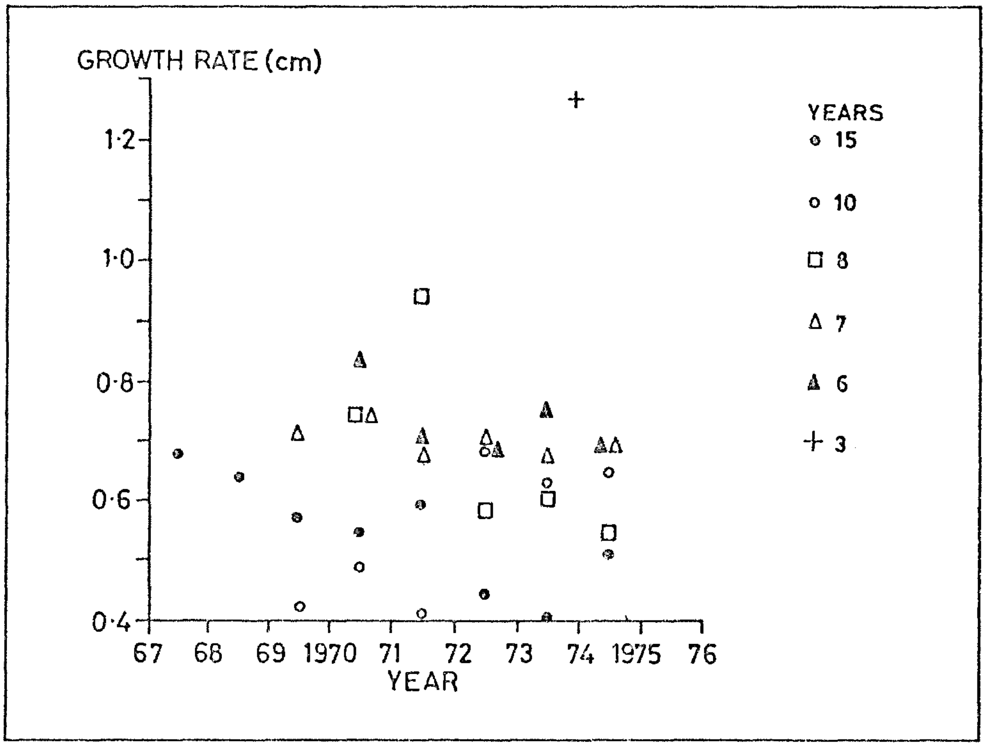


Figure 3.2 Age-Growth Rate Plot for 28 Colonies of *P. lobata* from Small Pool on Fairey Reef.

increments were averaged, and plotted against the year in which they occurred (Figure 3.2). Younger colonies showed a faster annual growth than older colonies, i.e. the growth rate of all colonies decreased with age. The growth surfaces of the corals remained reasonably regular for the first 5-7 years of growth, but then began to break up into the irregular "bumps" or lenticular prominences typical of the species.

Each of the annual growth increments may be expressed as a percentage of that of the previous year, and plotted (Figure 3.3). Thus, a point plotted at 100% for 1972-73 meant that during this time the specimen grew the same amount as it did in 1971-72. It was assumed that the last obvious low point in the traces represented the southern winter of 1976. Growth since this time was excluded from the calculations. From the growth data, it was found that the maximum annual increase in growth rate for any colony was 200%, and the maximum decrease was 48%.

Increase in the size of the coral *Goniastrea aspera* has been correlated with a decrease in the multiplication rate of the polyps (Motoda 1940). It was suggested that senescence or a geometric effect accounted for this phenomenon. A geometric restraint on coral growth was later postulated by Barnes (1973). However, it was proposed that this restraint may be partially overcome by the development of irregularities in the growing surface of the colony. Data presented here confirm that colony growth rate decreases with size and age, but the sample was too small to distinguish the effect of size from that of age. Although the development of surface irregularities was found in these specimens after about five years' growth, the data were insufficient to accurately determine whether a change in surface form always corresponded to a change in growth

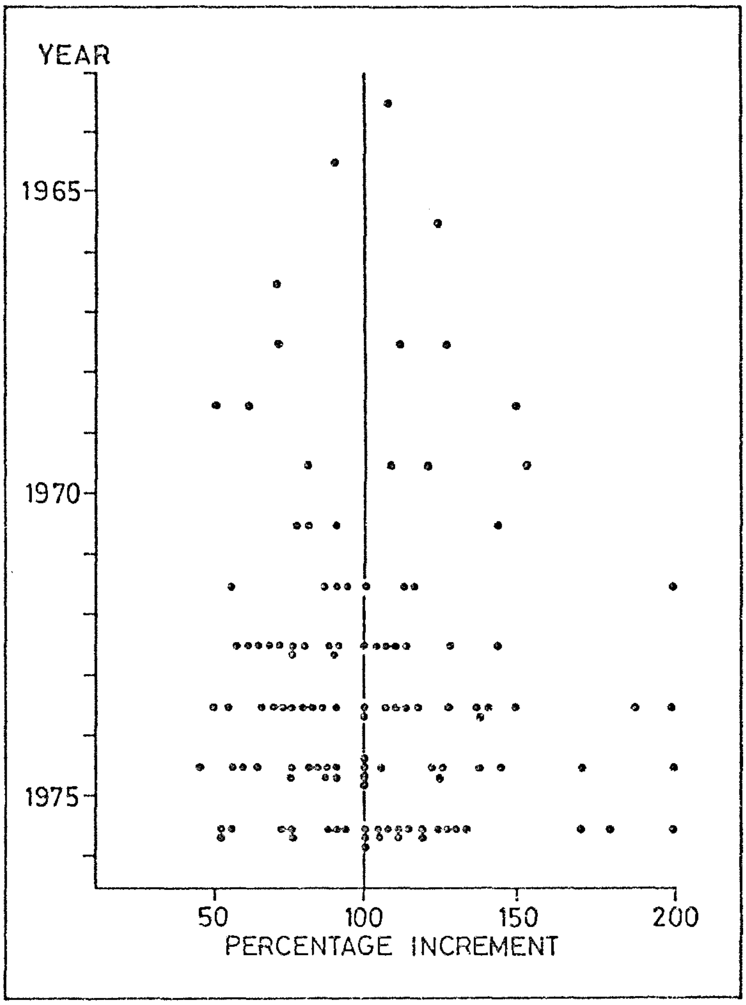


Figure 3.3 Colony Growth Increment (% of Previous Year) from 28 Colonies of *P. lobata* from Fairey Reef *vs* Year of Growth

The 28 colonies did not show similar growth trends at the same time. Figure 3.3 indicates that in any one year some colonies grew more than in the previous year, while others grew less. Since the corals grew in the same small area, it is unlikely that they were subject to different macroconditions of light, temperature, salinity or wave action, all of which are considered to have a major effect on coral growth (see Stoddart 1969). If any of these factors had acted to increase or decrease the annual growth, then all the data points would fall to one side of the central (100%) line in any given year. There may be several reasons why this did not occur, all of which have implications for the basic premise that underlay the Fairey Reef experiment. These may be summarised as follows:

(i) the gross environmental factors mentioned above are not major controls on growth rate;

(ii) the seasonal variation in environmental conditions during the life of the colonies has not been sufficiently distinctive to produce any recognisable similarity in growth rates in all corals;

(iii) environmental conditions varied, but those which stimulated growth were counteracted by those which depressed it;

(iv) the fact that the corals were assessed as being of the same species did not take into account the variability of individuals within the species category.

The first explanation is incorrect as the weight of evidence indicates that coral growth rate does respond to light and temperature changes, both in the long and the short term (Goreau 1961;

Shinn 1966; Muscatine 1973; among others). Consequently, it must be assumed that differences in gross environmental conditions from year to year on Fairey Reef were insufficient to cause all the colonies studied to exhibit a similar growth trend, and that there must have been finer exogenous or endogenous controls which caused adjacent colonies to show contrasting trends at the same time.

Two such controls appear obvious. Nutrition of corals need not be uniform, even over a small area of reef. It has been shown that the distribution of plankton on reefs is "patchy" (LIMER Expedition 1976). Alternatively, there may be genetic controls which act on the individuals within a specific population independently of gross environmental parameters (Buddemeier and Kinzie 1976, p.220). If one examines the argument that it is this intra-individual variation in response to external change within a species category that is in some measure responsible for the evolutionary process in natural systems, then the latter form of control appears more acceptable.

Whatever the conclusions reached above, the variability encountered in growth rates within a supposed uniform environment has important implications for the study of that same variability over a wider, more diverse range of environments, such as are to be found throughout the Great Barrier Reef Province. The question that must be answered is whether or not the Fairey Reef findings hinder the attempt to explain larger scale variability.

The conundrum resolves itself into a bivariate problem which can be approached in two ways: theoretical, and statistical. The first is best illustrated by analogy with climatic studies. Critchfield (1966) states the problem of climatic classification as follows:

> A complete classification of climate should provide a system of pyramiding categories, ranging from the many microclimates of exceedingly small scale areas, through macroclimatic types, to major divisions on a world scale. But the description of climates is not easily accomplished as the summation of a great number of micro-climates, nor are microclimates readily fitted into the pattern of major world climatic regions.

By analogy with the above, the variability of growth rates on a micro-scale (e.g. the pool at Fairey Reef) is not a determinant of the larger scale variability over the Province, although it is controlled by the same natural environmental factors in the same way as climate. In each case, the effect of *averaging by category or scale* rather than by accumulation becomes the basis for the next highest order. The coral problem is thus resolved by statistical means, such as analysis of variance procedures, which use this effect. Knowledge of the degree of variability which may take place in a small "uniform" area of the Great Barrier Reef thus provides a standard against which the wider spatial patterns can be tested.

In conclusion, the Fairey Reef study showed that a degree of variability existed in the growth rates of a population of corals of the same species within a uniform environment. It also showed that the growth rate of any colony within that group tended to grow more slowly with increasing age and size, although the degree of responsibility of each of these variables for the phenomenon is unknown, due to the small sample size employed.

CHAPTER FOUR

GROWTH RATE VARIATIONS ON A SINGLE REEF

Introduction

In the previous chapter, growth rate variations of *Porites* spp. were investigated over time, without the added effect of space being considered. The logical extension of this pattern of study is to include a small-scale spatial element, that is, in the present context, to look at growth rate variation over the scale of a single (preferably small) reef platform.

The distribution of reef organism taxa and morphological types on a reef platform is far from uniform. Rather, the distribution is based on several variables, such as morphological structure, reef orientation, depth parameters, and local oceanographic factors. This biological distribution forms the basis for the delineation of ecological zones. Wells (1954) refers to a zone as an area where local species assemblages and species dominance indicate local ecological differences. From the descriptive zonation studies in the literature, a general windward to leeward scheme has been adopted. In a platform reef example, the physiographic zones from windward to leeward would appear as follows: fore-reef slope, reef crest, algal rim, coral zone, reef flat, sand cay (if present), back-reef apron and patch-reef area, and back-reef slope (Figure 4.1).

The implications of this zonation for coral growth studies lie in whether or not a growth rate variation can be identified and associated with the various zones of the reef. The approach used here has been based on collection of *Porites* colonies from various zones on a reef and the statistical comparison of the growth data obtained.

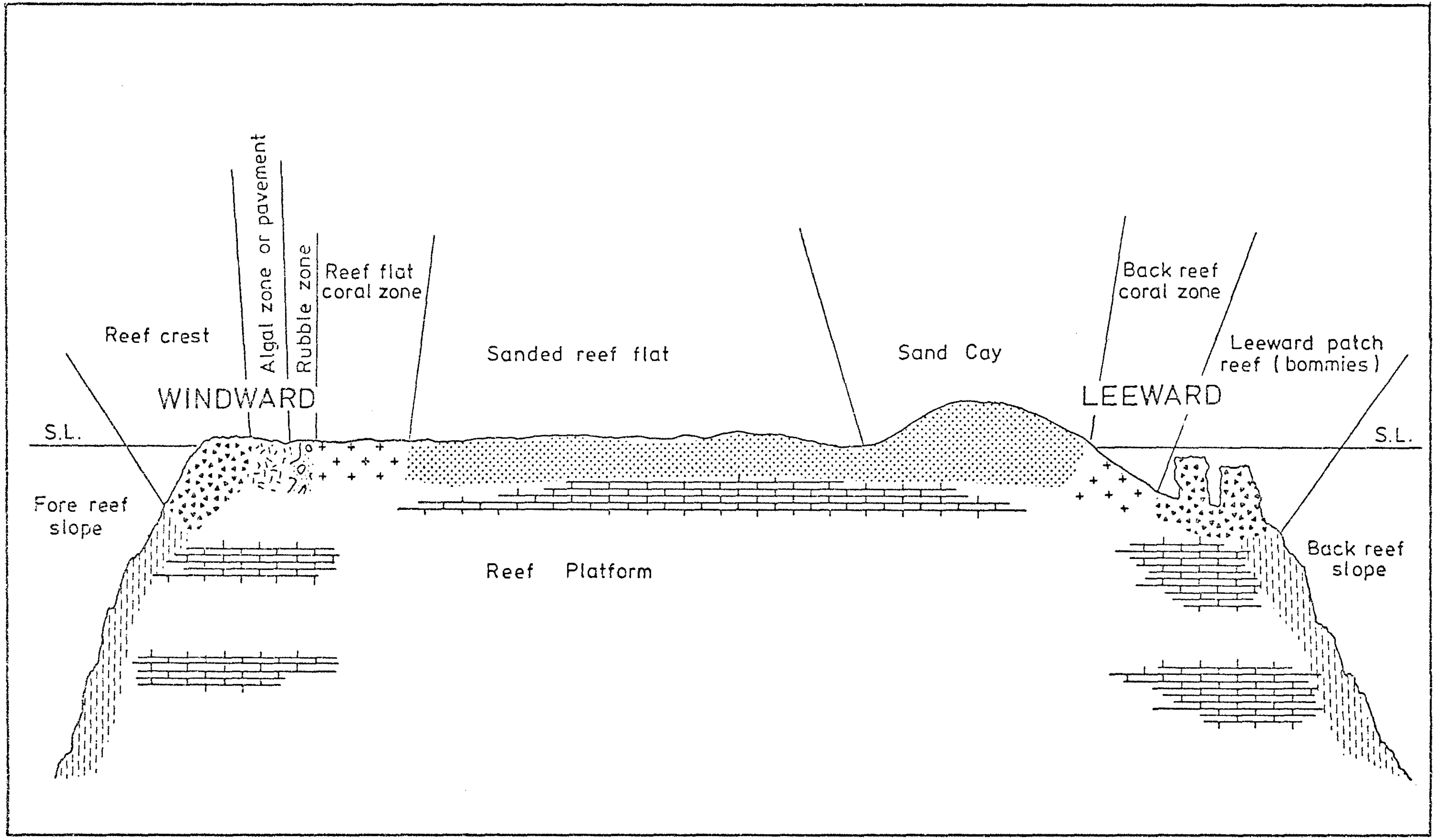


Figure 4.1 Hypothetical Platform Reef—Main Physiographic Zones.

The application of analysis of variance techniques to the data provides a measure of the ratio of the variance between the zones compared to that among the zones. The larger the ratio, the greater the difference between the group means.

Wheeler Reef (Figure 4.2), a small platform reef off Townsville, was selected, principally because of its structure (similar to the hypothetical reef in Figure 4.1), and accessibility. To test the effect of zonation on coral growth rates, the null hypothesis was constructed which stated that the growth rate of the whole reef population of the genus was not composed of separate or stratified sub-groups of population means whose variance differed significantly from that of the whole population. The expected hypothesis of course was that discrete groups of population means did exist. The analysis of variance routines used the mean growth rate data from each zone of the reef platform as the basis for grouping.

Wheeler Reef and Its Environment

Wheeler Reef is a small circular platform reef about $1.25km^2$ in area lying 55km north-east of Townsville. It is flat topped, devoid of large lagoonal features, and has a high reef flat relative to M.S.L. At mean low water springs, a small mobile sand cay is exposed on its leeward margin. Echo profiling by Harvey (1978) shows that the reef platform lies in about 54m of water on a circular bathymetric high, and that the reef flat is close to tidal datum at 0.3 metres above M.S.L. The reef edge is steeper on the windward side and trails off to a gentle sand slope to leeward. Wheeler Reef lies slightly to landward of the mid-point of the continental shelf, and is not well protected by any large reefs nearby.

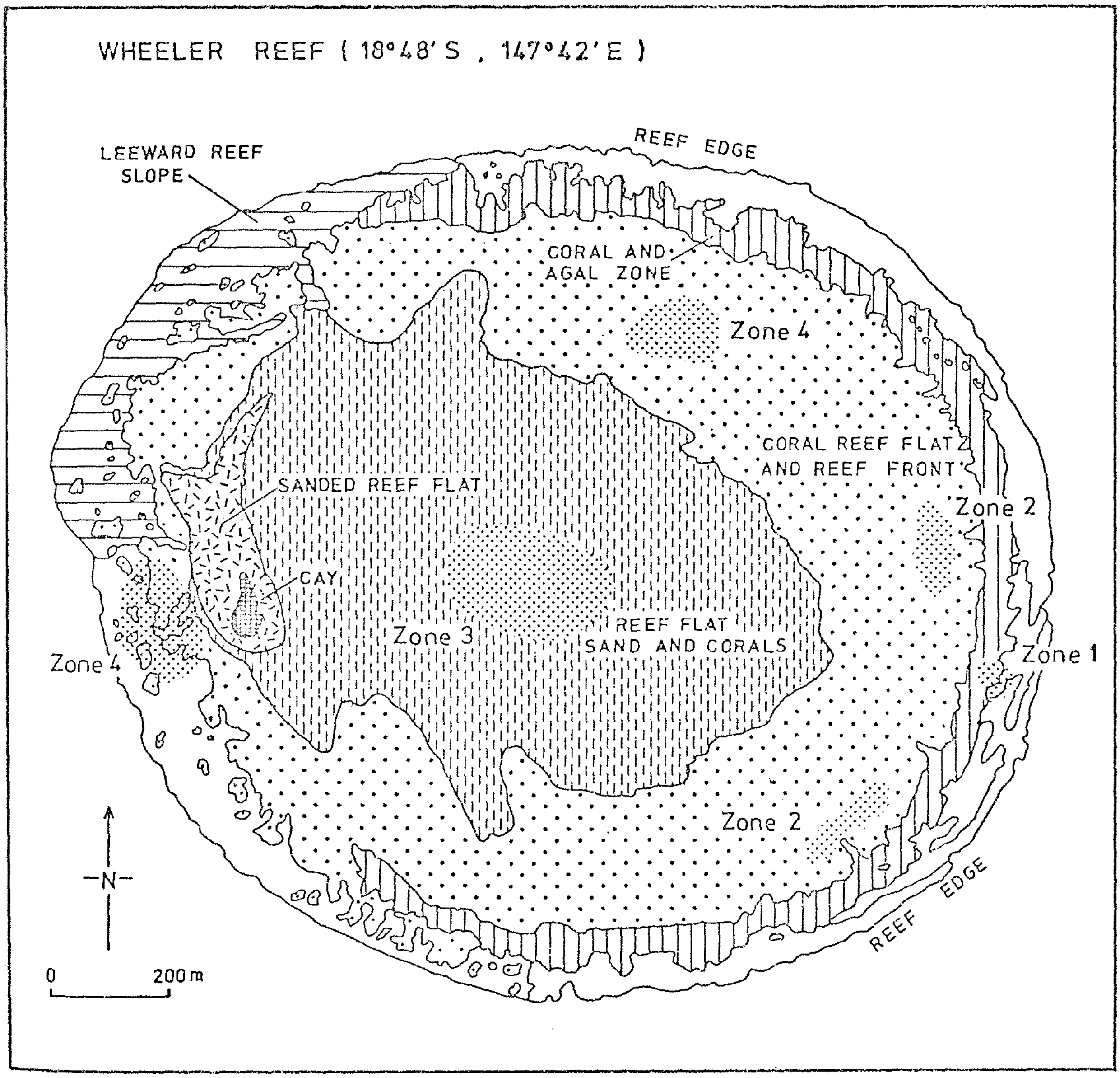


Figure 4.2 Wheeler Reef—Morphology and Surface Zonation. Collection Zones Numbered 1-4.

Drilling and subsequent radio-carbon dating of the cores reveals that the reef surface reached a level of 2.41m below present M.L.W.S. at 4390±100yrs B.P. (Hopley 1982). Since that time, the reef has reached the stage of a fully-formed platform reef, infilled and developing to leeward, in the scheme suggested by Davies (1977).

The closest meteorological station to Wheeler Reef is the lighthouse at Cape Cleveland, near Townsville. The use of Cape Cleveland weather data in an analysis of the climates of offshore areas such as Wheeler Reef poses the question of whether or not the separation of the two areas materially affects the data. Pickard (1977) has examined the question in relation to the findings of Brandon (1973) regarding the relationship between climatic data for Heron Island and that for Cape Capricorn. The former author concludes that the correct ratio between the rainfall statistics (in this case annual totals for seven years) is 1.23:1, i.e., the reef island rainfall totals are not more than 15% different from the land totals at the same latitude. However, he does point out some areas where very high coastal rainfall totals occur (e.g. the Innisfail area), may not follow this pattern due to the effects of orographic uplift close to the coast. In the light of the above, it was felt that the climatic data from Cape Cleveland could be used to represent the regime on Wheeler Reef.

Table 4.1 shows the breakdown of wind speed and direction at 0900 hours LST and 1500 hours LST for Cape Cleveland. The figures within each frame represent the percentage occurrence of each event. The most noticeable feature of the data is the predominant south-easterly component of the 0900 hours wind regime between January and September (inclusive). In the same period, the 1500 hours data show

TABLE 4.1

CAPE CLEVELAND—WIND DATA

CAPE CLEVELAND (LIGHTHOUSE) 19°11'S, 147°01'E

JANUARY 0900 HOURS LST — SPEED (KM/HR) — CALM 5

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	1	3	3	1	*			7
NE	1	4	5	1	1		*	12
E	1	3	4	3	2	1		14
SE	1	4	16	14	5	2		42
S	1	1	1	1	*	*		5
SW	2	2	1	1	*			6
W	*	1	1	*				2
NW	*	2	3	1	*			6
ALL	7	18	35	22	9	3	*	

NO OF OBS. 648

JULY 0900 HOURS LST — SPEED (KM/HR) — CALM 6

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	*							*
NE								
E	*	1	1	*				2
SE	2	6	13	26	14	4	*	67
S	1	3	3	2	1	1	*	11
SW	3	5	2	2	*	*		12
W	*	*	*					1
NW	*		*					*
ALL	7	15	19	30	16	5	*	

NO OF OBS. 647

JANURARY 1500 HOURS LST — SPEED (KM/HR) — CALM 1

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	1	3	8	3	*	*		16
NE	1	6	16	7	*	*		30
E	1	2	9	14	7	2	1	35
SE	*	1	1	5	4	2	1	14
S		*	*	*		*		*
SW			*					*
W								
NW		*	1	1	*	*		3
ALL	3	13	36	30	11	5	1	

NO OF OBS. 651

JULY 1500 HOURS LST — SPEED (KM/HR) — CALM 2

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	1	4	1	*				6
NE	2	7	5	2	*			17
E	1	6	12	14	7	1	1	41
SE	*	2	5	10	8	2	*	28
S	*	*	*	*		*		1
SW	*	*	1	1		*		2
W	*	*	*					*
NW	*	*	*					1
ALL	5	20	26	28	15	3	1	

NO OF OBS. 649

Source: Bureau of Meteorology, Surface Wind Analysis, 1978.

a more easterly trend. Oliver (1977) suggests that the latter figures more closely reflect the regional pattern. The summer months (November-January) are periods of more variable north-west to north-east winds. This time also corresponds to the cyclone season in North Queensland. Wave and current patterns therefore give Wheeler Reef an "energy zonation" with highest water movement values on the south-east rim of the platform, grading to the most sheltered region on the north-west rim.

The mean annual rainfall for Cape Cleveland is 1253mm/yr, with the largest proportion falling in summer (January-March = 72% of annual total) (Table 4.2). This has major significance for the growth patterns of the reef flat corals especially, since the occurrence of recurrent heavy storms in the "wet" can have a bearing on the reef flat salinity, not to mention the fluvial input to the closer reefs inshore which are susceptible to turbidity from the larger river systems. The latter effect has been found not to apply to Wheeler Reef, as studies show that the Burdekin River plume does not reach far out to sea at this location (Wolanski 1981).

The tidal characteristics of the standard port of Townsville, directly to the south-west of Wheeler Reef, are similar to those experienced at the reef itself, though the tidal range may be slightly higher at Townsville due to the shallowing of the shelf near the coast. Tides are semi-diurnal, with a range of 2.5 metres at Townsville between M.H.W.S. and M.L.W.S. Maxwell (1968, Figure 43A, p.76) shows the flood stream over the shelf adjacent to Wheeler Reef tending south towards the coastline around Cape Cleveland. In the open waters of the shelf, most authors agree that the predominant component of the water movement is the wind driven current of the

TABLE 4.2

CAPE CLEVELAND—TEMPERATURE AND RAINFALL DATA

CAPE CLEVELAND

	JAN	FEB.	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
AVERAGE DAILY MAX. TEMP.	30.6	29.8	28.8	27.6	24.9	22.9	22.3	23.5	25.4	28.1	29.6	31.1	27.1
AVERAGE DAILY MIN. TEMP.	24.6	24.3	23.6	22.3	20.0	17.9	17.3	18.1	19.9	21.9	23.5	24.5	21.5
AVERAGE DAILY MEAN TEMP.	27.6	27.0	26.2	25.0	22.4	20.4	19.8	20.8	22.6	25.0	26.5	27.8	24.3
AVERAGE MTH AND YR RAIN	243.0	350.0	233.0	56.0	31.0	40.0	17.0	10.0	13.0	21.0	47.0	78.0	1139

south-easterlies, setting the current to the north or north west (see Pickard 1977). This set or drift causes the total movement to resemble a northerly current with tidal perturbations superimposed upon it.

Six collection areas on the reef platform were chosen as representative of four specific ecological zones (Figure 4.2). The four zones are described as follows:

Zone 1—The windward margin or reef crest. Only one colony of *Porites* with discrete enough banding to be able to determine any annual growth data was found at this location. The few other *Porites* present in the area were flattened, irregular, encrusting forms. The coral was collected from a small, exposed location on the south-east extremity of the platform, where the water depth at M.L.W.S. was between 0.5 and 1.0 metres. The fore-reef slope rose from about 50 metres in depth to this point in a series of well defined spur-and-groove structures, the deeper areas of which were covered in the larger forms of plate-like *Acropora hyacinthus* and smaller colonies of *Pocillopora* spp. The upper two metres of the reef crest area contained the more robust forms of branching *Acropora* species, such as *A. palifera* and *A. robusta*, along with a few encrusting or stunted massive corals, such as the *Porites* mentioned above. This zone was characterised by fast water movement and strong turbulence as a result of wave action. At the top of this surf zone, the surface cover was almost entirely coralline algae.

Zone 2—The windward flat. The colonies used in the analysis were collected from two sites in this zone, both about 200 metres back from the reef edge. The substrate in this zone was characterised by scattered clumps of coral, mainly small branching types such as *Acropora humilis* and *Porites cylindrica*. The spaces between the coral patches were sand, and colonised by holothurians. The water depth at M.L.W.S. was about 1 metre, except for some small lagoons where the depth reached 3-4 metres. Thirty-two colonies of *Porites* were collected from these sites.

Zone 3—The mid-reef flat. This area was characterised by very sparse coral cover (about 5%), and the predominance of sanded reef flat. Those species that were in evidence were mainly small *Pocillopora damicornis* colonies and small *Porites lutea* heads, usually found in clumps, in association with fleshy masses of the brown alga *Padina* sp., calcareous *Halimeda macroloba*, and the pale green *Caulerpa racemosa*. The relative rarity of massive *Porites* colonies here dictated that only eight suitable colonies were taken for analysis.

Zone 4—The leeward reef margin. This area was located in the lee of the small mobile cay referred to above, and further around the reef platform edge towards the northern margin. The water here was deeper, ranging from 2-6 metres below M.L.W.S., and the principal coral growth form was made up of large bommies, or compound patch reefs. These bommies hosted a wide variety of coral species, from the most delicate branching forms to the larger massive heads, in some cases up to 2 metres in diameter. In between the bommies were sediment chutes, taking the sand from the reef flat to the deeper water to leeward. The outer margins of these chutes provided a fine sanded substrate, which was widely colonised by the staghorn coral, *A. formosa*. Ten regularly-shaped, massive *Porites* corals were taken from this location for study.

Zonation *vs* Growth Rate: Hypothesis

As discussed above, the variables which determine the placement of different reef platform locations into discrete eco/morphological zones are also the variables which are thought to have a significant effect on the growth rate of scleractinian corals. Chapter One examined these in detail.

The fact that coral species on a reef platform are not homogeneously distributed throughout all the habitats on the reef indicates that some species react differently to environmental factors compared to others. In the case of adaptation to water movement, for example, both growth form and corallite size have some bearing on the ability of a colony to thrive in either very low or very high energy conditions. Porter (1974) describes the highly efficient carnivory of *Montastrea cavernosa* in feeding on zooplankton, while Franzisket (1964) points out the relative inefficiency of corals with smaller polyps at the same task. Depending on the size of a species' corallites, increasing rates of water movement over a colony tend to inhibit rates of tentacular entrapment of food items such as zooplankton. At the other extreme, no water movement at all would reduce the amount of food reaching the colony surface. Further complications to this scheme arise with the knowledge that zooplankton are not always an important source of energy for reef corals (Johannes and Tepley 1974). These authors found in the same study that *Porites lobata* in particular was an inefficient captor of zooplankton, and Jokiel (1978) postulates that corals with small corallites (such as *Porites* spp.) are better suited to autotrophic nutrition.

Few data are available on the relationship between the population numbers of coral species and the growth rates of those colonies. It could be argued that the number of individuals of a species in any location reflects its success as a coloniser and suitability of the local environmental conditions for its growth. If this proves to be the case, it may be assumed that growth rates for the species in that location (or zone) will reflect this suitability. Thus, a species will tend to grow faster where it is best represented on the reef platform. According to the scheme from Rosen (1975), and following the above argument, *Porites* species should be found to grow faster in calmer water, principally from the back reef areas, and at depth.

The relationship between growth form and growth rate in the scleractinians has been discussed by Chappell (1980). In his simulated reef development model, form and diversity are shown to be related to the spatial balance of four stress factors operating on a simple reef section. These are: exposure, light, wave stress, and sedimentation. Diversity is shown to be greatest when the sum of the four stress factors (environmental stress) is small. Chappell suggests that growth may be limited by the same factors as those which control diversity, and tests this by constructing a model of reef growth which successfully compares with existing real reef morphologies. Chappell's Figure 2 (p.250) suggests that growth rates should be highest in the more protected, mid-depth back-reef zone, grading though the reef flat margins and central areas, to the M.L.W.S. mark on the reef flat. This study tests that hypothesis by examining the mean growth rates of colonies from those areas.

Rosen (1975) constructed a scheme of gradations of coral associations based on the degree of water movement at any location on a hypothetical reef platform. Figure 4.3 shows the scheme, for Indo-Pacific reefs, representing the theoretical distribution of shallow

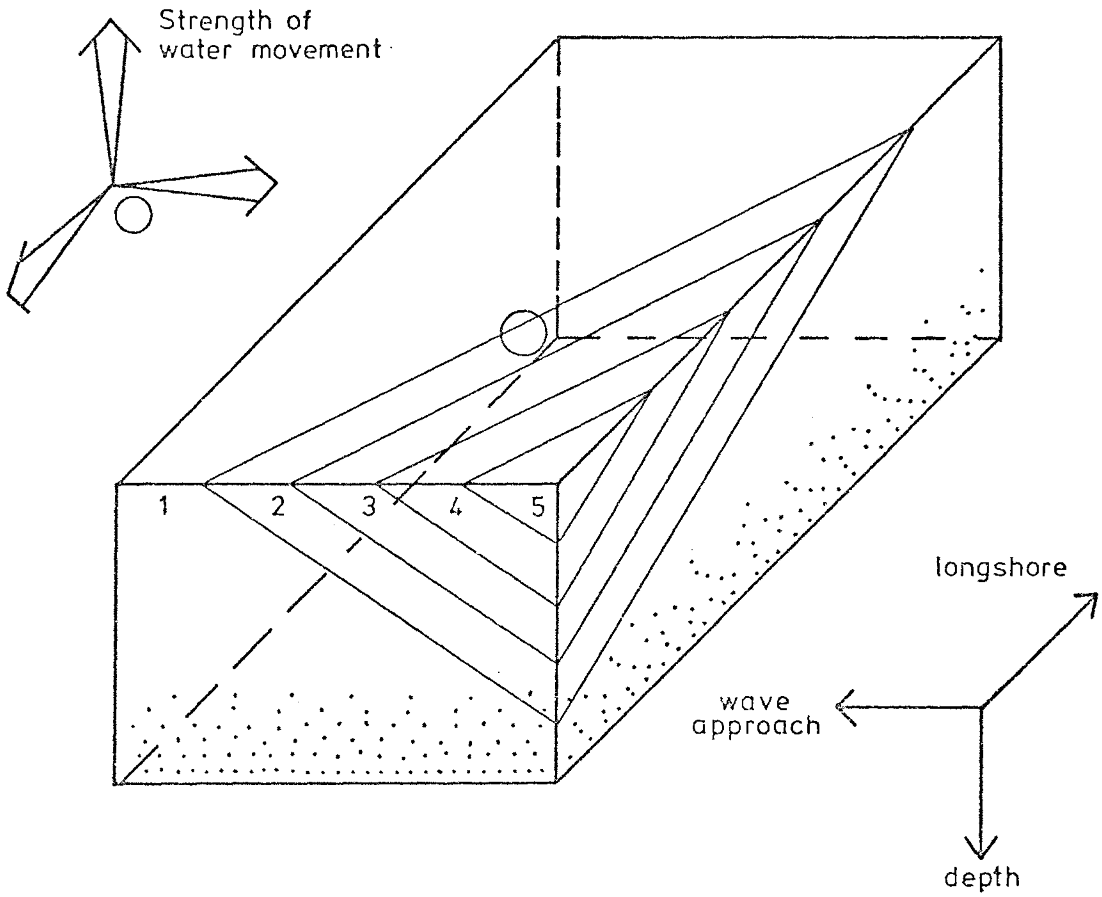


Figure 4.3 Spatial Scheme of Major Indo-Pacific Shallow Water Coral Associations (From Rosen, 1975)

water associations. The *Porites* assemblage occurs wherever the minimum water movement conditions are found. Thus *Porites* is a genus which prefers a low energy, leeward existence.

Analysis and Results: Wheeler Reef Zonation Study

A total of 51 colonies of *Porites* were collected from the above-mentioned areas on the Wheeler Reef platform. The mean annual growth rate for each coral was calculated and the group means from each zone plotted with 95% confidence limits (Figure 4.4). Zone 1 had only one colony, and was excluded from the statistical analysis. The number of replicates from each of the other three zones was unequal, so the statistical design was balanced by random sampling the two more numerously represented zones to match the number of replicates (colonies) in the smallest (n=8). The variances from each zone were tested for homogeneity, and a one-way analysis of variance performed on the means.

The null hypothesis that there were no significant differences between the growth rates of the colonies from different zones was rejected (Table 4.3, F-ratio, $P<.05$).

TABLE 4.3

	SS	df	MS	F	Sig.
BETWEEN ZONES	.005	2	.003	4.796	.019
WITHIN ZONES	.001	21	.001		
TOTAL	.016	23	.001		

Wheeler Reef. One-way analysis of variance testing effect of habitat/zonation on growth rates of *Porites*. (Cochran's C=0.582, variances homogeneous.)

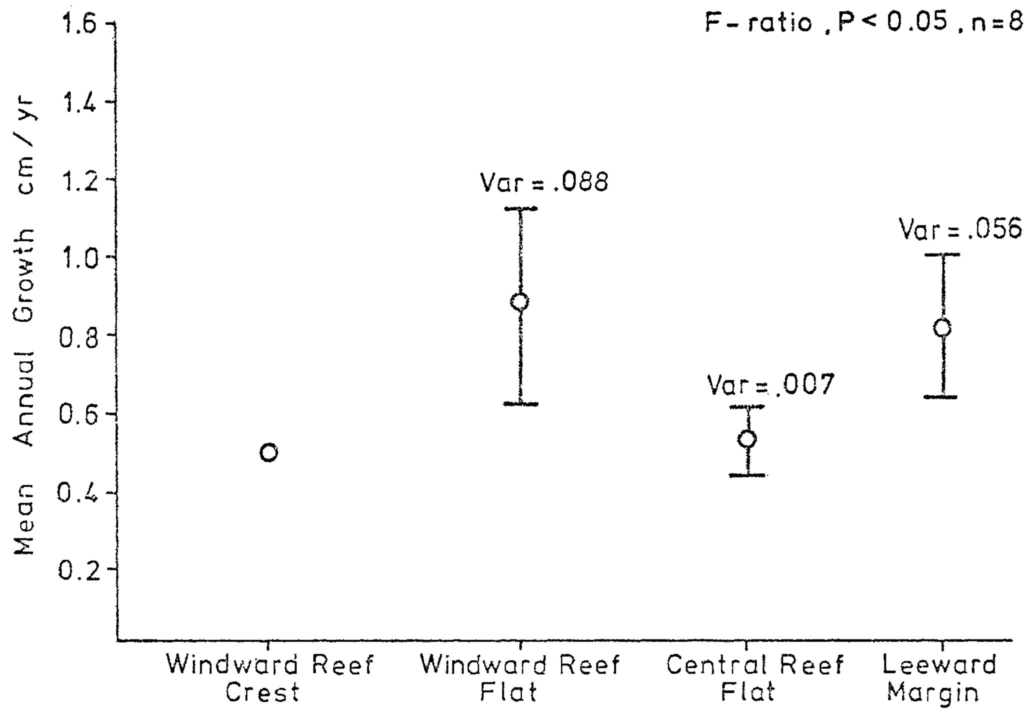


Figure 4.4 Mean Annual Growth Rate for Wheeler Reef Colonies, By Zone (95% Confidence Limits)

The data in Figure 4.4 show that the lowest growth rate zone for *Porites* was that of the single colony from the windward crest in Zone 1. This data must be regarded with caution because of its singularity. The next highest zonal mean growth rate was that of Zone 3, the central reef flat. The remaining zones (2=windward reef flat, 3=leeward reef margin) had the highest growth rates, but the confidence intervals in Figure 4.4 reveal that their respective means are not significantly different from each other. That their values are statistically indistinguishable may be a reflection of the physical proximity of the collection sites (a sampling error).

Discussion

General conclusions which may be made from the pattern of growth rate variation in *Porites* colonies on Wheeler Reef include the observation that geographical location on the reef platform in relation to the wave energy regime seems to have a significant effect on the growth rate of those corals. The pattern of fastest growth on the leeward margins and windward reef flat grading to slowest at the windward crest accords with the hypothesis of Chappell (1980) in terms of the relationship between diversity and growth of corals on a reef platform, and the balance of stress factors in each growth location. Rosen's (1975) scheme for the location of generic assemblages for Indo-Pacific reefs (Figure 4.3) also fits the pattern of growth variation found on Wheeler Reef. Although no numerical measures of the distribution of *Porites* on the reef platform were made, qualitative field observations revealed that the genus was more abundant in the zones in which it was found to grow fastest.

No relationship between growth rate and zonation was tested for at the specific level, although since 40 of the 51 colonies used in the sampling exercise were of the one species (*P. lutea*), it would not be expected that any specific effect should be found in the data analysed. The relative variability of growth in each zone proved to be of interest. Figure 4.4 shows that Zone 2 (windward reef flat) had the highest variance, followed by the leeward margin, while the reef flat in the central area of the platform showed very low variability. The conclusion that may be drawn from this ordering is that those reef edge zones encounter much more variable environmental conditions than does the centrally located mid-reef area. The changing wave energy patterns between the winter and summer periods may be a contributing factor, since the summer, variable north to north-west winds would certainly affect the leeward (west to northern) edges much more than they had been in the winter months.

The findings presented here do not conflict with those of others on total reef carbonate productivity (e.g. Davies 1977), which is described as being at a maximum on the windward side. *Porites* is not a major carbonate producer on the windward edge, as is reflected in its abundance at that location. The results suggest that for other species (e.g. *Acropora* sp.) abundance may be an indicator of growth rate. If so, then these other species, together with the coralline algae, are responsible for the maximum total carbonate production here.

CHAPTER FIVE

VARIATION IN GROWTH RATES BETWEEN REEFS

Introduction

The previous chapters have shown that the growth rates of *Porites* in the Great Barrier Reef Province vary through time and between morphological zones on a single reef. In this chapter the geographical scale of investigation is enlarged and growth rates on different reef types and at different locations on the continental shelf are examined. Finally, variations over the whole latitudinal extent of the Province are analysed. The effect of depth on growth is assessed, and variability in growth rate between different species of *Porites* are discussed.

SECTION ONE: Growth Rates on Different Reef Types

This section looks at the differences in mean annual growth rate of 81 colonies of massive *Porites* from three corresponding zones on each of three different reefs. The particular reefs were selected on the basis of their different locations, contrasting morphologies, and depths. They were Wheeler Reef (see previous chapter), Barnett Patches, and Three Isles.

The three reefs have contrasting morphologies and are representative of common reef types of the Province. As indicated in the previous chapter, Wheeler Reef (18°48'S, 147°31'E) is a small platform reef, most of its reef flat being at or just below M.L.W.S., with scattered corals over most of the surface on a sandy substrate. Radiocarbon dating of reef cores (Hopley 1982, and personal communication) indicate that the windward side of this reef reached modern sea-level about 4000 years B.P. In contrast, Three Isles ($15^{\circ}07$'S, $145^{\circ}25$'E) is typical of the low wooded island reef (Stoddart *et al.* 1978) common to the inner shelf of the Great Barrier Reef Province north of Cairns. These reefs are characterised by outer shingle ramparts, and rampart rock platforms in the lee of which lie mangrove swamps. Vegetated sand cays occupy the lee side of the reef platform. A high proportion of the reef is occupied by these subaerially exposed cays, while most of the reef flat is moated behind the ramparts at levels up to mean sea level. Radiocarbon ages from the low wooded island reefs have exceeded 6000 years (Polach *et al.* 1978) and some retain evidence of slightly higher (c.1m) mid-Holocene sea levels. Barnett Patches (18° 04'S, $146^{\circ}50$'E) is composed of a series of irregular reef patches, most of which are at or below Tidal Datum. An age of 3820±110 years B.P. from a depth of 3.7 metres (Hopley 1982) suggests that this reef flat is younger than those of the other reefs. The reef is typical of the resorbed reef of the Maxwell (1968) classification which he considered to be the end product of reef development. However, Hopley (1982) has shown that these irregular reef patches are relatively young and reflect the deep and irregular nature of the pre-Holocene substrate upon which the modern reef is growing. Both Wheeler Reef and Barnett Patches possess sand cays but both are small, ephemeral, and could not be compared with the major islands of the Three Isles reef.

1. Barnett Patches

Barnett Patches ($18^{\circ}04$'S, $146^{\circ}50$'E) is an unofficial local name for an area of small (c.0.5km^2), irregularly shaped patch reefs near the edge of the continental shelf, about 78km from the coastline, east of Dunk Island. The total area of the patches covers an area of approximately $50km^2$, and the irregular-shaped features rise from a general shelf depth of about 65 metres. All the patches have a veneer of living coral, and the largest has an unvegetated cay, which is surrounded by sanded reef flat. This cay is probably mobile, and is only inundated at the very highest of spring tides, and then only when its aspect is at a morphological low. This can be deduced from the presence of nesting sea-birds during the spring months, principally the Brown Booby (*Sula leucogaster*) and the sooty tern (*Sterna fuscata*).

Climatic records for Barnett Patches are not available, but as pointed out in the previous chapter, coastal records from nearby may be used to provide a guide to annual weather patterns for the reef area. The nearest coastal weather station is at Cardwell Post Office. Wind data for Cardwell are reproduced in Table 5.1. This reveals the typical North Queensland pattern of strong consistent south easterly winds during the winter months (especially for the 0900hrs readings—the 1500hrs figures reflect the confusing effect of the sea-land breeze at the particular location), and more variable north to north-east wind patterns in the summer months. Thermal and rainfall data are summarised in Table 5.2. The figures show a very similar pattern to that of Cape Cleveland records (previous chapter) with a mean annual rainfall of just less than 2000mm per year, 66% of that total falling in the period January to March. From these data it may be concluded that Barnett Patches enjoys a similar, though slightly wetter climate than Wheeler Reef.

The tidal range (M.H.W.S.-M.L.W.S.) at Goold Island near the coast at about the same latitude is 1.9 metres. The range may be expected to be slightly lower at Barnett Patches than at Goold Island due to the shallowing effect of the shelf closer inshore increasing

TABLE 5.1

CARDWELL WIND DATA

CARDWELL POST OFFICE 18°16'S, 146°02'E

JANUARY 0900 HOURS LST

SPEED (KM/HR)

CALM 17

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	5	3	*					8
NE	11	7	1	*				20
E	5	4	1	*				9
SE	12	11	4	3				30
S	4	2	*	*	*			7
SW	3	1	*					5
W	1	*						1
NW	1	2						3
ALL	40	30	6	3	*			

NO OF OBS. 648

JULY 0900 HOURS LST

SPEED (KM/HR)

CALM 13

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	1	*	*					2
NE	3	2	1					6
E	3	3	1	*				8
SE	11	19	13	5	2	*		51
S	6	4	2	1	*	*		13
SW	4	1	1	*				5
W	*	*						*
NW	*	*	*					1
ALL	29	29	18	7	2			

NO OF OBS. 650

JANUARY 1500 HOURS LST

SPEED (KM/HR)

CALM 5

DIRN	1 TO	6 TO	11 TO	21 TO	31 TO	41 TO	51 &	ALL
N	2	7	5	1	*			15
NE	4	14	13	11	2	*	*	44
E	2	3	1	*				6
SE	5	7	6	4	*			22
S	1	2	1	*				4
SW	1	*	*					2
W	*	*	*					1
NW	1	1	*					2
ALL	16	33	27	17	2	*	*	

NO OF OBS. 640

JULY 1500 HOURS LST

SPEED (KM/HR)

CALM 1

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	3	6	3	1				13
NE	4	12	10	3	*			29
E	2	3	3	*	*			8
SE	3	12	13	7	2	*		36
S	1	2	1	1	*	*		5
SW	1	*	1					2
W	*	*	*					*
NW	*	*	*					
ALL	15	36	31	13	3	1		

NO OF OBS. 642

Source: Bureau of Meteorology, Surface Wind Data, 1978.

TABLE 5.2

CAPE CLEVELAND, CARDWELL, COOKTOWN—TEMPERATURE AND RAINFALL DATA

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
						CAPE CLEVELAND							
AVERAGE DAILY MAX. TEMP.	30.6	29.8	28.8	27.6	24.9	22.9	22.3	23.5	25.4	28.1	29.6	31.1	27.1
AVERAGE DAILY MIN. TEMP.	24.6	24.3	23.6	22.3	20.0	17.9	17.3	13.1	19.9	21.9	23.5	24.5	21.5
AVERAGE DAILY MEAN TEMP.	27.6	27.0	26.2	25.0	22.4	20.4	19.8	20.8	22.6	25.0	26.5	27.8	24.3
AVERAGE MTH AND YR RAIN	243.0	350.0	233.0	56.0	31.0	40.0	17.0	10.0	13.0	21.0	47.0	78.0	1139
						CARDWELL							
AVERAGE DAILY MAX. TEMP.	30.9	30.5	29.9	28.6	26.3	24.6	24.1	25.2	26.9	28.5	29.9	31.1	28.1
AVERAGE DAILY MIN. TEMP.	22.1	21.9	20.9	19.0	16.3	14.1	12.5	12.8	20.8	17.4	19.6	21.1	17.7
AVERAGE DAILY MEAN TEMP.	26.5	26.2	25.4	23.8	21.3	19.3	18.3	19.0	23.6	22.9	24.7	26.1	22.9
AVERAGE MTH AND YR RAIN	419.0	422.0	363.0	186.0	90.0	53.0	30.0	27.0	35.0	52.0	99.0	176.0	1956
						COOKTOWN							
AVERAGE DAILY MAX. TEMP.	31.2	30.9	30.0	28.9	27.4	26.2	25.7	26.4	27.7	29.2	30.5	31.4	28.8
AVERAGE DAILY MIN. TEMP.	23.9	23.7	23.4	22.7	21.1	19.7	18.7	19.3	20.8	22.4	23.5	23.9	21.9
AVERAGE DAILY MEAN TEMP.	27.6	27.3	26.7	25.8	24.2	17.9	22.2	22.9	24.2	25.8	27.0	27.6	25.3
AVERAGE MTH AND YR RAIN	364.0	348.0	408.0	204.0	66.0	53.0	26.0	23.0	13.0	25.0	40.0	154.0	1724

the magnitude of the range. The tidal streams and circulation patterns in the region of Barnett Patches are similar to those found in the Wheeler Reef are, as described in Chapter Four.

Twenty-two colonies of *Porites* were collected from four different locations, with each collection site being chosen as representative of a distinctive ecological zone (see Figure 5.1). The zones were:

Zone 1: A fore-reef area on a small isthmus of the largest patch reef. This area was 2-4 metres deep at M.L.W.S., and fully exposed to south-easterly waves. The surface cover consisted of scattered colonies of hard corals, very stunted in form, with a total cover of about 10 percent. In between the corals the surface was almost completely covered with coralline algae, forming a dense, cemented substrate. Heavy turbulence in this area made collection difficult, as did the relative scarcity of large *Porites* colonies. The conditions described above have ensured that most of the corals tend toward encrusting growth forms, and these were unsuitable for X-radiographic work. One colony only from this area was found to be suitable for analysis.

Zone 2: A transitional area on the south-east side of the large patch (see Figure 5.1). This area was the same depth as the collection site above, and possessed a similar cemented substrate. More of the larger *Porites* were present, and coral cover was estimated to be about 25%. The proportion of coralline algal cover was correspondingly smaller. It was also noted that more species of coral were represented in this area. The number of colonies taken from this area was seven.

Zone 3: The reef flat. This area was situated on the southern tip of the largest patch (see Figure), but was much more sheltered

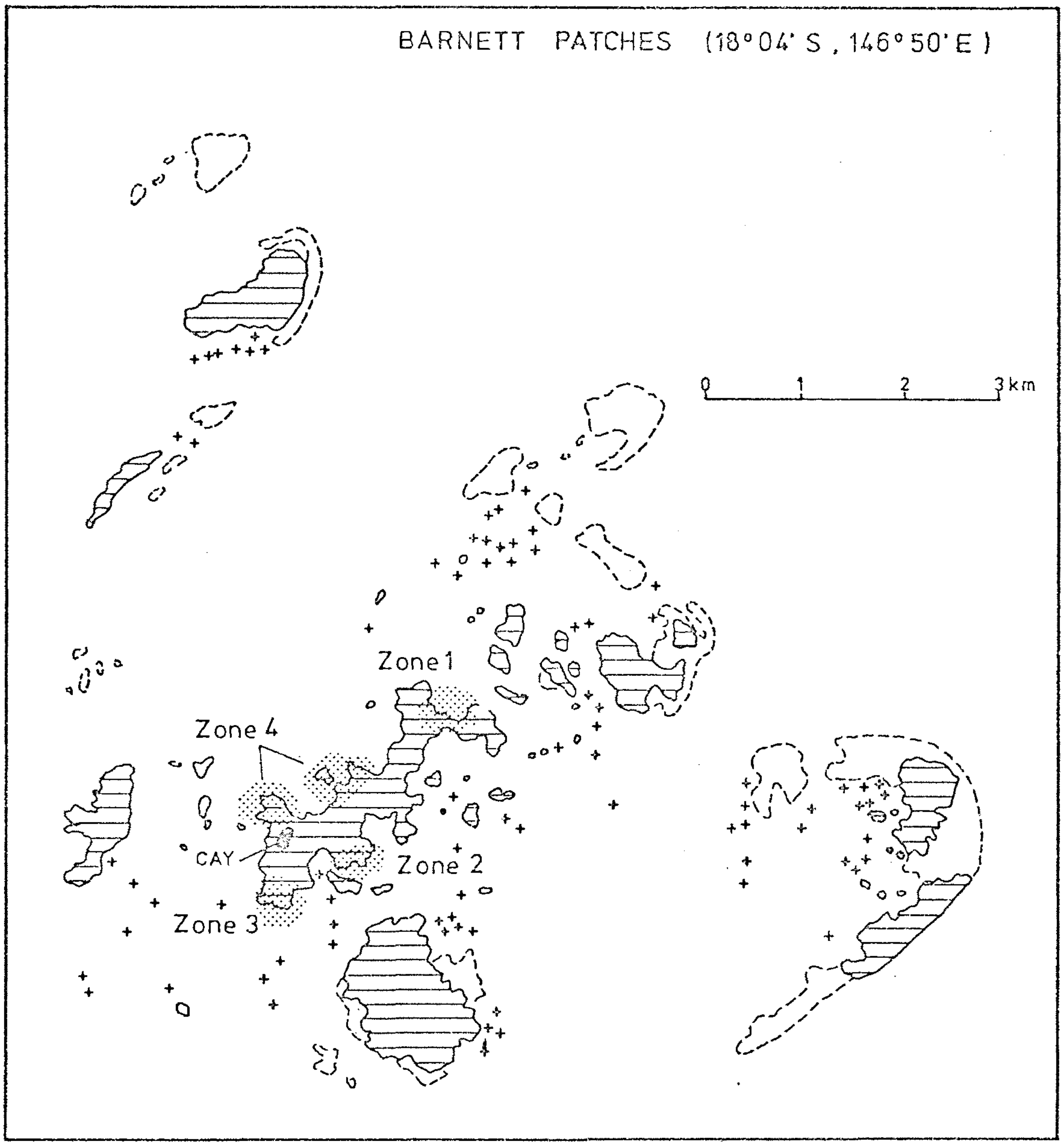


Figure 5.1 Barnett Patches—Morphology and Surface Zonation. Collection Sites Numbered 1-4.

from the prevailing weather than both of the above areas. It lay in 1-2 metres of water at M.L.W.S. Coral cover was estimated at about 20%, with a similar number of species present as in Zone 2. The intervening areas were predominantly sanded, with small patches of soft green and brown algae present. Seven corals were collected.

Zone 4: The leeward zone. This collection area was composed of two similar sections in the shelter of the body of the reef patch itself. Many species of coral were represented in these areas, ranging from the larger forms of the family Faviinae, to the plate and digitate forms of the Acroporids. Mobile sediment fans covered the slopes from the reef top to the deeper back reef areas. Many green and brown algae attached themselves to the substrate between the colonies, whose basal portions were often cemented by coralline algae. The seven *Porites* used in the survey were taken from the upper portions of several large bommies lying to leeward of the reef margin proper.

The areas sampled from around the large patch at Barnett Patches were thought to represent the largest range of environments in ecological terms, as described in the literature (e.g. Stoddart 1969). The dispersed pattern of reef patches within the area and the general lack of clear zonation necessitated that the zones chosen were based on location with respect to wave energy only rather than on purely morphological grounds, in order that comparisons could be made with the zones of the other two reefs studied.

2. Three Isles

Three Isles ($15^{\circ}07$'S, $145^{\circ}25$'E) lies in that part of the Great Barrier Reef Province which is protected by the large chain of ribbon reefs north from Cairns. It lies to the east of the main steamer channel, about a third of the distance to the ribbon reefs from the shore. The reef forms a low wooded island of the type described by Steers (1929), and Spender (1930), and is about 133ha in area. The platform has three principal above-water elements, a large vegetated sand cay on the north-west edge, and two mangrove islets, each with complex rampart and moat systems. First mapped by Spender in 1930, the reef has been more fully described by Stoddart *et al.*(1978). It represents a senile stage in the development of reef platforms.

Climatic data from the nearest land station at Cooktown show that the predominant wind regime from March to November is the south-easterly trade wind system, with a north to north-westerly influence, becoming more important in January and February. April is the month of most calms. These data are summarised in Table 5.3. Thermal and rainfall data are rpesented in Table 5.4. The mean annual rainfall is quite seasonal, with 63% of the yearly total falling between January and March. The reef, being so close to the mainland, comes under the direct influence of fluvial runoff from rivers to the south, such as the Endeavour River, during the wet season. The strength of this effect can be gauged by the presence around the cay of large driftwood trees, still containing mainland-originated rocks entwined in the roots. It could be expected that important salinity changes might occur during heavy wet periods, combining precipitation on the reef flat at low tide with strong terrestrial runoff, with consequences for coral growth.

The tidal range (M.H.W.S.-M.L.W.S.) at Low Wooded Island near Three Isles is 1.7 metres. Admiralty Chart Aus 832 (1978 ed.) shows tidal streams of 0.5 knots in velocity running approximately north-west and south-east in direction in the vicinity of Three Isles.

TABLE 5.3

COOKTOWN—WIND DATA

COOKTOWN POST OFFICE 15°28'S, 145°15'E

JANUARY 0900 HOURS LST

CALM 15

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	2	*						2
NE	4	1	1	*				7
E	3	1	1	*				5
SE	11	13	12	3	1	*	*	41
S	1	*						1
SW	4	3	2	*	*			9
W	3	2	1		*			6
NW	8	3	2	1	*			14
ALL	35	24	18	5	2	*	*	

NO OF OBS. 643

JULY 0900 HOURS LST

CALM 11

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	*							*
NE	*	*						*
E	*	*	*					1
SE	6	15	19	17	15	9	2	83
S								
SW	*		*					1
W	*	*						*
NW	3	1						4
ALL	10	17	19	17	15	9	2	

NO OF OBS. 647

JANUARY 1500 HOURS LST

CALM 4

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N	2	1	1	*				4
NE	7	8	5	*	*			21
E	2	3	2	*	*			8
SE	7	13	18	7	1	1		46
S	1	*	*					1
SW	1	1	*	*		*		3
W	*	1	1	*				2
NW	3	2	2	1	*			10
ALL	24	30	30	10	2	1		

NO OF OBS. 644

JULY 1500 HOURS LST

CALM 1

DIRN	1 TO 5	6 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 & UP	ALL
N								
NE	3	2	*					5
E	1	1	*					2
SE	5	15	24	22	15	7	2	91
S		*	*	*		*		*
SW			*					*
W								
NW								
ALL	9	18	25	22	15	7	2	

NO OF OBS. 642

SPEED (KM/HR)

Source: Burear of Meteorology, Surface Wind Data, 1978

TABLE 5.4

CAPE CLEVELAND, CARDWELL, COOKTOWN—TEMPERATURE AND RAINFALL DATA

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
CAPE CLEVELAND													
AVERAGE DAILY MAX. TEMP.	30.6	29.8	28.8	27.6	24.9	22.9	22.3	23.5	25.4	28.1	29.6	31.1	27.1
AVERAGE DAILY MIN. TEMP.	24.6	24.3	23.6	22.3	20.0	17.9	17.3	18.1	19.9	21.9	23.5	24.5	21.5
AVERAGE DAILY MEAN TEMP.	27.6	27.0	26.2	25.0	22.4	20.4	19.8	20.8	22.6	25.0	26.5	27.8	24.3
AVERAGE MTH AND YR RAIN	243.0	350.0	233.0	56.0	31.0	40.0	17.0	10.0	13.0	21.0	47.0	78.0	1139
CARDWELL													
AVERAGE DAILY MAX. TEMP.	30.9	30.5	29.9	28.6	26.3	24.6	24.1	25.2	26.9	28.5	29.9	31.1	28.1
AVERAGE DAILY MIN. TEMP.	22.1	21.9	20.9	19.0	16.3	14.1	12.5	12.8	20.8	17.4	19.6	21.1	17.7
AVERAGE DAILY MEAN TEMP.	26.5	26.2	25.4	23.8	21.3	19.3	18.3	19.0	23.6	22.9	24.7	26.1	22.9
AVERAGE MTH AND YR RAIN	419.0	422.0	363.0	186.0	90.0	53.0	30.0	27.0	35.0	52.0	99.0	176.0	1956
COOKTOWN													
AVERAGE DAILY MAX. TEMP.	31.2	30.9	30.0	28.9	27.4	26.2	25.7	26.4	27.7	29.2	30.5	31.4	28.8
AVERAGE DAILY MIN. TEMP.	23.9	23.7	23.4	22.7	21.1	19.7	18.7	19.3	20.8	22.4	23.5	23.9	21.9
AVERAGE DAILY MEAN TEMP.	27.6	27.3	26.7	25.8	24.2	17.9	22.2	22.9	24.2	25.8	27.0	27.6	25.3
AVERAGE MTH AND YR RAIN	364.0	348.0	408.0	204.0	66.0	53.0	26.0	23.0	13.0	25.0	40.0	154.0	1724

The southerly drift caused by the north-west monsoon may be greater than the tidal flood to the north (Pickard 1977) but the lighter nature of the winds in this season do not affect the flow as much as the consistent south-easterlies in winter.

The coral colonies used in this survey were taken from three discrete zones, representing different energy conditions (see Figure 5.2). These were:

1. The shallow moated area on the north-west end of the platform between the cay and the end of the cemented rampart.
2. The front of the windward platform on the south-east edge, between the largest mangrove islet and the small mangrove patch referred to in Spender's map.
3. The moat system on the northern side of the reef between the cay and the largest mangrove islet.

The first area was a very shallow, sandy bottomed zone of coral and coralline algal cover (c.50%) off the north-west tip of the cemented rampart system. It is an area of strong tidal runoff, being the lowest part of the moating system on the windward side of the reef platform. Most of the colonies collected from this area were *Porites lutea*, although many Favids were present, mainly *Favites* spp. and *Favia* spp. Much soft algal growth occurred here, with long strands of the brown alga *Hydroclathrus* sp. attached to each coral patch. Small patches of *Thalassia* sp. appeared among the coral clumps. Twenty-one colonies of *Porites* were collected from this area.

The second collection area lay on the windward side of the platform, in a series of moats along the surf zone, formed by

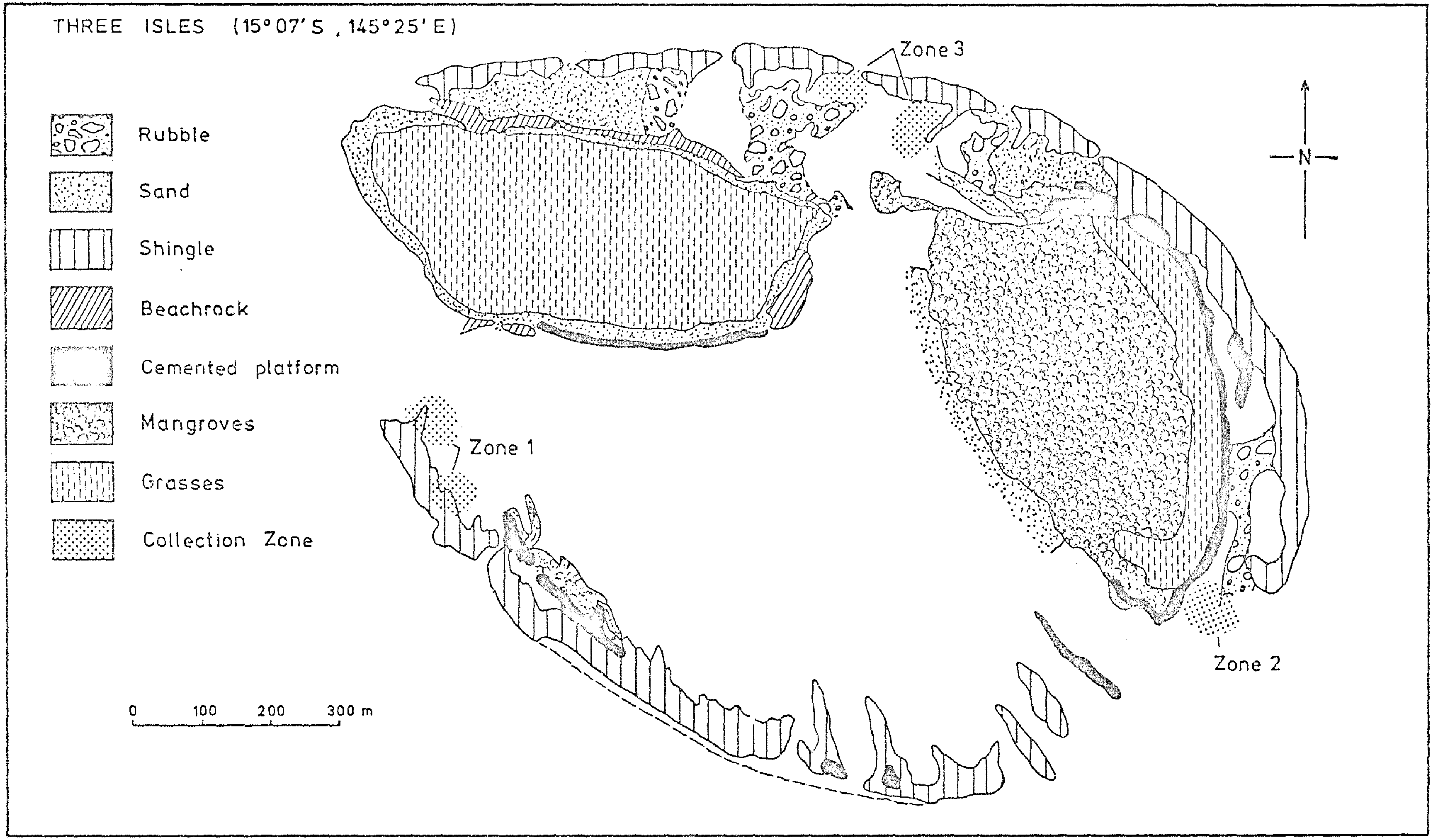


Figure 5.2 Three Isles—Morphology and Surface Zonation. Collection Sites Numbered 1-3.

heavily cemented ramparts. The moated pools ranged from 0.5 to 1.0m in depth at M.L.W.S., with the principal coral growth form being *Porites* microatolls, with typical dimensions of 12-15cm in height and 20-80cm in diameter. The substrate consisted of sand and shingle, quite bare and relatively mobile. Fourteen corals were taken for analysis.

The third collection area lay in a fairly deep (c.1m) moat behind a very large consolidated shingle rampart system. In places, this cemented wall of *Acropora* shingle reached 2.5 metres in height, and up to 50 metres in width. Small breaches in the narrower sections of the rampart allowed much of the impounded water to escape at low tide, but isolated pools remained. As in the previous area, the colonies of *Porites* in these moated pools were almost the sole scleractinian genus found there. They were principally *P. lutea* and very regular in shape and size. The substrate is *Acropora* shingle, cemented in some places, but mostly unconsolidated. The moated water probably reaches about 30°C during mid-day neap tides in the summer months, as many were found to be quite warm at that time, though no quantitative measurements were undertaken. Nineteen colonies were collected from this area.

The areas sampled at Three Isles represented the widest possible range of shallow water environments that could be found on the reef platform, in terms of exposure to wave energy and possible low tide temperature and salinity effects.

Analysis and Results

The results of analysis of the variances between the zones on Wheeler Reef have been presented earlier. In a similar fashion, data are presented here for the two remaining reefs involved in this section of the study, Barnett Patches and Three Isles. The Barnett Patches colonies show slow growth at the windward and leeward margins, with faster growth on the central reef flat. The zone of maximum annual growth was the windward reef flat. The zonal pattern of growth rates on Three Isles showed fastest growth on the leeward margin, followed by the windward reef flat, with the slowest on the central reef flat. The 95% limits of the means for the different zones are plotted in Figure 5.3(a),(b). After equalising the number of replicates in each zone, analysis of variance showed that the variations in growth rate between zones on both Barnett Patches and Three Isles was significant (Table 5.5).

TABLE 5.5

ONE-WAY ANALYSIS OF VARIANCE TESTS OF GROWTH RATE VARIATION BETWEEN DIFFERENT ZONES ON EACH REEF (COCHRAN'S C=.493, .452 RESPECTIVELY, VARIANCES HOMOGENEOUS)

Barnett Patches	SS	df	MS	F	Sig.
Between zones	.251	2	.125	4.165	.033
Within zones	.542	18	.030		
Total	.793	20	.040		

Three Isles	SS	df	MS	F	Sig.
Between zones	.857	2	.429	5.47	.009
Within zones	2.586	33	.078		
Total	3.443	35	.098		

Having done this, the data for all three reefs (Wheeler Reef, Barnett Patches, and Three Isles) were analysed together. The analytical method used was again similar to that used for the single reef study in Chapter Four. The numbers of replicates within

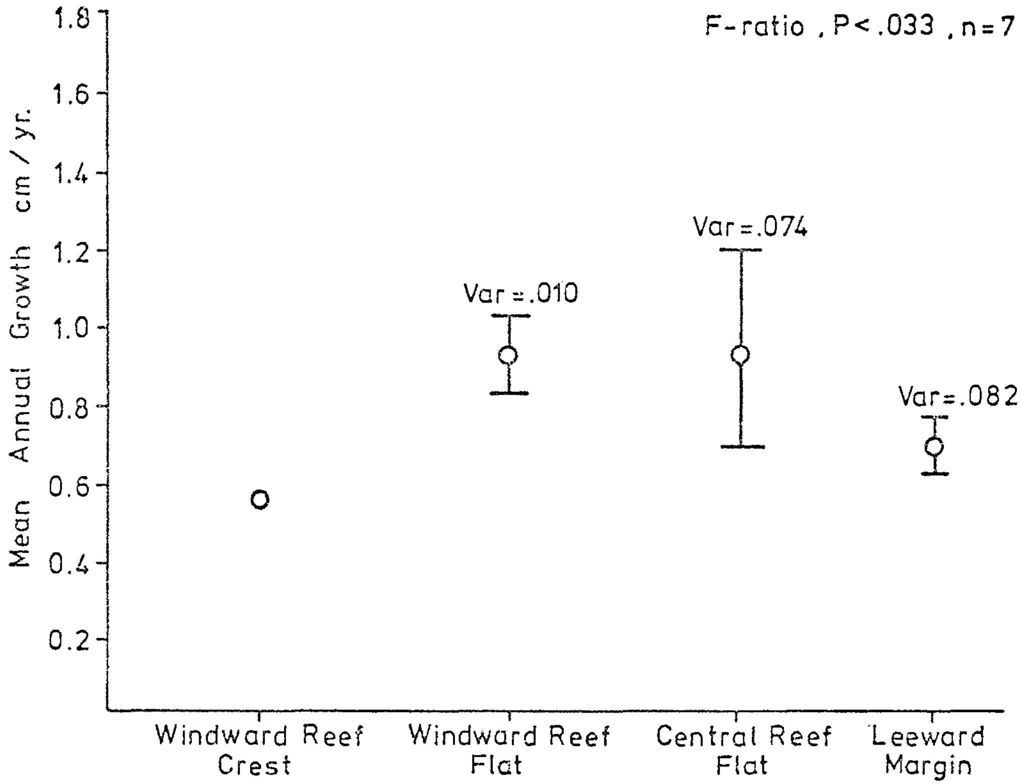


Figure 5.3(a) Barnett Patches—Zone Growth Means

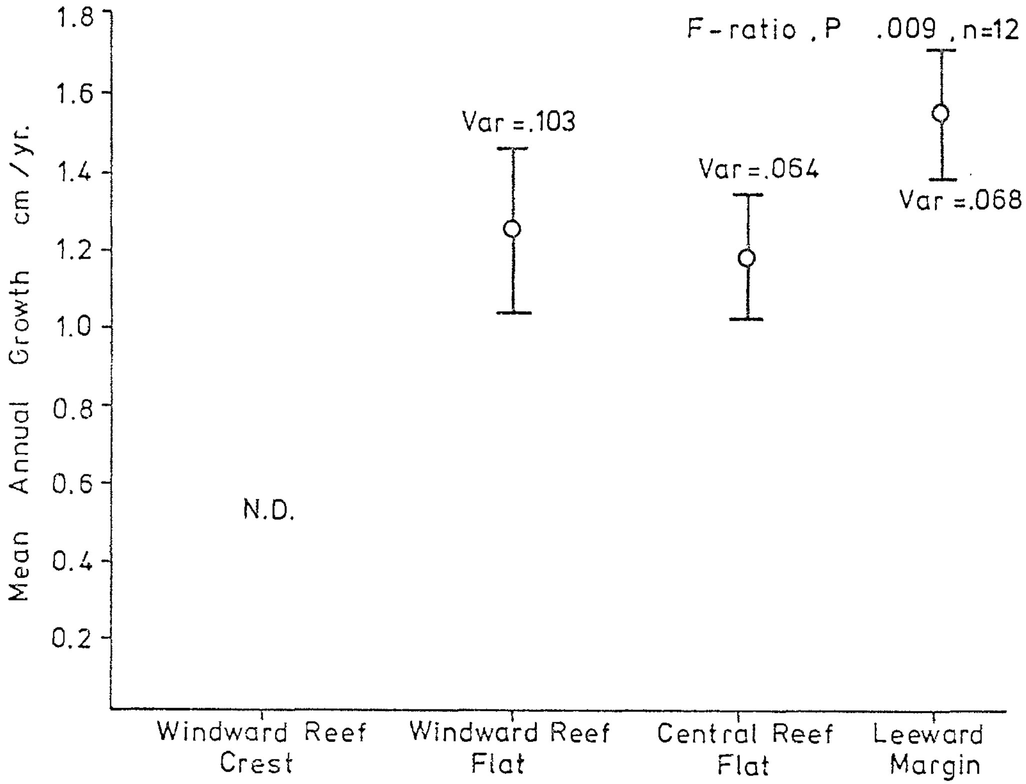


Figure 5.3(b) Three Isles—Zone Growth Means

each zone on each of the three reefs were random sampled to provide a balanced design for analysis of variance. The variances of the growth means on the three reefs were found to be homogeneous and significantly different from each other (Cochran's C=.479, variances homogeneous, F-ratio, P<.001). The results are given in Table 5.6.

TABLE 5.6

ONE-WAY ANALYSIS OF VARIANCE TEST OF GROWTH RATE VARIATION BETWEEN THREE DIFFERENT REEF TYPES

	SS	df	MS	F	Sig.
Between reefs	5.7	2	2.8	38.7	.000
Within reefs	5.7	78	.07		
Total	11.5	80			

The growth rate data from the three reefs were then subjected to a two-way analysis of variance to test for the existence of any interaction effects between reef variances and zone variances. (i.e. if similar zones did not show similar trends between reefs). Table 5.7 reveals just such an effect in the present case. There is a significant interaction between zones of one reef and different zones on the others (F-ratio, P<.001). The plot of the zone means for each of the reefs (Figure 5.4) shows the nature of the interaction. The leeward reef margin zone growth mean for Barnett Patches is lower than that of the central reef flat on that reef, whereas the opposite holds true for the other two reefs.

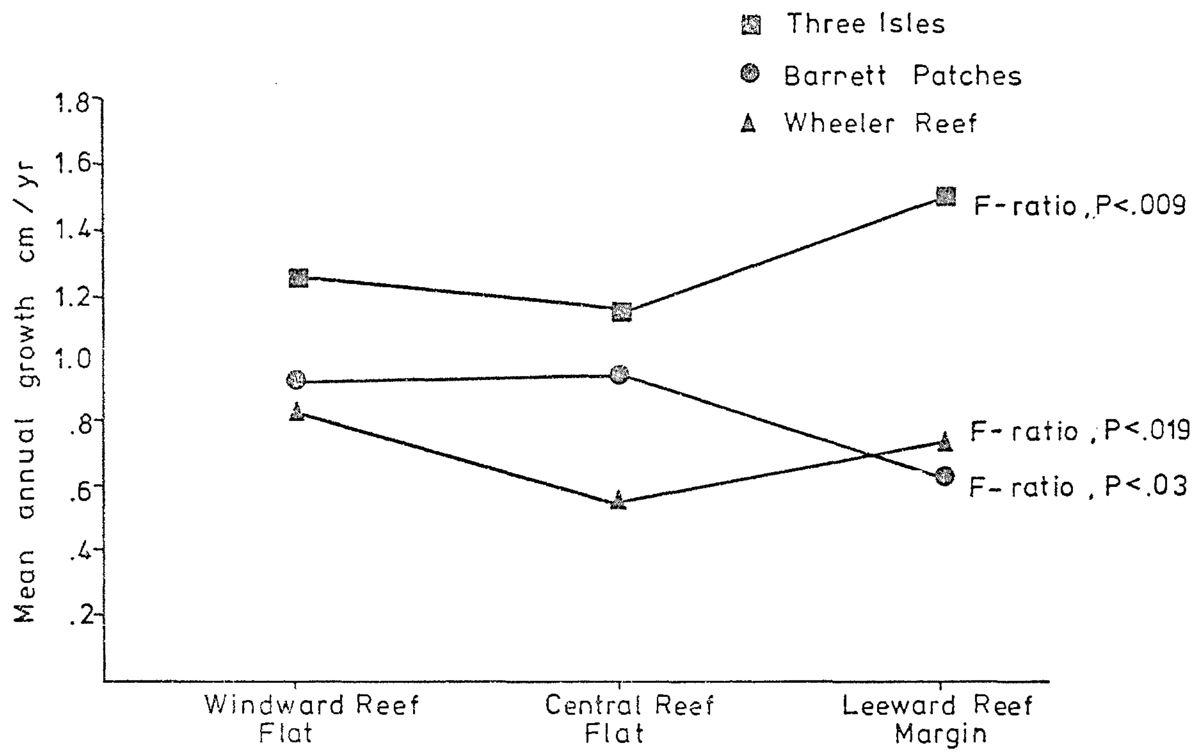


Figure 5.4 Wheeler Reef, Barnett Patches, Three Isles—Zone Growth Means and Interaction Effects

TABLE 5.7

TWO-WAY ANALYSIS OF VARIANCE TEST OF GROWTH RATE VARIATION AMONG REEFS AND ZONES

Source of Variation	SS	df	MS	F	Sig.
Main Effects					
Reef	5.74	2	2.87	49.3	.000
Reef zone	.423	2	.211	3.63	.031
2-way Interactions					
Reef/Reef zone	1.17	4	.293	5.03	.001
Explained	7.332	8	.917	15.76	.000
Residual	4.188	72	.058		
Total	11.52	80	.144		

Discussion

In the previous chapter it was pointed out that significant differences existed between the mean growth rates of corals from different zones on a single reef platform. The analysis of the data in this section from three different *types* of reef platform supports the proposition that mean zonal growth rate also differs according to the type of reef upon which it occurs. The earlier contention that structural zonation of the reef platform is important to the ordering of habitats or zones in energy terms is supported by the data. Figure 5.2 shows that the highly structured reef, with distinct vertical, as well as horizontal zonation (Three Isles) has discrete growth rate zonation patterns. The least structured reef (Barnett Patches) shows a distinct zonation in growth rate pattern, but in a different order to that of Three Isles. The reef version which lies in between these two reef types (Wheeler Reef) has a more concentric zonal pattern, although similar in order to that of Three Isles.

It is possible to explain these findings in terms of the reef descriptions given in the earlier part of this chapter. The higher the reef platform, the more the zonal pattern reflects the prevailing water movement (energy) regime. Thus the high reef platform of Three Isles reef is strongly zoned with very distinct variation in energy levels and height with respect to tidal fluctuation. This distinctiveness of the zones is paralleled by the growth behaviour of the corals. In contrast, the much lower and more uniform Barnett Patches shows a much less distinctive pattern of growth rates. Wheeler Reef is intermediate between these two extremes in terms of both its zonation pattern and the distinct nature of its growth patterns.

SECTION 2: Variation in Growth Rates Across the Continental Shelf

The continental shelf that forms the foundation of the Great Barrier Reef Province varies in width from less than 16kms (at 14°S) to more than 200kms (at 21°30'S). The influence of terrestrial inputs such as fluvial sediments, fresh water, and coastal biogeographical entities (e.g. mangroves) declines outward across the shelf. Thus, while the shelf edge reef communities in the Swains or Pompey Complexes (more than 150kms from the coast) are not influenced to any degree by terrestrial inputs, the ribbon reefs and mid-shelf reefs around the Cape Melville area can be affected by factors originating on the coast and hinterland. The existence of driftwood logs on Three Isles with rocks enmeshed in their root systems illustrates this point. The influence of the large circulating masses of oceanic water outside the Province margin is less well documented, though the principal effect of this impinging on the shelf is probably as much a function of its lack of organic nutrients as any more positive influence.

This section studies the effect of location on the shelf on the growth rates of 30 colonies of *Porites* from similar zones on four reefs near Townsville. The reefs used in the analysis were Viper Reef, on the extreme edge of the shelf west of Townsville, Wheeler Reef, towards the mid-line of the shelf, and the fringing reefs of Magnetic Island and Rattlesnake Island, slightly north of Townsville (considered jointly). The three sites lie in a relatively evenly spaced sequence along an east-west line across the continental shelf. The colonies from each reef were collected from the leeward margins (the leeward zone, shown to be the most conducive for *Porites* growth at Wheeler: previous section) in similar depths.

Viper Reef is a small platform reef which has a crescentic shape. Hopley (1978) has shown the reef to be relatively young, radiocarbon ages from the reef top being younger than 2700 years. To the east of the reef, the sea floor drops away to depths of over 100 metres in less than 3kms. Depths to the west of the platform are of the order of 30-40 metres. The corals used were taken from the leeward edge of the platform near the lagoon entrance in about 1 metre of water (M.L.W.S.).

The corals from Wheeler Reef used in the analysis were those from Zone 4, described in the previous section.

The fringing reefs of the two high granitic inshore islands, Magnetic and Rattlesnake, are similar to each other in appearance and structure. Both the collection sites on these islands were close to the shoreline in water less than 2 metres deep (M.L.W.S.). Small non-perennial creeks or gullies flow through the Quaternary sediments and decomposed granite fans and out over the reef flats.

The reef edges support a variety of species of hard corals, principally Favids and small branching *Millepora* spp. The inner part of the reef is covered with brown algae among the numerous massive *Porites* heads, which form microatolls where moating occurs. Radiocarbon ages in excess of 5000 years have been obtained from Rattlesnake Reef (Hopley 1980), which is slightly emerged on its inner edge.

Analysis and Results

Ten colonies from the leeward margin zone (or its fringing reef equivalent) were used as the basis for an analysis of variance routine to determine whether the location of those sample groups with respect to their locations across the continental shelf had any effect on growth rate. The null hypothesis that there was no significant difference between the variances of the group means on each reef was rejected (F-ratio, P<.05). Results of the analysis are presented in Table 5.8.

TABLE 5.8

ONE-WAY ANALYSIS OF VARIANCE TEST OF GROWTH RATE VARIATION BETWEEN SIMILAR ZONES FROM SELECTED REEFS ACROSS THE CONTINENTAL SHELF NEAR TOWNSVILLE. (COCHRAN'S C=.645, VARIANCES HOMOGENEOUS)

	SS	df	MS	F	Sig.
Between reefs	.470	2	.235	7.70	.0023
Within reefs	.824	27	.031		
Total	1.295	29			

Figure 5.5(a) shows the respective group means plotted with 95% confidence limits. The growth rates of the Viper Reef corals are lower and less variable than those of the two locations further

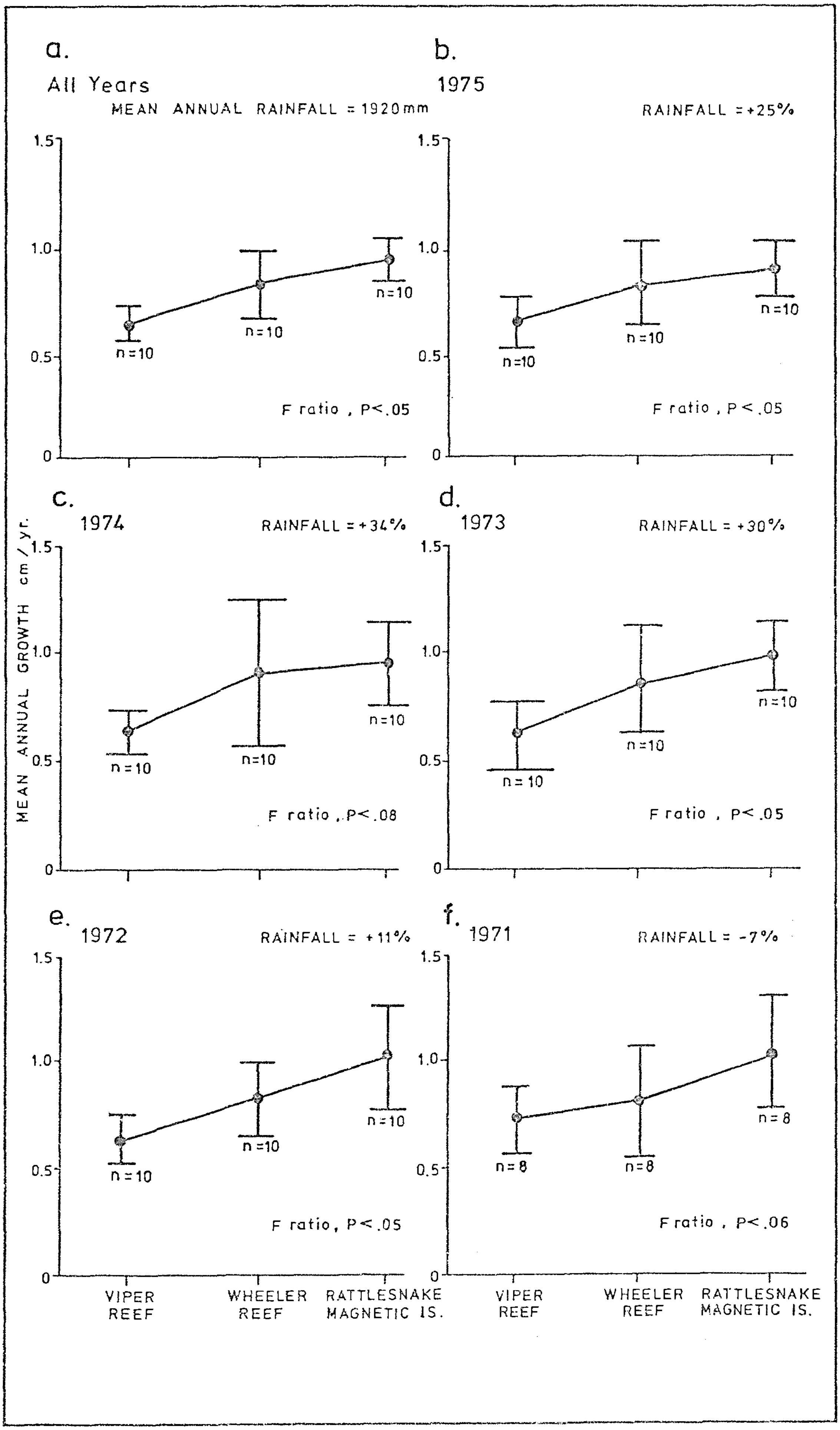


Figure 5.5 Cross-shelf Variation—Leeward Zone Means Plot

inshore. Maximum growth rates (more than 1.0cm/yr) are obtained from the fringing reef colonies on Magnetic Island and Rattlesnake Island. The values for the Wheeler Reef corals lie between those of the shelf edge and the inshore reefs.

The annual growth increment of each colony for every year between 1971 and 1975 was obtained, and analysis of variance performed on the data on the same cross-shelf basis. In each year significant differences between growth rates were found (F-ratio, $P<.05$). Figure 5.5(b)-(f) shows that the overall sequence of a slow, consistent growth at the shelf edge grading to faster but more erratic inshore was maintained, although the values of the group mean for the mid-shelf reef corals (Wheeler Reef) varied with respect to the outer and inner reef colonies.

Discussion

The results of the analysis of growth rate data in the first part of this section (see Table 5.8) suggest that there are one or more environmental variables operating in a selective fashion on growth rates as the distance from the coast increases. The most obvious group of factors are those which are attributable to fluvially based salinity and organic nutrient variations. Fresh-water inputs to the nearshore fringing reefs such as Magnetic and Rattlesnake are certainly large enough during the summer wet season to lower the ambient salinity values. Pickard (1977) concludes that the lowest inshore salinity values occur in February in the Townsville region, in conjunction with the coastal rainfall maximum. Recent work reports that the inshore salinity values in the area to the immediate north of the Burdekin River outfall drop to as low as 10 parts per thousand in flood periods (Wolanski 1981). The fringing reefs on Magnetic Island are only a few kilometres from the mouth of the Ross River, which has a heavy seasonal outflow. The Rattlesnake Island reefs lie somewhat further out to sea in Halifax Bay, but are still within the range of the wet season flow from the Bohle River and adjacent coastal streams. Whether the terrestrial runoff has any major effect on the mid-shelf reefs in the region such as Wheeler Reef is unresolved. Wolanski (1981) reports that the Burdekin plume at peak discharge does not reach that far out to sea. Surface salinities are also affected by rainfall directly, although to a smaller degree than river runoff. The proximity of the shelf edge reefs to the Coral Sea waters has a moderating influence on the salinity variation in these areas, as data from CSIRO (Rep. No. 88, Div. Fish. Oceanog. 1979, Figure 15) show.

The importance of organic inputs from terrestrial sources in the present scheme can only be subjectively evaluated, due to a lack of knowledge of the exact requirements of *Porites* from this source, and the dearth of quantitative information on the subject for this region. It is recognised that the oceanic waters of the Coral Sea are less endowed with organic nutrients than the waters in the vicinity of the coast. The principal source of these nutrients inshore is assumed to be fluvial runoff, although extended periods of turbulence caused by strong south-easterly winds in the winter months (dry period) may dampen the seasonality of this feature by resuspension and mixing of sediments inshore. The relative growth means of the colonies for each year (Figure 5.5) were examined to attempt to determine the magnitude of the effects of such factors as river runoff-induced salinity changes and food availability. Rainfall data for each year are included for each year on the plotted growth data. The percentage values on each graph refer to the amount of rainfall in that year relative to the 21 year annual mean precipitation. The years are subjectively described as either dry, normal, wet, or very wet. It can be seen that the growth rate values for the corals from Viper Reef and the inshore fringing reefs are relatively stable through time. The apparent oscillation of the mean growth values from the mid-shelf reef (Wheeler Reef) follows a pattern that is consistent with the trend of annual rainfall over the five-year period. The Wheeler Reef coral growth rates are depressed during drier years, and elevated with respect to the rates from the other two shelf locations during wetter years. The mean salinity values over the whole of each year may be said to be lower inshore, and higher at the shelf edge, yet the growth rates of the inshore corals were greater in all cases. This either indicates a negative growth-salinity relationship, or is an artifact caused by the exclusion of other more important variables from the case. The former conclusion is supported by the increased rates of growth for the mid-shelf reef during wetter years, although one must assume that salinity drops sufficiently in the region of that reef during those periods. The positive effect of increased nutrient supply on growth rates during wet years is easier to postulate from the data, as comparison between Figure 5.5(c) and Figure 5.5(f) shows. It is clear from the above that more environmental data would be an asset to the construction of any hypothesis concerning growth rates and terrestrial *vs* oceanic influences. For example, the conjunction of high rainfall periods with increased cloud cover may introduce the latter as a factor of importance. The results suggest a positive relationship between growth rate and cloud cover. This conflicts with the findings of Glynn (1977), who found that the growth rate of *Pocillopora* on Saboga Reef in the Gulf of Panama declined with increasing cloud cover. A test of the strength of the terrestrial/ oceanic influence on growth is made later in this chapter.

SECTION 3: Cross-Shelf Variation Among Different Reef Types

It has been shown that there is a significant difference between growth rates of colonies of *Porites* from different zones on different types of reef. We also know that the location of those reefs on the continental shelf has a singificant effect on the value and variability of the colonies' growth rates. This section combines the two types of reef division made in the last sections and analyses the variability of growth among different types of reef which are also spread across the shelf.

Early workers noted the cross-shelf change in reef morphology north of Cairns. Hedley (1925) described the shelf between 17^{o}S and 19^{o}S as "recovering from a drowning movement." Spender (1930) proposed a scheme of classification for the reefs and reef-islands of this area in terms of their height, which in turn dictated the type of sediments found on the reef platofrms. He formed the opinion that the inner reefs of the shelf had reached the upper limit of growth in sheltered water, while the outer reefs were lower and had not yet reached their upper limit. The idea of outer shelf subsidence was also referred to by Fairbridge (1950), principally for the area to the south of Cairns, where the outer barrier is well below modern sea level. He noted also that the inner reefs south of Cairns were small, with large sediment trains, and described them as being "more juvenile" than those north of Cairns. Hopley and Harvey (1981) have used C^{14} datings and level surveys to confirm the decline in elevation to seawards, concluding that the shelf edge reefs are younger and that significant downwarping has occurred between Cairns and Townsville. There is, therefore, in this area a combination of the factors which in the previous sections were shown to have influence on the growth rates of *Porites*, i.e. with increasing distance across the shelf there is a distinctive change in reef morphology. The arrangement is such that the two factors should reinforce each other and provide very distinctly different populations of growth rates across the shelf from the different reef types.

To test this assumption, this section examines the growth rates of 48 colonies of *Porites* from three different morphological reef types lying across the continental shelf just north of Cooktown. The reef types chosen represented the island-reefs of Spender, found in the inner section of the shelf, the mid-shelf reefs such as Eyrie Reef, which are mostly platform reefs with unconsolidated sediments, and either well-formed or incipient sand cays, and the third type, the elongated shelf-edge ribbon reefs. A total of 16 colonies was selected from three zones on each reef.

Analysis and Results

The group mean growth rates for each reef zone (windward reef flat, central reef flat, and leeward reef margin) were plotted according to the reef type on which the colonies were found (Figure 5.6). Two-way analysis of variance techniques were employed to examine the differences between zones among reef types. Table 5.9 shows that the group means between zones were significantly different, as were the reef means. A significant interaction effect was also evident.

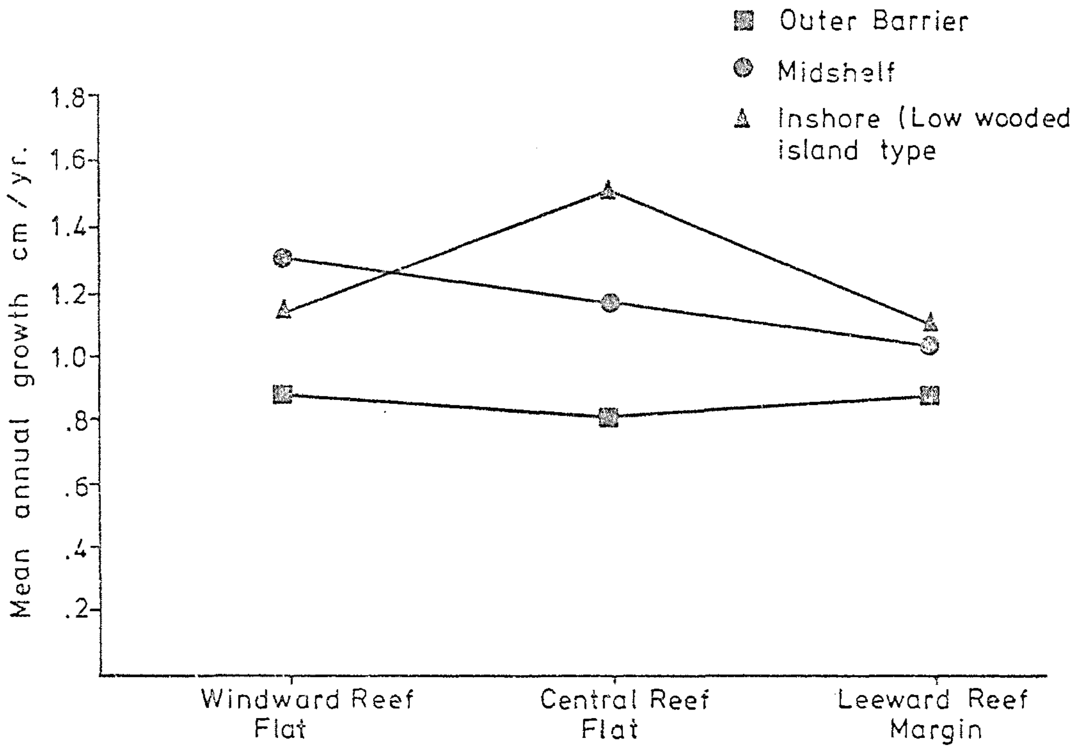


Figure 5.6 Cross-shelf Variation—Contrasting Reef Types—
Zonal Means Plot

TABLE 5.9

TWO-WAY ANALYSIS OF VARIANCE TEST OF GROWTH RATE VARIATION AMONG DIFFERENT ZONES ON DISSIMILAR TYPE CROSS SHELF REEFS

Source of Variation	SS	df	MS	F	Sig.
Main Effects					
Reef type	2.67	2	1.33	18.65	.000
Reef zone	1.36	2	.682	9.52	.000
2-Way Interactions					
Reef type/Reefzone	1.214	2	.607	8.48	.000
Explained	5.478	6	.913	12.76	.000
Residual	7.801	41	.072		
Total	13.279	47	.115		

Discussion

The data from this analysis support the findings in Chapter Four and those of the first two sections of this chapter. Mean zonal growth rate differs significantly according to the type of reef it occurs on, and a significant interaction effect is found between reef zone variance and reef type variance. The very distinct differences in the growth rate population indicated by the degree of significance of the results from this exercise clearly support the original premise that a combination of different reef types aligned across the shelf will produce contrasting growth rates.

SECTION 4: Cross-Shelf Variation on a Provincial Scale: Terrigenous *vs* Oceanic Influences

From the foregoing section we can say that at a particular latitude, coral growth changes in both rate and variability as we move from the shoreline towards the edge of the continental shelf. This section tests the relative strengths of the oceanic and terrestrial influences on growth rate, using the total data collected by the survey, allowing for the fact that the continental shelf varies in width by factors of up to 12 times. The hypothesis takes account of the fact that there must be a finite limit on the distance over which any of the sourced variables can operate significantly by introducing an absolute value for each colony in terms of distance from shore and shelf edge. It postulated that variability in growth rates should be more influenced by the more changeable influences from the landward side, since the principal feature of oceanic influences is their constancy or lack of variability of intensity.

Analysis and Results

The distance of each reef coral population from open ocean and from shore was measured in nautical miles from the relevant Admiralty Chart. The northernmost colonies were from Port Moresby, and the southernmost from Heron Island (see Figure 2.1). Landward distance was termed "L" and oceanward "O". Spearman Rank correlation coefficients were computed for the relationships between mean colony growth rate, standard deviation, and L and O (Table 5.10).

TABLE 5.10

CORRELATION BETWEEN GROWTH RATE AND DISTANCE TO LAND/OCEAN

Mean with L	-0.4584	sig. $P<.001$
Mean with O	0.2200	sig. $P<.001$
S.D. with L	-0.2089	sig. $P<.001$
S.D. with O	0.1719	sig. $P<.001$

Discussion and Results

The relationship between growth rate and both distance variables was highly significant. There was a much stronger correlation between landward distance and growth (negative) than between open ocean distance and growth (positive). The standard deviation of mean annual colony growth rate followed the same pattern, although the strength of these relationships was weaker, but still significant.

The hypothesis was supported by the data. Terrestrial influences on growth rate (producing higher but more variable annual growth) are more important than oceanic influences (producing lower but less variable annual growth rates). It is suggested that the more consistent nature of the open ocean environmental variables induce less departure from the "normal" growth rate pattern because of their passive nature, while the terrestrial factors induce greater variability in growth because of their wider range of intensity and erratic nature. An example of this phenomenon would be the moderating effect of oceanic salinity levels as compared with the widely varying effect of fluvial runoff.

SECTION 5: Other Province-Scale Variations

The moderating effect of a more stable environmental regime such as that occurring on the edge of the continental shelf has a vertical counterpart which operates over the whole Province depth. Variables such as temperature (especially on shallow reef flats), light availability, and to some extent salinity, show a fairly large range of variation with depth. While the latter two vary only over large depth ranges (greater than, say, 10 metres), water temperature on reef platforms varies considerably within the tidal range of a reef. Moated pools on exposed reef flats often reach more than 30°C during summer mid-day low spring tides.

Much work has already been done on the effect of depth on coral growth rates (see summary by Buddemeier and Kinzie 1976, and Highsmith 1979). This study examines some of the simple relationships between growth rate and selected independent variables, taking into account the depth ranges from which the experimental colonies were taken.

Analysis and Results

The corals from the whole of the Great Barrier Reef Province were graded into two classes: those from water less than 1 metre deep, and those from deeper areas.

Analysis of the data was undertaken using discriminant analysis. This technique distinguishes between two or more groups of cases on the basis of discriminating variables. These variables measure the characteristics on which the groups are expected to differ, while ancillary tests provide measures of the success of the classification. In the present example, the colonies, having been divided into "surface" and "deeper" corals, were discriminated on the basis of their means and standard deviations. Almost two-thirds of the 452 colonies used in the analysis were "classifiable" on the basis of their growth rate and variability (Table 5.11).

TABLE 5.11

CLASSIFICATION RESULTS-DISCRIMINANT ANALYSIS, GROUPS DEFINED BY DEPTH, N=452

Actual Group	No. of Cases	Predicted Group Membership	
		(Surface)	(Deeper)
Surface Corals (0.00-1.00m)	224	130 58.0%	94 42.0%
Deeper Corals (1m +)	228	82 36.0%	146 64.0%

Percentage of "grouped" cases correctly classified: 61.06%

Discussion

The analysis supported the proposal that depth was a discriminating variable in determining growth rate, and growth rate variability (as measured by the standard deviation). The relative importance of the discriminant functions (mean and standard deviation) is shown in the summary table (Table 5.12).

TABLE 5.12

SUMMARY TABLE-DISCRIMINANT ANALYSIS-GROUPS DEFINED BY DEPTH

Step Entered/Removed	Vars. In.	Wilk's Lambda	Sig.
1. Standard Dev.	1	.978	.007
2. Mean	2	.946	.000

From the order of inclusion in the stepwise analysis, the standard deviation is seen to be the most important discriminant function of the two. We may conclude that the variability of the growth rate has higher powers of correctly classifying the colonies into populations according to the depth at which they grew.

The technique does not describe the *direction* of the function "variability" with respect to the action of the variable DEPTH. However, from the knowledge gained in Section 2 of this chapter regarding the effect of more stable environments such as those found on the outer edge of the continental shelf on growth rate variability, we may surmise that the relationship is negative in direction, i.e. the greater the depth at which a coral grows, the less variable is the growth rate, a finding which is supported by previous work (e.g. Dodge and Vaisnys 1980).

SECTION 6: Province-Scale Variation in Month of Mid-point HD Band Deposition

Introduction

During the course of this study, it was noticed that the time of deposition of the HD bands in colonies varied from reef to reef. While these findings do not conflict with the idea of seasonality of banding in hard corals, they are interesting in their spatial pattern.

Analysis and Results

The X-radiographs of the coral slices were examined in conjunction with the data concerning their date of collection, and reef location. Many colonies from reef flat areas possessed the smaller (lunar monthly) bandings within the annual density band regime. From these colonies, the months of HD banding deposition were calculated. The mid-point of this month range was then determined to ± one month, one per reef. These values were then regressed against latitude (Figure 5.7).

The data revealed that there was a positive, significant correlation between decreasing latitude and the passage of time throughout the year. The mid-point of the HD band was laid down progressively later in the year the further north the corals grew, from October/November at 21°S, to April at 15°S.

Discussion

The literature concerning the environmental factors which influence density banding in hermatypic corals is summarised by Dodge (1978, unpub. thesis) up to that date, revealing a confusing

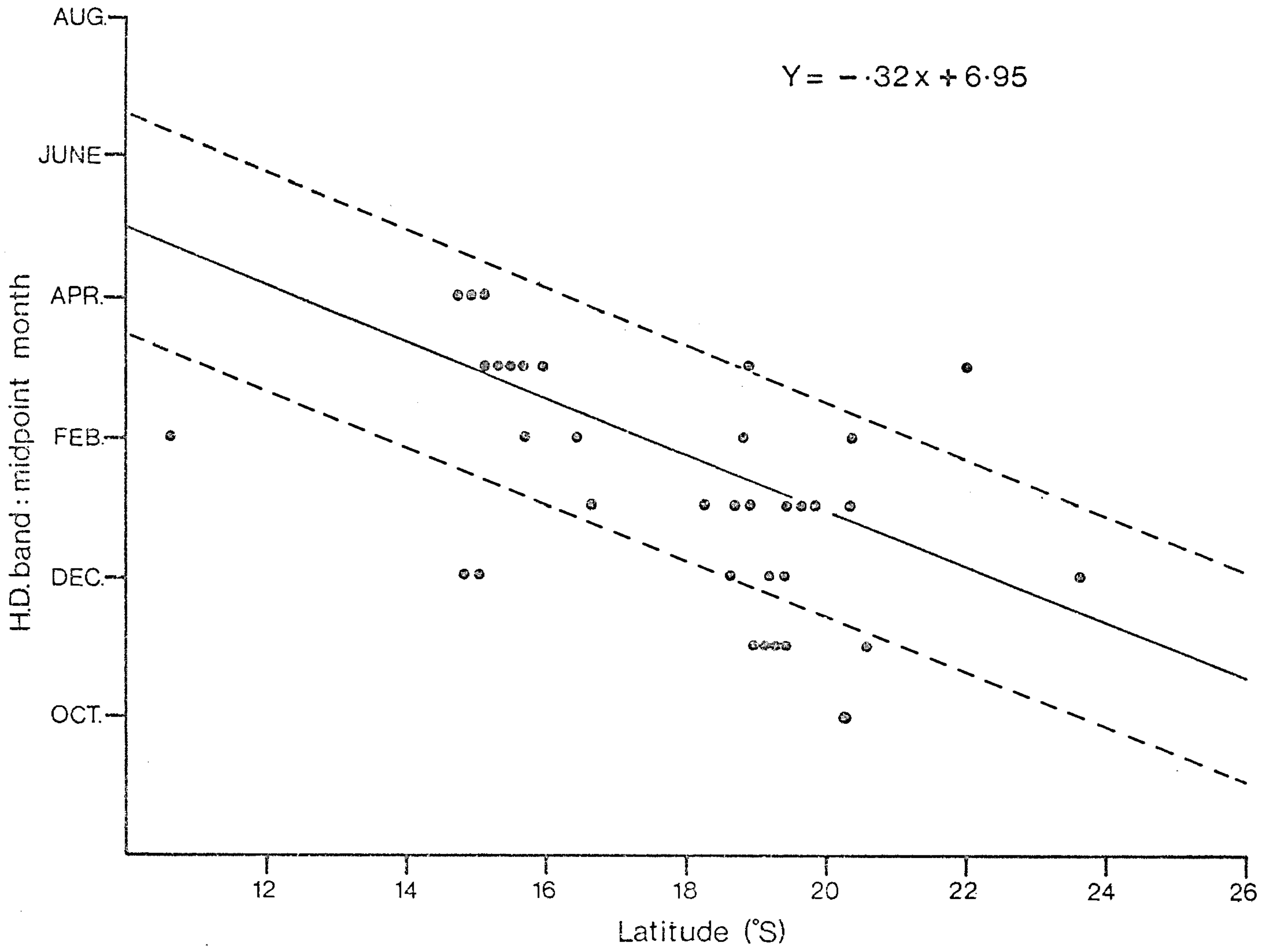


Figure 5.7 HD Band Mid-Point Deposition Time *vs* Latitude

pattern of findings in respect of the seasonal timing of density band formation and the contributing variables to that phenomenon. Among other factors reckoned to be important to the production of the HD bands in coral skeletons, Dodge's summary quotes high rainfall, warm water, and reduced light. In contrast, Buddemeier and Kinzie (1975) report a LD band/warm water relationship from Hawaii. The same authors found that the nature of the HD band consisted of a thickening of the trabecular walls of the corallites. This agrees with the findings of Dodge and Vaisnys (1980) who equate HD bands with thickening of the skeletal elements such as septa and dissepiments. Highsmith (1979) proposed a model of density band formation which states that the production of the skeletal matrix of the coral is accelerated relative to the rate of extracellular calcification about an optimum temperature of around 27^{o}C, forming a LD band at that point. The HD bands are formed either side of these optimum conditions. He also states that extracellular calcification is not independent of light intensity, suggesting that decreasing light levels may reduce the widths of the LD bands relative to those of the HD bands.

As reported in Chapter Two, the density peaks in the colonies collected from the Great Barrier Reef Province for this study occurred in the late summer, with densities reaching their minima in late winter. The late summer months (January to April) form the period when the ten-year average temperature field isotherms retreat northward, the 27^{o}C contour moving from Moreton Bay to north of Cooktown in that time. The data for the movements of this isotherm and the 28^{o}C isotherm are plotted against the months of the year in which they occur in Figure 5.8 (data from CSIRO 1978). The regression line for the northward migration of the HD band mid-point is super-

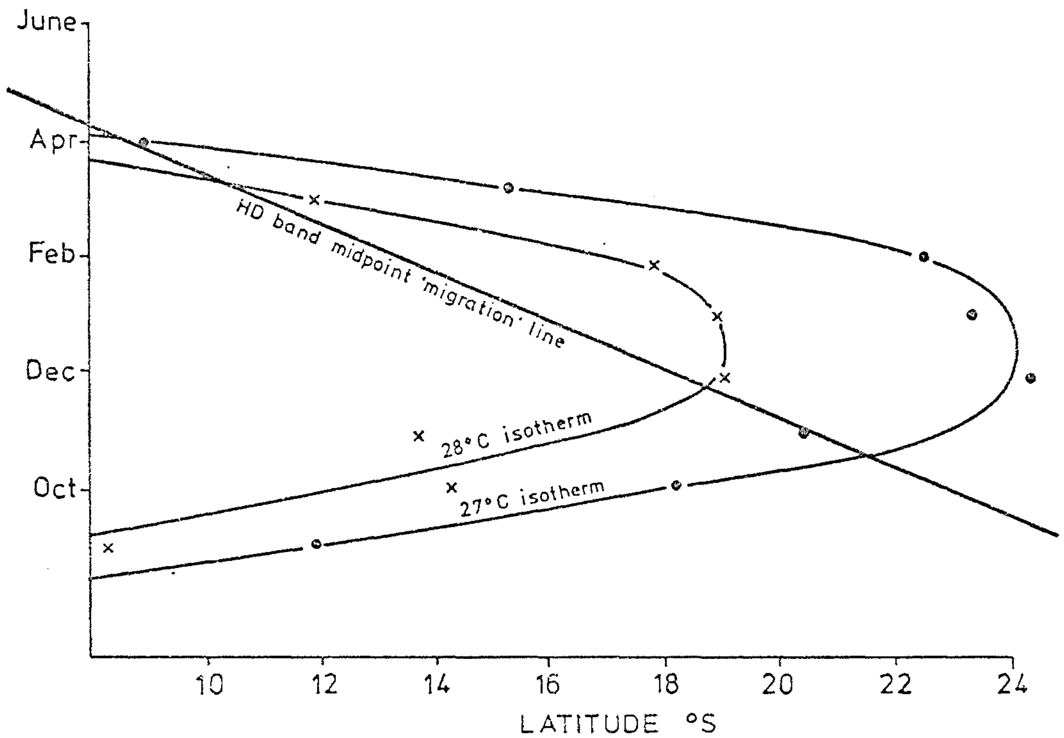


Figure 5.8 Isotherm Movements, Surface Waters of Province *vs* Latitude

imposed on the plot. Examination of the residuals in this graph reveals that the regression line most closely fits the data derived from the movement of the 27^{o}C isotherm along the coastline. If the line is phase-shifted, the fit becomes weaker in the case of both lines at the ± one month level, although a slight shift of about half a month forward in time indicates that a fit as good as the in-phase fit is obtained (Figure 5.9). This shows that there may be a small lag-time response of HD deposition to water temperature change. The line of "migration" of the high density banding parallels the northward movement of the 28^{o}C isotherm after about December.

The latitudinal movement of these surface water isotherms does not entirely explain the shift in the time of deposition of the HD band mid-point. It seems that water temperature is not the only controlling variable of density banding. Highsmith's model is not supported with regard to increase in density under reduced light levels, since the onset of the "wet season" occurs in December-January in most years (see Table 5.2), with greater cloudiness in the wetter north of the Province, and the density mid-point does not reach this area until after March. It is clear that more data are needed on other "migrating" influences in order to find an explanation.

SECTION 7: Latitudinal Variation Among Species

As it was not possible to statistically describe the species of *Porites* collected at anything more than a nominal level, the consideration of the effect of this factor on growth rate was treated separately from other variables. The question of genetic controls on growth was alluded to in Chapter One. A great deal of evidence is available to show that different genera of scleractinians

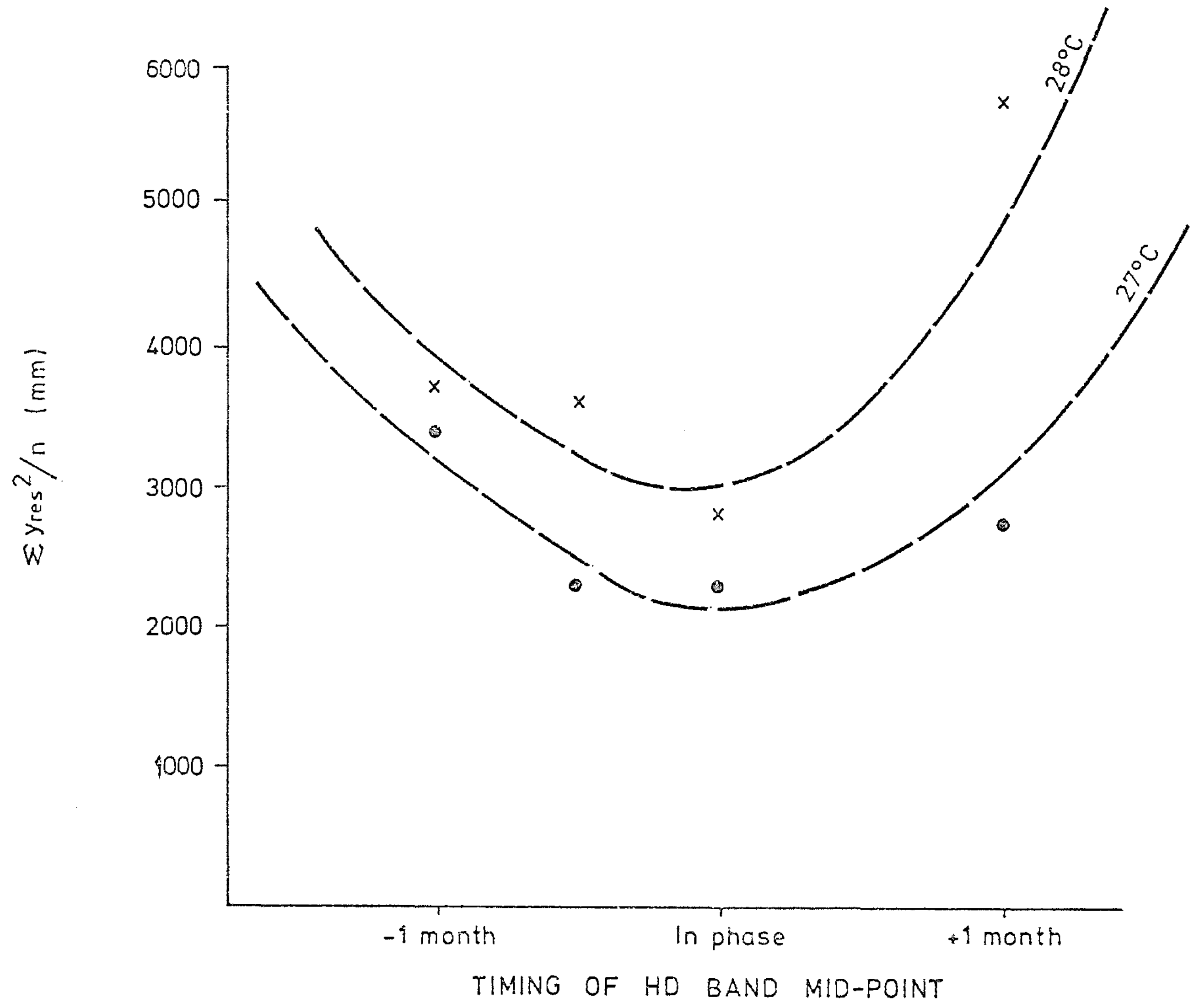


Figure 5.9 Best Fit of HD Band Timing to Surface Isotherm Movement

grow at different rates, even among similar morphological types (see Highsmith 1979, p.107, for example). What is not so well documented is inter-specific growth rate variation, especially among the massive Indo-Pacific corals.

Genetic "blueprints" determine the growth form of a coral colony within the constraints of the local environment. Among the Acroporidae, some species form stunted branching colonies on the high energy reef crest, while the same species take on a more elongated staghorn form in the sheltered waters of the back-reef slope (Veron and Pichon 1976). This same effect can be seen in *Porites* on most reefs, with flattened, encrusting forms living on the reef front, and large rounded colonies on the reef flat.

This section describes the analysis of growth rate patterns according to species. Five species were used (see Table 5.14), the criterion for selection being a sample number of replicates exceeding 30 colonies (more than 5% of the total *Porites* collected). The species are all similar in gross morphology when found in similar environments, but the finer skeletal characteristics of the coralla may differ.

The aim of the study was to identify differences between the species growth means, and determine any spatial patterns of species growth responsė. The variable LATITUDE was selected as a surrogate variable containing elements of many other factors (such as available light, salinity, and surface water temperature), against which the pattern of species growth response was to be measured. This had the additional benefit of forming a model of preferred latitudinal distribution for each species.

Analysis and Results

The mean annual growth rates for each of the five species chosen was plotted, with 95% confidence limits (Figure 5.10). One-way analysis of variance was used to test for the significance of differences between the means for each species (Table 5.13). Significant differences did exist (F-ratio, P<.000) with the order of rank of the species means as shown in Figure 5.10. The mean annual growth rate was correlated with latitude for each species (Table 5.14).

TABLE 5.13

ONE-WAY ANALYSIS OF VARIANCE TEST OF DIFFERENCES BETWEEN SPECIES GROWTH MEANS. (COCHRAN'S C=0.216, VARIANCES HOMOGENEOUS)

Source of Variation	df	SS	MS	F	Sig.
Between Species	4	4.03	.57	6.45	.000
Within Species	448	38.11	.088		
Total	434	43.15			

TABLE 5.14

SPEARMAN RANK CORRELATION COEFFICIENTS : SPECIES MEAN GROWTH *vs* LATITUDE

Species	Mean	Standard Dev.	Spearman Rank (R)	Sig.
P. lobata	.893	.32	-.322	.003
P. lutea	.841	.26	-.206	.012
P. australiensis	1.046	.31	-.110	.114
P. mayeri	.834	.26	-.192	.032
P. murrayensis	1.069	.34	-.367	.015

The five species fall into two distinct categories of growth means, the "slow growers" (*P. lobata*, *P. lutea* and *P. mayeri*), and the "fast growers" (*P. australiensis* and *P. murrayensis*). All of the slow

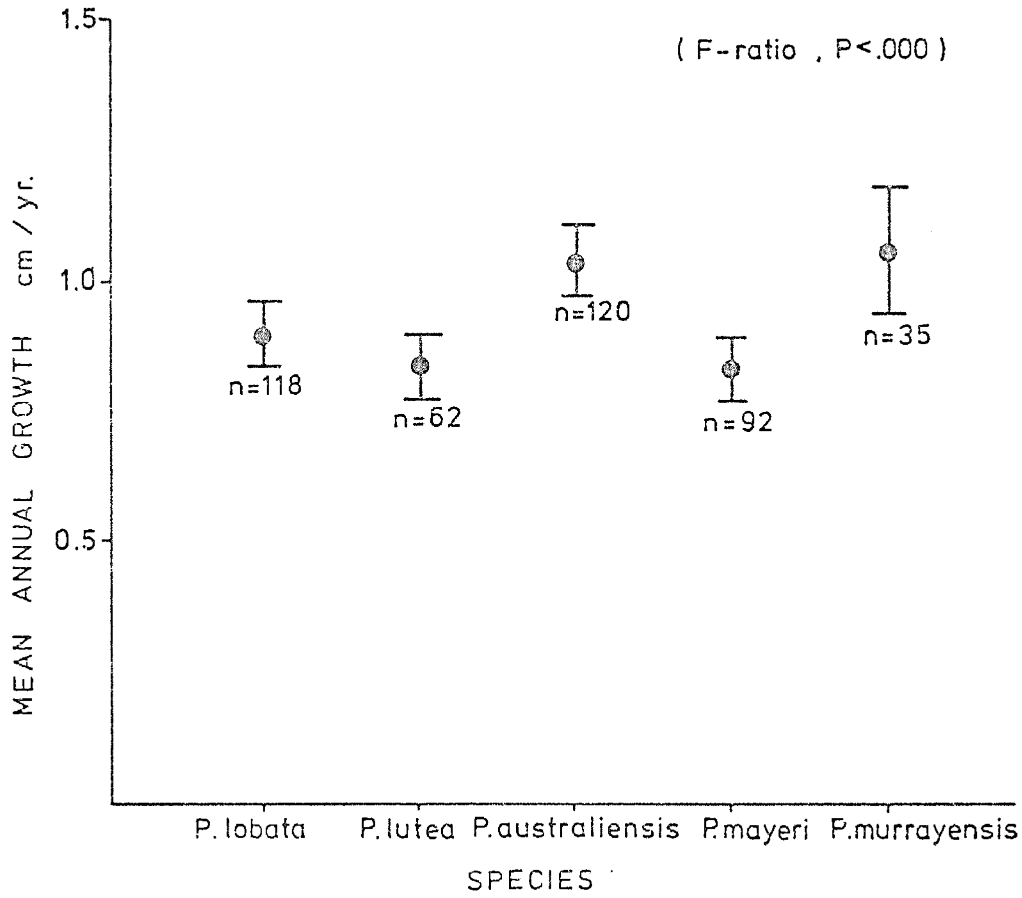


Figure 5.10 Mean Annual Growth Rate of Five Species of *Porites* (95% Confidence Limits)

growers showed a significant relationship with latitude, while only one of the faster growers was significantly related. *P. australiensis* was not significantly related to latitude.

Discussion

The ranking of the significantly-related species in terms of their R-value gives an index of preferred latitudinal range for each. Those with higher coefficients of determination (*P. lobata* and *P. murrayensis*) are more growth responsive to the latitude at which they grow, while those with low R-values are the least particular about their location (*P. lutea* and *P. mayeri*). Further down the scale, the corals which are not significantly related to latitude at all may not have any locational preference (*P. australiensis*). Each of the species above is found throughout the latitudinal range of the Province, although two (*P. lobata* and *P. lutea*) may be found further south in the Solitary Island area, off the coast of New South Wales (Veron and Pichon, in press).

CONCLUSIONS

This large-scale approach to growth rates of *Porites* has demonstrated a number of geographically significant characteristics:

1. Morphologically different reef types produce growth rates which cluster into distinct populations.
2. Patterns of growth change with distance out across the continental shelf. This appears to be related to terrigenous influences more than oceanic ones.
3. Where different morphological reef types are aligned across the shelf, these patterns are reinforced.
4. It is confirmed that the depth at which the corals grow

also has an effect on skeletal extension rate. Variability was at a maximum on the reef flat where environmental fluctuations are greatest, a situation which is similar to that produced across the shelf, where the largest environmental fluctuations occur closest to the mainland.

5. The different species of *Porites* show at least two patterns of growth, varying in both rate and response to parameters controlled by latitude.

6. The timing of the deposition of the mid-point of the HD band varies with latitude over a five month period.

The significance of these findings will be discussed in the final chapter.

CHAPTER SIX

PATTERNS OF CORAL GROWTH RATES

This investigation has been concerned with the patterns of coral growth rate variation which exist within the Great Barrier Reef Province. Studies were carried out into the nature and timing of sequential density banding in massive *Porites* colonies, and the data from these findings were used to analyse the geographical patterns of variance in coral growth. The scale of investigation ranged from small reef pools to Province-wide.

X-Radiography and Density Banding in *Porites*

The X-radiographic techniques utilised in this research were based on the work of Knutson *et al.* (1972), Buddemeier *et al.* (1974), Moore and Krishnaswami (1974), Macintyre and Smith (1974). However, they were modified to allow faster screenings, so that as large a number of corals as possible could be used in the project. Most industrial-type X-ray machines and processes use exposure times of between 30 seconds and two minutes, whereas the medical machines such as the one used in this research use rapid exposures at higher voltages. Buddemeier (1978) warns that faster exposures mean loss of contrast and resolution. This research has shown that the use of low-density contrast mammography film removes this limitation, producing very reasonable results (see Figure 2.4(a)-(c)). Parallax error at the specimen edge is avoided by the use of a fine focal spot and large object distance. Some colonies of *Porites* which were X-rayed did not show a sequential density banding of light and dark bands on the X-radiographs. These colonies were found in association with others which did produce banding, indicating that some factor in addition to micro-environmental controls must have been influencing the formation of density bands. The nature of these is unknown.

The application of microdensitometric measurement to X-radiographs required careful theoretical reasoning. Plates were scanned along only one line of growth—the axis of maximum length. The justification for this approach lies in the fact that only relatively hemispherical colonies were used in the research, so that there was seldom a large discrepancy between the greatest and smallest axis of colonial growth. Further, the parameter "axis of maximum growth" is comparable between colonies in absolute terms.

The annual nature of the pairs of high and low density bands in hermatypic corals has been demonstrated by many comparative methods, such as radioactive labelling in the skeletal framework, and vital staining of growth surfaces. These have been summarised by Buddemeier and Kinzie (1976). This research confirms the annual spacing of density bands in *Porites* from the Great Barrier Reef Province, by using Alizarin stainings at seasonal intervals to compare with X-radiographically determined bands. The periodicity of stainings allowed each type of density variation within a year's growth to be correlated with a season of the year. High density deposition occurred between October and March, while low density skeleton was laid down from April to September. The use of the date of collection of each colony as a time marker against which to align the type of density band deposited at the growth surface made possible the determination of the month(s) of HD band deposition of colonies from each of the 34 reefs examined in the Province. As shown in Chapter Five, the timing of the mid-point of the HD deposition period is latitude dependent. The mid-point of the band occurred later in the year as one moved north. Recent work (Schneider and Smith, in press) on the correlation of density banding in *Porites* from the Hawaiian chain of islands with environmental changes indicated that thinner sections (0.45cm) for X-radiographic analysis reveal that the change from low to high density is relatively abrupt. The densitometer traces described in Chapter Two show that *Porites* colonies from the Great Barrier Reef Province have no such abrupt density shift. The continuum of density is a symmetrical curve for every annual cycle. Experimentation with thinner sections at the beginning of the research did not alter this phenomenon, but reduced the contrast between HD and LD bands. There appears to be no Great Barrier Reef counterpart to the rapid density shift reported by Schneider and Smith (in press) from Hawaii.

These authors introduce an alternative to the annual "pair-band" method of assigning seasonal effects to changes in skeletal density, noting that in both Hawaiian and Abrolhos Reefs, banding consists of one band per year. This band is composed of an abrupt shift followed by a gradation in density. They contend that improving or deteriorating conditions produce the density changes and claim they are "explaining some of the disagreement in the literature about season-density relationships." This disagreement has arisen from attempts to correlate environmental variables, principally water temperature and light intensity, with shifts in density in coral skeletons, (e.g. Buddemeier 1974; Macintyre and Smith 1974; Weber *et al.* 1975; Hudson *et al.* 1974; Dodge and Thomson 1974; Buddemeier and Kinzie 1975). While the oxygen isotope method of Weber *et al.* (1975) and later authors has tended to confirm the positive temperature-density relationship, the work of Schneider and Smith (in press) using Sr thermometry, shows no "systematic correlation" between the two. The results from this study suggest that the correlation between water temperature and/or related seasonal factors and density is positive.

The *Porites* from the Great Barrier Reef Province studied in this research exhibited a seasonal banding pattern coupled to a unique migratory northward shift. This could not be clearly correlated with any available environmental data for the region. No evidence of this type of shift has been reported elsewhere. The symmetrical density curves and the out-of-phase deposition periods within the Province may be a function of the large latitudinal range of the Great Barrier Reef, and the fact that it lies well within the limits considered conducive to coral growth. This may not be said about areas such as the Hawaiian Archipelago or the Abrolhos Group, which lie further towards the extreme latitudinal limits of growth.

Grigg (1981) examined the mean gross carbonate production for the Hawaiian Archipelago and reported that the rate for the northwest extreme of the chain was just sufficient to offset erosion and subsidence. Corals accounted for 20-60% of this production. Agegian (1981) refers to the increasing contribution of coralline algae compared to that of corals in carbonate production as the northern limits of the Archipelago are reached. The latter situation may explain the rapidity of density shifts in terms of sensitivity to environmental change, rather than the quality of the change itself. However, although these studies suggest changes in carbonate deposition latitudinally, there is no indication of any temporal variation in the laying down of HD and LD bands.

The occurrence of 12-13 very find high density bands within the annual "pair-band" sequence in shallow moated colonies of

Porites from Holbourne Island, north of Bowen, suggests that environmental changes on a lunar timescale may influence density variation within the skeleton. The central region of the Great Barrier Reef Province has a semi-diurnal tidal regime, with summer extreme low/spring tides mainly occurring at night, and winter lows in the daytime. Any radical temperature increases in moated waters tend to be ameliorated by this non-synchronisation. The intensity of any effect of solar radiation on a moated pool is a function of the time between isolation of the pool from the falling tide, and inundation from the flood. This period may be longer during spring tides. Buddemeier and Kinzie (1975) reported low density phases in skeletal deposition in *P. lobata* in association with the full moon on Oahu. These bands were only visible in the summer, low-density phase of the skeleton, and did not occur during the denser winter bands. In the discussion section of the same paper, Buddemeier suggests that periodic growth variation in corals such as *Porites* reflects the change in fullness of the moon. He suggests that bright moonlight may stimulate autotrophic genera to feed. Johannes and Tepley (1974) have shown *Porites* to be inefficient at catching zooplankton, so moonlight-response may be an important tool in the energy requirements of the genera.

Another suggestion for the lunar density variations in corals is based on reproduction activity. *Porites*, however, has been shown to have no lunar periodicity in spawning. Marshall and Stephenson (1933, p.237) demonstrated the release of planula from colonies of *P. haddoni* (cf. *P. australiensis* ?) extended from before January until May, 1929, and only decreased in June-July. The colonies from Holbourne Island used in this research presumably have no lunar spawning pattern. Thus, reproductive activity does not seem to explain any lunar variation in density banding for *Porites*. However, it may be of significance to the major seasonal banding observed in Great Barrier Reef corals, since the peak periods of planula release correlate with the deposition of densest skeleton. Final verification of this relationship awaits the acquisition of data showing whether the time of spawning alters as one moves up the coast, in the same manner as the HD band.

The resolution of discrepancies between density band data from the Great Barrier Reef Province and that from other areas may be aided by the collection of band-width ratios (HD:LD) according to latitude within the Province. Shifts in the proportion of one density type to another would indicate a closer liaison between changes in the environment and skeletal response.

Growth in a Uniform Environment

One of the most striking features about the growth rate, however measured, of any species of coral, even over short periods, is its variability. The work of Wood-Jones (1910) at Cocos-Keeling was the first to show that corals grew "in fits and starts" for no apparent reason. Mayor (1924) reported that a massive *Porites* in Pago Pago Harbour grew 37mm in diameter in 1917-18, not at all the following year, and a further 54mm in 1919-20. Buddemeier and Kinzie (1976) review variability in annual growth rates for the same species from equivalent macro-environments and report that both year-to-year intra-colony and inter-colony growth (on a larger time scale) vary by a factor of about two. The results of the analysis of growth rates of the *Porites* colonies from Fairey Reef in this research support this. As shown in Chapter Three, intra-colony growth rate varied year by year by almost exactly this factor (Figure 3.3).

Intra-colony variation occurs in most massive corals. Very few have perfectly regular hemispherical shapes. Differential radial growth may ensue in response to external or internal forces acting upon the colonial form. The example of microatoll formation is an indication of the extreme adjustment that a massive colony can make in response to adverse external influences. Exposure kills the upper surface of the growing hemisphere, so the colony expands laterally. Should the water level in the moated pool rise, the growing edge of the corallum begins to grow back inwards towards its dead centre, in an apparent effort to regain the original hemispherical shape. This desire to maintain a genetically determined form could be seen as an opportunistic response by individual corallites growing into newly created "free" space, were it not for the fact that groups of polyps are often found restructuring the growth surfaces of a colony to regulate the corallum's shape following injury or polypal crowding. Examples of both types of these activities can be seen in the section of the Holbourne Island microatoll in Chapter Two (Figure 2.9). In the present study, this intra-colony growth variation was excluded by using only those growth axes which had not experienced such modification.

Inter-colony growth variability is less explainable in terms of external influences. Within a micro-habitat, minor fluctuations in water quality/current/nutrient status conditions may exist. LIMER 1976 illustrated the patchy nature of plankton distribution on a reef flat. Either the selection of the small habitat on Fairey Reef in the present case failed to mask this variability, or some mediated response was being generated by the corals. Although the colonies selected for study were all identified as the one species on the basis of skeletal morphology, it is possible that sub-groups were being examined for similar growth trends. The difficulty of ensuring that identical (clonal?) sub-groups are investigated is presumably incapable of solution at present.

One approach to the total problem may be to look for zonation in growth responses within the microhabitat, by mapping colony positions prior to analysis. Checks could then be made for gradations or patterns within the pool population.

Growth on Single Reefs

Significant differences between the growth means of *Porites* colonies from discrete zones on the Wheeler Reef platform (as reported in Chapter Four) may have implications for the development of the reef itself. Differential coral growth rates at specific locations on the platform cause preferential growth of the reef surface where those corals are a major source of carbonate, in either sediment or matrix form. The nature of the contribution of corals to upward reef development depends largely on the species and growth form of the colonies in question. Mayor (1924) speculated that reef growth was probably three times faster in the Pacific because of the more rapid growth of the dominant coral *P. astraeoides* in that ocean, than in the Atlantic, where the slower growing *Orbicellar annularis* (*Montastrea*?) is the dominant massive coral. Corals such as *Acropora* species contribute to upward reef growth by producing a porous open framework and easily-broken down fragments, making them a major source of sediment in the reef system. The massive corals form a more wave-resistant matrix, and may contribute sediment only through the activities of bioeroders such as boring bivalves and sponges.

The differential rate of upward reef building is thus dependent on species and growth form distribution as well as growth rate. In the present study, the distribution of *Porites* on the Wheeler Reef platform precludes it from being a major carbonate producer since it is not common on the windward edge. Smith and Kinsey (1976) have published carbonate productivity measurements from both windward (seaward) and leeward (lagoonal or protected) environments. The figures, which are derived using the alkalinity reduction method on several reefs and atolls, show that windward area $CaCO_3$ production is five times that of the protected leeward or lagoonal environments. This phenomenon is interpreted by the authors to be "largely a function of variable water motion" (p.938). As Rosen's (1975) scheme postulates, the *Porites* biotype is confined to the deeper and/or more sheltered parts of the reef environment, unlike corals such as *Acropora* which are among the major carbonate producers of the windward regions.

Porites growth rates are important factors in the development of reef flats on the inshore fringing reefs of the Province. Kinsey and Davies (1979), from calcification values, propose a maximum vertical growth of 3.1mm/yr around the perimeter zone at One Tree Reef, using the figure of 50% porosity after normal aragonite compaction. They postulate that the central zones of the reef flat would have been subjected to growth-limiting factors, and lagged behind the vertical accretion rates of the perimeter. More recently, Kinsey (1981) proposed a model of calcification and community metabolism of increased complexity, forming the opinion that there are three modes of metabolic levels, from high energy environments, grading through a mixed mode of relatively high energy, and a low energy mode. This suggests that the vertical accretion rates from different parts of the reef flat may be higher than the 3.1mm/yr figure stated above. In zones of high coral cover, rates as great as 7mm/yr may be achieved. The zone of most favourable growth conditions for *Porites*, the leeward reef flat margin, should present rates of accretion approaching those of the colonies themselves. Where *Porites* is the dominant reef flat coral, the growth rates of the colonies are almost solely responsible for the upward growth of the flat. Hopley *et al.* (in press) report colonial growth rates of 11.3mm/yr (average) from Orpheus and Rattlesnake Islands, north of Townsville. Dating of cores from these same fringing reefs indicates vertical reef flat accretion rates of 6.7-7.3mm/yr. The cores reveal that the principal reef flat builders are the massive corals such as *Porites*. These colonies remain relatively intact within the cemented sediments after being buried, forming a solid matrix. The reef flat uses this matrix as a platform for further upward growth. Thus, where *Porites* is a dominant genus, as on a fringing reef or leeward patch reef, the the rate of reef accretion may be largely controlled by the rates of colonial growth, particularly when a small negative factor is introduced into the rate of skeletal deposition to account for bioerosion.

Growth Rates on Contrasting Reef Morphologies

The development of a reef platform from a veneer of corals on a deep substrate into a highly structured and vertically differentiated biolith standing above mean sea level, covers a period of changing environments within the boundaries of the platform itself. These changes are wrought by the development of the platform surface, in relation to sea level, becoming progressively more significant as mean sea level is attained. Hopley (1982, Chap. 10) describes the development in terms of change in the degree of environmental fluctuation, from the relative stability of the deeper water, to the diurnal and seasonal variability of shallow waters. Pichon (1974), working in Tulear, shows how energy gradients develop, differentiating windward environments from leeward. Sedimentary regimes and biological processes are affected, producing small variations in platform surface morphology and height. Feedback mechanisms among the biological components may develop, producing even greater differentiation in reef zonation over time.

The three contrasting reefs studied in Chapter Five are examples of different stages in the development of reef platforms as discussed above. Barnett Patches is a comparatively young, largely submerged, reef, Wheeler Reef is older and at or about M.S.L., while Three Isles is a senile, highly structured platform which, because of moating, rises to above M.S.L. The zonal growth rates revealed from the three reefs in this study are suggestive of the degree of change in zonal growth patterns which parallel the development of the reef platform, as it progresses from the Barnett Patches type, through the Wheeler configuration, to the senile Three Isles stage.

The zonal growth means plotted in Figure 5.4 show the sequence of development through time of the environments on a reef platform. The zonation on Barnett Patches is less discrete than on the other reefs. This is especially true of the different in growth means between the windward reef flat and the central flat, which is negligible, while it is significantly different on both Wheeler Reef and Three Isles. In energy terms, the windward and central reef flat environments are similar, principally due to the depth of the substrate, and the scattered location of the reefal elements. The leeward reef zone on Barnett Patches has a significantly different growth rate mean to the other two zones. The integrity of this zone may be a function of its location with respect to the protection of the largest of the reef patches (see Figure 5.1).

The zonation growth pattern on Wheeler Reef is an intermediate stage in the sequence. All the zonal means are significantly different, with the central reef flat becoming distinctive from the windward reef flat in zonation. This development parallels the upward growth of the platform at about M.S.L., with depth becoming a less important energy manipulator than reef platform configuration. Zonation becomes more concentric, with platform perimeter energy conditions determining windward/leeward zonation in growth rates.

Three Isles has a discrete zonation in the growth patterns of corals on the platform. The growth rate means in Figure 5.4 show that by the time the Three Isles stage of development is reached, the height of the reef flat *above* M.S.L. has become a significant factor in energy zonation.

The protection offered by the reef platform to its leeward perimeter sites is almost complete, with consequent improvement in the growth conditions of the calm water types such as *Porites*. This is reflected in the leeward growth figures for Three Isles (Figure 5.4).

The reef development sequence described by Hopley (1982, Chap. 8; reproduced in Figure 6.1) refers to Barnett Patches as an example of a juvenile reef, with irregular reef patches rising from substrate highs in the pre-Holocene surface (Type III). Wheeler Reef lies between the Type IV and Type VI reef, as an infilled multiple-lagoonal reef (Type V). The author

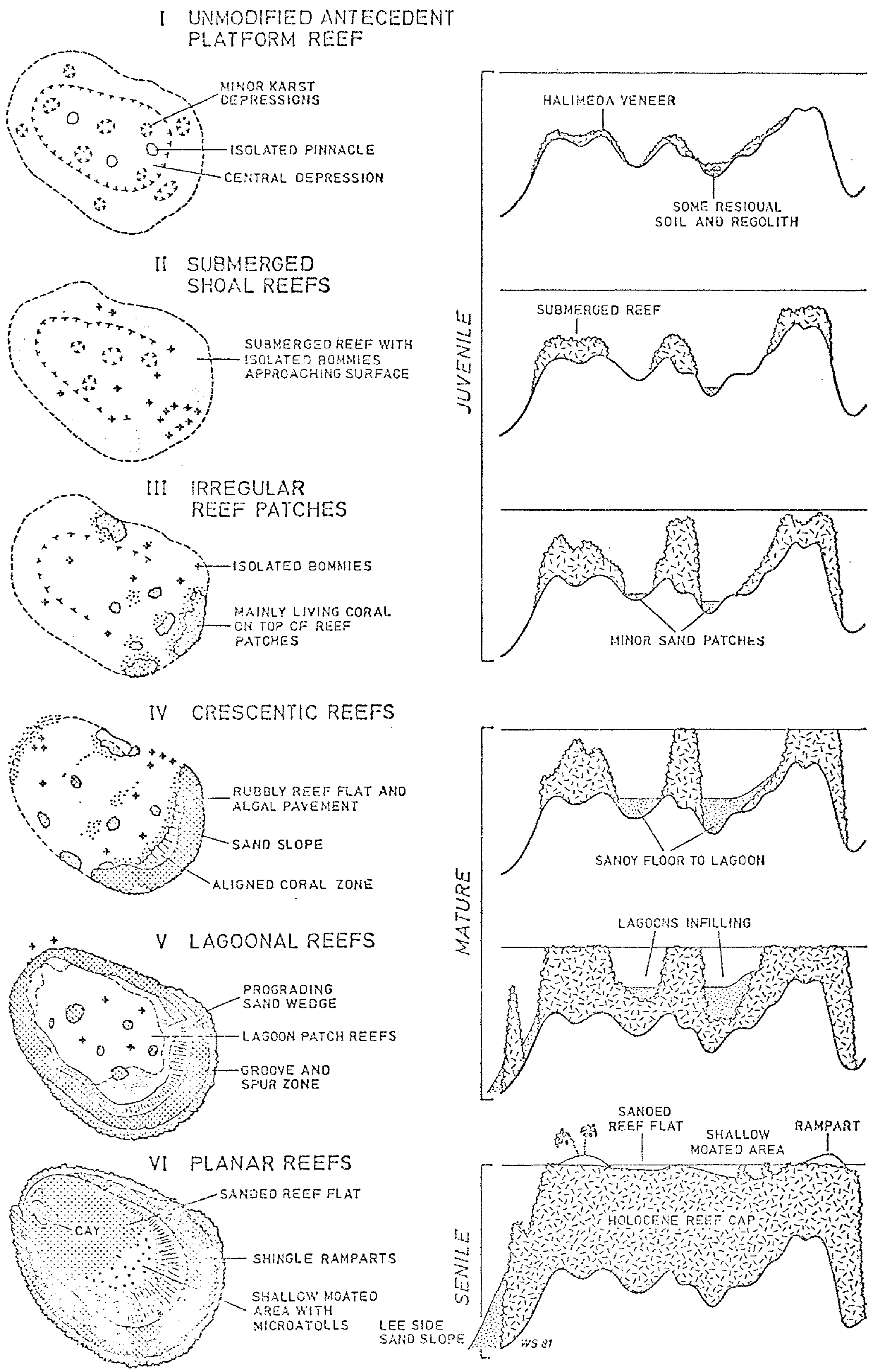


Figure 6.1 Reef Classification Scheme (Hopley 1982)

suggests that the multi-lagoonal (Type V) reefs can have relatively short existences, especially if the pre-Holocene surface upon which it grew was shallow or lacked significant relief. Three Isles is represented in the scheme as a senile planar reef (Type VI). It has reached the last stage in the development of the sequence, and consists of the sanded reef flat with microatoll formation in depressions, significant coral populations mainly on the leeward margins, and is colonised by mangroves behind a well developed rampart system.

The growth rates of the zonal coral populations concur with a changing pattern of energy-controlled environments through the sequence of reef development discussed above. The relative zonal growth means show the changing morphology of the platform as it approaches and passes M.S.L., turning from a juvenile collection of patch reefs to a senile planar reef. The occurrence of *Porites* increases through this sequence, beginning with few colonies among the dominant *Acropora* on the juvenile reefs, then becoming more in evidence in the lagoonal reefs, especially on the leeward reef flats, and finally dominating the coral assemblages in the moated margins and leeward shelves of the senile reefs.

For the above reasons, coral growth rates within a zonal framework may aid the classification of reef types into those sub-groups proposed by Hopley (1982) at some future stage.

Growth Rates Across the Continental Shelf

The relative growth rates of corals from the inner shelf reefs and those of the outer barrier reefs affect differential reef platform development according to shelf location. The data in Chapter Five reveal faster, erratic growth in corals on inshore reefs, grading to slower, more consistent growth on the outer reef platforms.

The intensity and frequency of occurrence of the environmental variables controlling coral growth determine the cross-shelf patterns. Intensity influences the growth rate, while frequency of effect alters the variability. Both the intensity and frequency of these controls decrease to seaward. This gradient suggests that controls on growth which are important in other parts of the world may not be as significant on the continental shelf margins of the Great Barrier Reef Province. Variability in growth rate is lower at the shelf edge, indicating the effect of distance from the coast on controlling-variable intensity, resulting in a lack of stimulation and/or repression of growth. Shelf edge conditions such as seasonal upwelling do not appear to be significant influences in the Province (compare with the findings of Glynn 1977, in the Gulf of Panama).

The depression of growth rates in the shelf centre during years with less-than-average rainfall indicates the centre section may be a transition zone, with the intensity of climatic events being the limiting factor. The influence of terrestrial factors can be seen to be more important than those from oceanic regions, since it is clear that there are no "dry" season effects which vary from the ocean direction. The correlation coefficients measuring the significance and relative strengths of the land/ ocean influences on growth (Chapter Five) support this conclusion.

The cross-shelf growth rate pattern for corals may have a parallel in the contrasts between continental shelf reef accretion rates and atoll growth. Hopley (1982, Chapter 8, Table 8.3) summarises the data from the literature on the published results of radiocarbon dating of reef cores from Caribbean and Indo-Pacific reef areas relating to accretion rates of different reef types. These show that fringing reefs from both oceans have the largest rate of upward growth, followed by shelf, bank, or barrier reefs, with atoll development being the slowest. It would be of interest to know whether growth rates for coral *colonies* reflect this pattern, but a search of the available literature reveals that not enough species have been measured from each location to make this comparison. The findings of this study suggest that coral growth rates should vary between fringing reefs, barrier reefs, and atolls in much the same manner as the cross-shelf pattern within the Great Barrier Reef Province.

Multivariate Relationships: Coral Growth and Environmental Controls

In Chapter Two it was pointed out that only those statistical techniques which could be used with non-normally distributed data were utilised in this analysis. The distribution of colony growth values from the Province is plotted in Appendix B. This spread of values is possibly within the ambit of parametric analyses, so the application of these methods was attempted, to provide an interesting, if less robust, measure of the combined influences on coral growth rate. The results of this statistical exercise should be regarded as indicators of relationships rather than definitive measurements.

Several independent variables were chosen against which to regress growth rate. These were variables which had shown that they were related to growth in earlier analyses. Age of colony was chosen as a genetic parameter, latitude, shelf-zone, and reef zone and depth as locational variables, and the mean annual rainfall as an environmental variable. With this mix of independent variables, the relative effects of each type of influence on growth rate could be found.

Multiple regression runs on the annual growth values with the independent variables indicated that the total portion of the variability of growth rate which could be explained in terms of those variables was very low (Table 6.1).

TABLE 6.1

MULTIPLE REGRESSION: SELECTED VARIABLES AGAINST GROWTH RATE (DEPENDENT VARIABLE: MEAN ANNUAL GROWTH RATE)

Variable	Mult. R	R. Square	beta
Age	.311	.096	-.28
Latitude	.419	.175	-.26
Shelf-zone	.469	.220	.213
Mean ann. rainfall	.501	.251	-.206
Reef zone	.505	.256	-.113
Depth	.513	.264	.105

The indication for this type of analysis is that, for any large ecosystem such as the Great Barrier Reef, the selection of variables against which to regress such measures as growth data is of prime importance. In the present case, the independent variables used may not be the most influential variables, or there may not be enough independent variables in use in the analysis. The development of a reliable data base from which to choose measures of environmental variables seems essential if more than a cursory effort is to be made to describe the patterns of coral growth using multivariate techniques.

REFERENCES

Agegian, C. (1981) The growth of coralline algae in the Hawaiian Archipelago. *Abstracts, 4th Int. Coral Reef Symp.* Manila, Philippines.

Aller, R.C. and R.E. Dodge (1974) Animal-sediment relations in a tropical lagoon—Discovery Bay, Jamaica. *J. Mar. Res.* 32: 209-232.

Backshall, R.G., J. Barnett, P.J. Davies, D.C. Duncan, N. Harvey, D. Hopley, P.J. Isdale, J.N. Jennings and R. Moss (1979) Drowned dolines—the blue holes of the Pompey Reefs, Great Barrier Reef. BMR. *J. Aust. Geol. and Geophys.* 4:99-109.

Baker, P.A. and J.N. Weber (1975) Coral growth rate: variation with depth. *Earth and Planet. Sci. Lett.* 27:57-61.

Banner, A.H. (1968) A fresh-water "kill" on the coral reefs of Hawaii. *Tech. Rept No. 15.* Hawaii Inst. Mar. Biol., Univ. of Hawaii.

Barnes, D.J. (1971) A study of growth, structure and form in modern coral skeletons. PhD Diss., University of Newcastle-Upon-Tyne.

———— (1972) The structure and formation of growth-ridges in scleractinian coral skeletons. *Proc. Roy. Soc. Lond.* 182(B): 331-350.

———— (1973) Growth in colonial scleractinians. *Bull. mar. Sci.* 23:280-298.

Barnes, D.J. and C.J. Crossland (1980) Diurnal and seasonal variations in the growth of a staghorn coral measured by time-lapse photography. *Limnol. Oceanogr.* 25(6):1113-1117.

Bernard, D.M. (1905) *Porites* of the Indo-Pacific region. *Brit. Mus. (Nat. Hist.) Cat. Madreporarian Corals* (London). Vol. 5.

Brandon, D.E. (1973) Waters of the Great Barrier Reef Province. In O.A. Jones and R. Endean (eds), *Biology and Geology of Coral Reefs.* Vol. 1., Geology I. N.Y.: Academic Press.

Buddemeier, R.W. (1974) Environmental controls over annual and lunar monthly cycles in hermatypic coral calcification. *Proc. 2nd Int. Coral Reef Symp.,* Vol. 2. Brisbane: GBRC.

———— (1978) Coral growth: retrospective analysis. In D.R. Stoddart (ed.), *Handbook of Coral Reef Research.* SCOR/UNESCO.

Buddemeier, R.W. and R.A. Kinzie (1975) The chronometric reliability of contemporary corals. In G.D. Rosenberg and S.K. Runcorn (eds), *Growth Rhythms and the History of the Earth's Rotation.* London: John Wiley and Sons.

Buddemeier, R.W. and R.A. Kinzie III (1976) Coral Growth. *Oceanogr. Mar. Biol. Ann. Rev.* 14:183-225.

Buddemeier, R.W., J.E. Maragos and D.W. Knutson (1974) Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. *J. exp. mar. Biol. Ecol.* 14:179-200.

Chappell, J. (1980) Coral morphology, diversity and reef growth. *Nature* 286:249-252.

Chave, K.E., S.V. Smith and K.J. Roy (1972) Carbonate production by coral reefs. *Mar. Geol.* 12:123-140.

Clausen, C.D. and A.A. Roth (1975) Estimation of coral growth rates from laboratory ^{45}Ca-incorporation rates. *Mar. Biol.* 33:85-91.

Coles, S.L. and P.L. Jokiel (1977) Synergistic effect of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Mar. Biol.* 40:187-195.

Critchfield, H.J. (1966) *General Climatology*. N.J.: Prentice-Hall.

Daly, R.A. (1910) Pleistocene glaciation and the coral reef problem. *Am. J. of Sci.* 30:297-308.

Darwin, C. (1842) *The Structure and Distribution of Coral Reefs*. London: Smith, Elder and Co. (Repr. University of California Press, Berkeley, L.A.), 1962.)

Davies, P.J. (1977) Modern reef growth—Great Barrier Reef. *Proc. 3rd Int. Coral Reef Symp.* Vol. 2. Miami, U.S.A.

Dodge, R.E. (1978) The natural growth records of reef-building corals. PhD Diss. Yale University, New Haven.

Dodge, R.E., R.C. Aller and J. Thomson (1974) Coral growth related to resuspension of bottom sediments. *Nature* 247:574-577.

Dodge, R.E. and J. Thomson (1974) The natural radiochemical and growth records in contemporary hermatypic corals from the Atlantic and Caribbean. *Earth and Planet. Sci. Lett.* 23:312-322.

Dustan, P. (1975) Growth and form in the reef-building coral *Montastrea annularis*. *Mar. Biol.* 33:101-107.

Edmondson, C.H. (1929) Growth of Hawaiian corals. *Bull. Bernice P. Bishop Mus.* 58:1-38.

Edwards, R.J. (1979) Tasman and Coral Sea ten year mean temperature and salinity fields, 1967-76. *Rept. No. 88*, Div. Fish. and Oceanogr. Sydney: CSIRO.

Fairbridge, R.W. (1950) Recent and Pleistocene coral reefs of Australia. *J. Geol.* 58(4):330-341.

Franzisket, L. (1964) Die Stoffwechselintensitat der Riffcorallen und ihre okologische, phylogenetische und sociologische Bedeutung. *Z. Vergl. Physiol.* 49:91-113.

Gardiner, J.S. (1902) On the growth rate of some corals from Fiji. *Proc. Camb. phil. Soc. math. phys. Sci.* 11:214-219.

Glynn, P.W. (1974) Rolling stones among the Scleractinia: Mobile corallliths in the Gulf of Panama. *Proc. 2nd Int. Coral Reef Symp.* Vol. 2. Brisbane: GBRC.

——— (1977) Coral growth in upwelling and non-upwelling are off the Pacific coast of Panama. *J. Mar. Res.* 35:567-585.

Goreau, T.F. (1959) The ecology of Jamaican coral reefs. 1. Spec composition and zonation. *Ecology* 40:67-90.

——— (1961) Problems of growth and calcium deposition reef corals. *Endeavour* 20(77):32-39.

Goreau, T. and N. Goreau (1960) The physiology of skeleton formation in corals. III. Calcification rate as a function of colony weight and total nitrogen content in the reef coral *Manicina aerolata*. *Biol. Bull. mar. biol. Lab., Woods Hole* 118:419-429.

Goreau, T.F., N.I. Goreau and T.J. Goreau (1979) Corals and coral reefs. *Sci. Am.* August, pp.110-120.

Grigg, R.W. (1981) Coral reef development at high latitudes. *Abstracts, 4th Int. Coral Reef Symp.* Manila, Philippines.

Grigg, R.W. and J.E. Maragos (1974) Recolonisation of hermatypic corals on submerged lava flows in Hawaii. *Ecology* 55: 387-395.

Guppy, H.B. (1889) The Cocos-Keeling Islands. *Scott. geogr. Mag.* 5:281-297.

Harvey, N. (1978) Wheeler Reef: morphology and shallow reef structure. In D. Hopley (ed.), *Geographical Studies of the Townsville Area.* Dept. of Geog., James Cook Univ. of North Qld, Monogr. Ser. Occ. Pap. 2, pp.51-53.

Hedley, C. (1925) The natural destruction of a coral reef. *Rep. Gt Barrier Reef Comm.* 1:35-40.

Highsmith, R.C. (1979) Coral growth rates and environmental control of density banding. *J. exp. mar. Biol. Ecol.* 37:105-125.

——— (1980) Passive colonisation and asexual colony multiplication in the massive coral *Porites lutea*. *J. exp. mar. Biol. Ecol.* 47:55-67.

Hopley, D. (1978) The Great Barrier Reef. In D. Hopley (ed.), *Geographical Studies of the Townsville Area.* Dept. of Geog., James Cook Univ. of North Qld, Monogr. Ser. Occ. Pap. 2, pp.49-50.

Hopley, D. (1980) Mid-Holocene high sea levels along the coastal plain of the Great Barrier Reef Province. *Mar. Geol.* 35: M1-M9.

———— (1982) *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs.* N.Y.: John Wiley-Interscience.

Hopley, D. and P.J. Isdale (1977) Coral microatolls, tropical cyclones and reef flat morphology: a North Queensland example. *Search* 8:79-81.

Hopley, D., A.M. Slocombe, F. Muir and C. Grant (in press) *Nearshore fringing reefs in north Queensland: structure, growth and classification.*

Hudson, J.H., E.A. Shinn, R.B. Halley and B. Lidz (1976) Sclerochronology: a tool for interpreting past environments. *Geology* 4:361-364.

Jell, J.S. (1974) The microstructure of some Scleractinian corals. *Proc. 2nd Int. Coral Reef Symp.* Vol. 2. Brisbane: GBRC.

Johannes, R.E. and L. Tepley (1974) Examination of feeding of the reef coral *Porites lobata in situ* using time-lapse photography. *Proc. 2nd Int. Coral Reef Symp.* Vol. 1. Brisbane: GBRC.

Johnston, I.S. (1980) The ultrastructure of skeletogenesis in hermatypic corals. *Int. Rev. Cytol.* 67:171-214.

Jokiel, P.L. and S.L. Coles(1974) Effects of heated effluent on hermatypic corals at Kahe Point, Oahu. *Pac. Sci.* 28:1-18.

Kinsey, D.W. (1981) The absolute modal distribution of reef community metabolism and calcification. *Abstracts, 4th Int. Coral Reef Symp.* Manila, Philippines.

Kinsey, D.W. and P.J. Davies (1979) Inorganic carbon turnover, calcification and growth in coral reefs. In P. Trudinger and D. Swaine (eds), *Biochemistry of Mineral Forming Elements.* Amsterdam: Elsevier.

Kinsman, D.J.J. (1964) Reef coral tolerance of high temperature and salinities. *Nature* 202(4939):1280-1282.

Knutson, D.W., R.W. Buddemeier and S.V. Smith (1972) Coral chronometers: seasonal growth bands in reef corals. *Science* 177:270-272.

Lamberts, A.E. (1974) Measurement of Alizarin deposited by coral. *Proc. 2nd Int. Coral Reef Symp.* Vol. 2. Brisbane: GBRC.

Lewis, J.V., F. Axelsen, I. Goodbody, C. Page and G. Chislett (1968) Comparative growth rates of some reef corals in the Caribbean. *Mar. Sci. Manus. Rept.* No. 10. Montreal: McGill University.

LIMER 1975 Expedition Team (1976) Metabolic processes of coral reef communities at Lizard Island, Queensland. *Science* 7(11-12):463-468.

Macintyre, I.G. and S.V. Smith (1974) X-radiographic studies of skeletal development in coral colonies. *Proc. 2nd Int. Coral Reef Symp.* Vol. 2. Brisbane: GBRC.

Maragos, J.E. (1972) A study of the ecology of Hawaiian reef corals. PhD Diss., University of Chicago.

Marshall, S.M. and T.A. Stephenson (1933) The breeding of reef animals. Part 1. The corals. *Sci. Rept. Great Barrier Reef. Expedition* 3(8):219-245.

Maxwell, W.G.H. (1968) *Atlas of the Great Barrier Reef.* London: Elsevier.

Mayer, A.G. (1915) The lower temperature at which reef corals lose their ability to capture food. *Yearbook Carn. Inst. Wash.* 14:212.

——————— (1918) Ecology of the Murray Island coral reef. *Carn. Inst. Wash. Publ.* 213:1-48.

Mayor, A.G. (1924) Structure and ecology of Samoan reefs. *Pap. Dept. mar. Biol. Carnegie Instn. Wash.* 19:1-25.

Mayr, E. (1976) *Evolution and the Diversity of Life.* Harvard: Bellknap Press.

Milliman, J.D. (1974) *Marine Carbonates.* Berlin, Heidelberg, N.Y.: Springer-Verlag. (Chapter 6)

Moore, W.S. and S. Krishnaswami (1974) X-radiographic studies of skeletal development in coral colonies. *Proc. 2nd Int. Coral Reef Symp.* Vol. 2. Brisbane: GBRC.

Motoda, S. (1940) A study of growth rate in the massive reef coral, *Goniastrea aspera.* Verrill: Palao. Trop. *Biol. Sta. Stud.* 2:1-6.

Muscatine, L. (1973) Nutrition of corals. In O.A. Jones and R. Endean (eds), *Biology and Geology of Coral Reefs,* Vol. II. Biology I. N.Y., London: Academic Press.

Oliver, J. (1977) The climatic environment of the Townsville area. In D. Hopley (ed.), *Geographical Studies of the Townsville Area.* Dept. of Geog., James Cook Univ. of North Qld, Monogr. Ser. Occ. Pap. 2.

Orr, A.P. and F.W. Moorhouse (1933) Variations in some physical and chemical conditions on and near Low Isles Reef. *Sci. Rept. Great Barrier Reef Expedition* 2:87-98.

Pichon, M. (1974) Free-living scleractinian coral communities in the coral reefs of Tulear (Madagascar). *Proc. 2nd. Int. Coral Reef Symp.* Vol. 2. Brisbane: GBRC.

Pickard, G.L., J.R. Donguy, C. Henin and F. Rougerie (1977) A review of the physical oceanography of the Great Barrier Reef and Western Coral Sea. *AIMS Monogr. Ser.* 2.

Polach, H.A., R.F. McLean, J.R. Caldwell and B.G. Thom (1978) Radiocarbon ages from the northern Great Barrier Reef. *Phil. Trans. Roy. Soc. London, A.* pp.139-158.

Porter, J.W. (1974) Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa*. *Proc. 2nd Int. Coral Reef Symp.* Vol. 1. Brisbane: GBRC.

Rosen, B.R. (1975) The distribution of reef corals. *Underwater Ass. Rep. 1* (NS), pp.1-16.

Salvat, B., J.P. Chevalier, G. Richard, G. Poli and R. Bagnis (1977) Geomorphology and biology of Taiaro Atoll, Tuamotu Archipelago. *Proc. 3rd Int. Coral Reef Symp.* Vol. 2. Miami.

Saville-Kent, W. (1893) *The Great Barrier Reef of Australia: its products and potentialities.* London: Allen.

Schneider, R.C. and S.V. Smith (in press) *Skeletal Sr content in* Porites *in relation to environmental factors.*

Shinn, E.A. (1966) Coral growth rate, an environmental indicator. *J. Palaeont.* 40:233-40.

Slack-Smith, R.J. (1960) An investigation of coral deaths at Peel Island, Moreton Bay, in early 1956. *Zool. Pap. Univ. of Qld.* 1(7):214-221.

Sluiter, C.P. (1889) Einiges uber die Ensterhung der Korallenriffe in der Javasee und Branntweinsbai, und uber neue Korallenbildung bei Krakatau: Natuurk. *Tidjschr. Nederl.-Indie* 49:360-380.

Smith, S.V. and D.W. Kinsey (1976) Calcium carbonate production, coral reef growth, and sea level change. *Science* 194:937-939.

Spender, M.A. (1930) Island reefs of the Queensland coast. *Geog. J.* 76:194-214, 273-297.

Stephenson, T.A. and Anne Stephenson (1933) Growth and asexual reproduction in corals. *Sci. Rept. Great Barrier Reef Expedition* 3(7):167-217.

Stoddart, D.R. (1969) Ecology and morphology of recent coral reefs. *Biol. Rev.* 44:433-498.

Stoddart, D.R., R.F. McLean, T.P. Scoffin, B.G. Thom and D. Hopley (1978) Evolution of reefs and islands, northern Great Barrier Reef: synthesis and interpretation. *Phil. Trans. Roy. Soc. A,* pp.149-159.

Vaughan, T.W. (1915) The geological significance of the growth rate of the Floridian and Bahaman shoal-water corals. *J. Wash. Acad. Sci.* 5:591-600.

Vaughan, T.W. (1918) Some shoal-water corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island. *Pap. Dep. mar. Biol. Carnegie Instn. Wash.* 9:49-219.

Veron, J.E.N. (1981) The species concept in "Scleractinia of Eastern Australia." *Abstracts, 4th Int. Coral Reef. Symp.* Manila, Philippines.

Veron, J.E.N. and M. Pichon (1976) Scleractinia of Eastern Australia. Families: Thamnasteriidae, Astrocoeniidae, Pocilloporidae. *AIMS Monogr. Ser. 1,* Part 1. Canberra, AGPS.

Veron, J.E.N., R.A. How, T.J. Done, L.D. Zell, M.J. Dodkin and A.F. O'Farrell (1974) Corals of the Solitary Islands, Central New South Wales. *Aust. J. mar. Freshwat. Res.* 25:193-208.

Weber, J.N. (1973) Incorporation of strontium into coral reef skeletal carbonate. *Geochim. et Cosmochim. Acta.* 37: 2173-2190.

Weber, J.N. and E.W. White (1974) Density banding in reef coral skeletons. Activation energy for skeletal aragonite deposited by the hermatypic coral *Platygyra* spp. *Mar. Biol.* 26:252-259.

——————————— (1977) Caribbean reef corals *Montastrea annularis* and *Montastrea cavernosa*—long-term growth data as determined by skeletal X-radiography. In Am. Assoc. Petr. Geol., *Studies in Geology,* Vol. 4, pp.171-179.

Weber, J.N., P. Deines, E.W. White and P.H. Weber (1975) Seasonal high and low density bands in reef coral skeletons. *Nature* 255:697-698.

Wells, J.W. (1954) Recent corals of the Marshall Islands. *Prof. Pap. U.S. Geol. Surv.* 206-I:335-346.

————— (1956) Scleractinia. In R.C. Moore (ed.), *Treatise on Invertebrate Paleontology(F) Coelenterata.* Lawrence, Kansas: University of Kansas Press.

————— (1957) Coral reefs. In J.W. Hedgepeth (ed.), *Treatise on Marine Ecology and Paleoecology.* Vol. 1. Geol. Soc. Am. Mem. 67.

Wolanski, E. (1981) Physical oceanography of the Great Barrier Reef lagoon. Paper presented to Conf. on Env. Engin., Townsville, 8-10 July 1981.

Woodhead, P.M.J. (1971) Report of the Committee appointed by the Commonwealth and Queensland Government on the problem of the Crown-of-Thorns starfish (*A. planci*). Ed. J.R. Welsh. House of Reps. Govt. of Australia, pp.31-33.

Wood-Jones, F. (1910) *Corals and Atolls.* London: Reeve and Co.

APPENDIX A

COLLECTION SITE DATA

Port Moresby—July 1977 (collection month)

- several small colonies from leeward side of small island off coast
- depth about 1 metre

North Triangle Reef—November 1975

- several small heads from top of bommie on leeward side of plug reef in surge channel
- depth about 1 metre

Carter Reef—June 1976

- large collection made from lee side of large bommie on leeward face of main reef
- depth about 2 metres

Nymph Island—June 1976

- two collections from west and south side of island platform.
- depth .3 metre

Eyrie Reef—December 1977

- several colonies 10-15cm diameter from back reef area to south of sand cay
- depth 2 metres

Long Reef—July 1976

- several colonies taken from reef in lee of platform
- depth 1 metre

Low Wooded Island—July 1976

- several larger heads *Porites* and three *Goniastrea* collected from leeward reef face
- depth 3-5 metres

Three Isles—July 1976

- see text, Chapter Five

Lark Pass Reef—July 1976

- several samples taken from under leeward anchorage, more from reef flat
- depth 12 metres and 1 metre

<u>Cairns Reef</u>—June 1976

- nine colonies taken from small bommie south of opening on NE side of reef
- depth 1-2 metres

<u>East Hope Island</u>—June 1976

- large collection from east face of bommie to north of anchorage
- depth 2-15 metres

<u>Pickersgill Reef</u>—June 1976

- small number of *Porites* collected from NW face of reef platform to leeward of cay
- depth 2-5 metres

<u>Yule Pt Reef</u>—June 1974

- three large heads taken from fringing reef approximately 150 metres from shore
- depth 0.5 metres at M.L.W.S.

<u>Barnett Patches</u>—October 1975

- see text, Chapter Five

<u>Pelorus Island</u>—May 1977

- large collection from reef shelf to lee of southern sand spit
- depth 2-5 metres

<u>Lodestone Reef</u>—April 1976

- small number of 15-20cm diameter heads from lee of reef platform
- depth 2 metres

<u>Keeper Reef</u>—October 1976

- several small colonies taken from reef flat at low tide
- depth 1 metre

<u>Eclipse Island</u>—February 1975

- three colonies 15cm diameter from leeward reef slat
- depth 1.5 metres at M.L.W.S.

<u>Wheeler Reef</u>—June 1975

- very large collection from all parts of platform
- see text, Chapter Four

<u>Pandora Reef</u>—May 1977

- several medium sixed colonies from leeward slope of platform behind shingle cay
- depth 1-5 metres

Viper Reef—June 1977

- large collection of small heads from back-reef slope of "lagoon"
- depth 2-3 metres

Bowden Reef—December 1975

- small number of colonies taken from reef flat in centre of south east platform
- depth 1-5 metres

Rattlesnake Island—March 1976

- fifteen coral heads from reef flat on NW side of high island (fringing reef)
- depth 1-2 metres

Leopard Reef—May 1977

- several colonies taken from eastern patch reef of group
- depth 15 metres

Magnetic Island—April 1978

- five medium colonies and wedges from three very large microatolls from Geoffrey Bay fringing reef
- depth 0.5 metres at M.L.W.S. (moated)

Kangaroo Reef—May 1977

- several medium colonies from south eastern tip of largest patch of the complex
- depth 1-2 metres

Fairey Reef—October 1976

- eighty small colonies taken from small pool
- see text, Chapter Three

Holbourne Island—May 1974

- several large sections of moated microatolls from middle "double ringed" pool close to shore on fringing reef
- depth 1 metre at M.L.W.S. (moated)

Parker Reef—May 1977

- six medium corals from leeward crest of reef platform
- depth 1-2 metres

Bushy Island (Redbill Reef)—October 1977

- eight small colonies from base of bommie in small lagoon near cay
- depth 3-5 metres

Molar Reef—October 1977

- several small to medium colonies from east face of platform near anchorage
- depth 1-3 metres

Cockatoo Reef—October 1977

- many small colonies from rim around "blue hole" (see Backshall *et al.* 1979 for map)
- depth 0.5 metres at M.L.W.S.

Mystery Cay Reef—July 1975

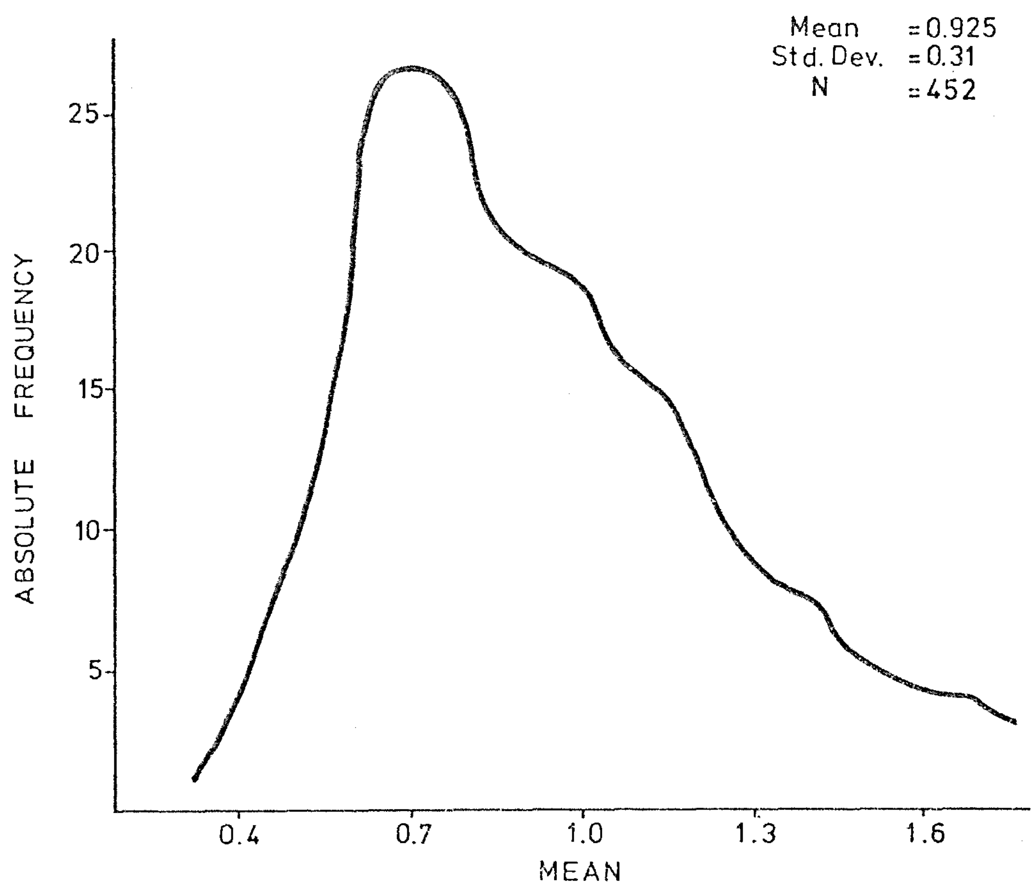
- six small to medium colonies from western tip of reef platform
- depth 1-2 metres

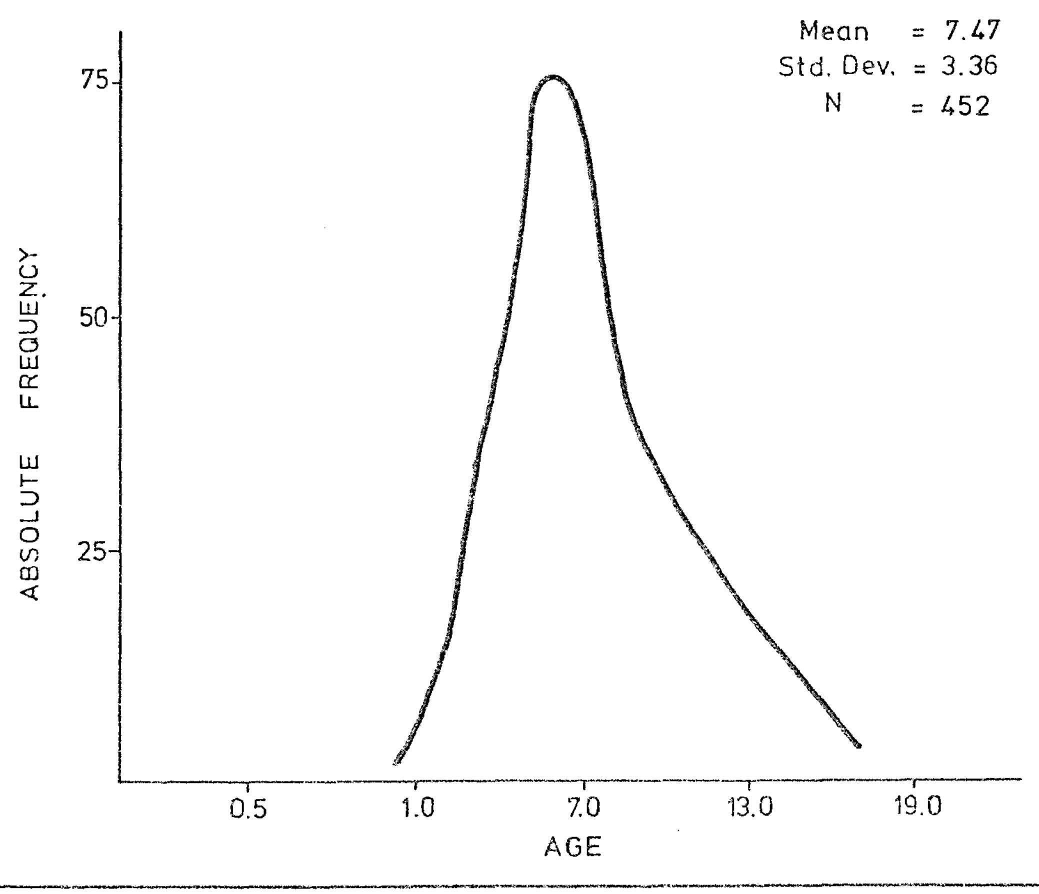
Heron Island—August 1977

- small collection made from reef platform due west of research station about 200 metres from beach
- depth 1 metre at M.L.W.S.

APPENDIX B

GROWTH DATA DISTRIBUTION


Mean = 0.925
Std. Dev. = 0.31
N = 452
ABSOLUTE FREQUENCY
25
20
15
10
5
0.4
0.7
1.0
1.3
1.6
MEAN


Mean = 7.47
Std. Dev. = 3.36
N = 452
ABSOLUTE FREQUENCY
75
50
25
0.5
1.0
7.0
13.0
19.0
AGE

APPENDIX C

COLONY DESCRIPTORS

ID.NO	MEAN	SDV	CVR	VOL	ID.NO	MEAN	SDV	CVR	VOL	ID.NO	MEAN	SDV	CVR	VOL	ID.NO	MEAN	SDV	CVR	VOL
1003	.84	.07	.08	1541.03	7005	1.17	.09	.08	891.80	10004	1.55	.10	.07	7058.23	16102	1.52	.17	.11	1141.34
1005	1.16	.18	.16	507.29	8044	1.30	.05	.04	7602.94	10001	1.16	.10	.08	2091.33	17003	1.01	.06	.06	2639.20
1042	1.20	.07	.06	287.54	8047	1.11	.05	.04	1210.26	10005	.94	.10	.10	1096.88	17005	1.29	.05	.04	1210.26
1030	1.10	.09	.08	1186.99	8045	1.15	.07	.06	1356.32	11038	1.09	.06	.06	7366.19	17007	.90	.08	.09	121.31
1047	.74	.12	.16	131.70	8043	1.16	.11	.10	1381.75	11035	.83	.07	.08	1096.88	17004	.94	.04	.04	2159.52
1027	1.16	.14	.12	261.42	8033	1.36	.08	.06	3320.95	11034	1.40	.12	.08	1541.03	18051	1.32	.08	.06	3053.03
1034	1.00	.08	.08	325.00	8034	1.40	.08	.06	1541.03	11020	.63	.04	.06	137.11	19001	1.20	.09	.08	2300.31
1021	.85	.07	.09	1568.71	8931	1.16	.11	.09	2924.65	11412	1.16	.09	.07	2091.33	19002	1.39	.06	.04	2372.95
2005	.91	.13	.15	665.72	8031	1.46	.12	.08	1011.44	11033	1.09	.06	.05	2447.10	20010	.53	.05	.10	48.39
2088	.75	.10	.14	70.20	8067	1.80	.07	.04	970.44	11044	1.37	.10	.07	1433.56	20015	1.01	.11	.11	172.72
2008	1.10	.17	.15	221.48	8066	1.24	.16	.13	619.65	11041	.97	.08	.08	1712.11	20151	.84	.06	.07	1513.68
2003	.84	.05	.06	334.85	8612	1.59	.06	.04	2264.56	11032	.71	.05	.06	1257.72	20033	.59	.05	.08	387.08
2001	.98	.02	.02	66.75	8068	1.19	.06	.05	3185.11	11045	.70	.03	.05	2424.69	20025	.55	.10	.19	11.68
2002	1.03	.08	.07	355.14	8614	2.00	.23	.12	561.60	11431	1.01	.09	.09	575.76	20021	.41	.04	.09	131.70
3048	1.01	.09	.09	334.85	8064	1.35	.10	.08	409.41	11046	1.14	.07	.06	2841.09	20027	.65	.04	.06	154.23
3051	.60	.04	.07	70.20	8610	1.73	.09	.05	2882.67	11031	.96	.09	.09	1682.76	20029	.50	.07	.14	40.63
3045	1.46	.09	.06	1741.80	8063	1.68	.13	.08	334.85	11048	1.38	.10	.07	3460.60	20034	.59	.02	.04	185.83
3024	.83	.04	.05	2600.00	8611	1.85	.30	.16	444.48	11051	.75	.08	.11	236.92	20022	.67	.04	.06	166.40
3001	1.33	.05	.04	1331.20	8041	1.64	.14	.08	1433.56	11371	1.08	.08	.07	1156.64	20067	.63	.05	.09	334.95
3006	1.09	.14	.13	214.01	8114	.91	.09	.10	1011.44	11317	.79	.05	.06	2841.09	20070	.82	.10	.13	179.19
3041	.67	.05	.07	166.40	8611	1.30	.12	.09	714.03	11410	1.04	.05	.05	2924.65	20076	.81	.06	.08	172.72
3046	.62	.05	.08	214.01	8613	1.81	.03	.02	990.80	11049	1.31	.07	.05	2024.59	20066	.71	.02	.03	315.35
3004	.54	.03	.06	547.68	8615	1.59	.10	.06	1306.40	12007	.60	.02	.04	409.41	20075	.95	.05	.05	1141.34
3044	.81	.03	.04	990.80	8069	1.62	.14	.09	296.62	12011	1.04	.08	.08	634.77	20077	.76	.06	.07	244.91
3007	.53	.04	.08	854.12	8061	1.33	.13	.10	1306.40	13001	.88	.08	.09	1281.90	20073	.52	.08	.15	185.83
3021	1.01	.04	.04	2639.20	8082	1.37	.12	.09	2300.31	13003	1.44	.20	.14	2678.78	20065	.58	.06	.11	106.77
3002	.63	.03	.05	2229.17	8081	1.84	.04	.02	1032.37	13005	1.54	.10	.06	6982.61	20069	.85	.10	.12	43.11
3003	1.20	.15	.12	287.54	8087	1.12	.06	.06	3604.11	13004	1.70	.18	.10	2759.14	20047	1.50	.22	.15	1895.40
4043	1.22	.07	.06	590.15	8810	.76	.04	.06	1541.03	14010	1.13	.10	.09	817.52	20042	.85	.02	.02	199.59
4023	1.02	.07	.07	344.89	8088	.79	.05	.06	3460.60	15002	1.46	.12	.08	2799.92	20002	1.13	.28	.24	29.62
4022	.82	.04	.05	179.19	8812	1.26	.16	.13	3751.53	15019	.69	.04	.06	1118.96	20006	1.04	.13	.12	185.83
4042	.86	.04	.05	2194.16	8085	1.75	.16	.09	376.23	15023	.81	.04	.05	468.94	20037	.77	.11	.14	31.63
5993	1.02	.09	.09	344.89	8312	1.38	.12	.09	854.12	15007	.95	.08	.08	481.50	20055	.73	.06	.09	63.41
5004	1.05	.08	.08	650.12	8210	1.73	.10	.06	2882.67	15021	.73	.08	.12	507.29	20129	.50	.11	.21	20.80
5001	1.06	.12	.12	387.08	8038	1.02	.07	.07	3701.95	15010	.76	.07	.09	244.91	20049	.38	.04	.10	31.63
5002	1.02	.10	.10	344.89	8035	1.02	.08	.08	2024.59	15020	1.07	.10	.09	398.14	20490	1.18	.11	.09	3096.64
5005	1.33	.12	.09	166.40	8310	1.31	.04	.03	2024.59	15056	.92	.06	.06	432.58	20149	.82	.07	.08	38.24
5006	1.36	.09	.07	817.52	8034	.76	.05	.07	3096.64	15011	.96	.10	.11	148.37	20041	.49	.07	.13	38.24
5007	1.00	.07	.07	891.80	8314	.92	.10	.10	1032.37	15028	.91	.09	.10	1959.28	20054	.83	.07	.08	315.35
5003	1.78	.21	.12	930.57	8311	1.01	.10	.09	1381.75	15001	1.03	.01	.01	179.19	20144	.53	.04	.08	85.20
5011	1.01	.05	.05	172.72	8313	1.26	.15	.12	650.12	15018	.86	.09	.10	355.14	20044	1.06	.08	.08	1075.08
5009	.91	.07	.08	681.57	8310	1.00	.03	.03	891.80	15053	.69	.02	.03	619.65	20046	1.01	.10	.10	1356.32
5010	1.00	.03	.03	325.00	8032	.91	.10	.11	3413.62	15057	.68	.07	.10	179.19	20050	.88	.06	.07	221.48
6010	.71	.04	.06	1596.72	8039	.91	.05	.05	3413.62	15023	.77	.11	.14	31.63	20052	.86	.10	.12	206.72
6006	.51	.03	.05	1682.76	8037	1.12	.10	.09	1863.99	15025	.54	.04	.07	25.84	20901	.77	.03	.04	2024.59
6057	.60	.05	.09	287.54	9051	1.30	.15	.12	5646.54	15024	1.42	.17	.12	60.19	20903	.94	.11	.12	728.94
6002	1.13	.19	.17	236.93	9007	1.08	.14	.13	637.67	15029	.76	.05	.07	590.15	20902	1.60	.30	.19	287.54
6001	1.09	.09	.08	2494.75	9004	.77	.07	.09	2095.78	15016	.70	.07	.09	111.48	20903	.80	.06	.07	1802.20
6009	.59	.03	.04	387.08	9151	.85	.06	.06	2799.92	15015	.63	.07	.11	221.48	20904	1.10	.14	.13	432.58
6006	.88	.11	.12	387.08	9011	.60	.04	.07	747.49	15017	.89	.09	.10	229.11	20905	.70	.08	.11	1164.91
6004	.97	.13	.13	296.62	9001	.48	.02	.04	634.77	15020	1.00	.09	.09	895.63	20912	.81	.04	.05	1832.92
6005	.91	.06	.07	8091.55	9017	.62	.03	.05	1682.76	16009	.97	.08	.08	3185.11	20910	.87	.06	.07	1712.11
7003	.94	.08	.08	2882.67	9035	.74	.05	.06	3555.84	16001	1.15	.09	.08	1356.32	20911	.70	.04	.06	1927.17
7008	.99	.11	.11	1281.90	9031	.90	.04	.05	1895.40	16008	1.68	.14	.09	2678.78	20915	1.24	.10	.08	1682.76
7004	1.03	.05	.04	970.44	10003	1.54	.08	.05	1186.99	16201	1.22	.15	.12	1625.07	20916	1.21	.10	.08	1568.71
7011	1.12	.07	.06	3701.95	10031	1.52	.06	.04	1141.34	16101	1.63	.12	.07	2447.10	20943	1.01	.06	.06	1927.17
7009	.91	.07	.07	2639.20	10002	1.19	.05	.04	1486.65	16106	1.19	.10	.08	2229.17	20935	.83	.08	.09	325.00

ID.NO	MEAN	SDV	CVR	VOL
20931	.94	.13	.14	269.94
20932	.82	.08	.10	305.89
21002	.97	.07	.07	1712.11
21001	.50	.03	.07	2600.00
21004	1.37	.16	.12	835.69
21007	.64	.04	.07	911.05
21008	1.14	.14	.12	1306.40
21009	.85	.08	.09	199.59
21111	1.14	.10	.08	1331.20
21211	1.02	.10	.10	2759.14
21212	.61	.04	.06	799.62
21107	1.25	.18	.15	325.00
21110	.72	.05	.08	970.44
21108	1.17	.11	.10	911.05
21109	.72	.05	.07	4006.08
21141	.65	.04	.07	1991.76
22018	.55	.03	.06	970.44
22019	.61	.04	.06	1032.37
22017	.67	.06	.09	575.76
22014	.70	.10	.15	57.08
22013	.75	.06	.09	236.92
22015	.78	.06	.07	1233.84
22016	.71	.03	.05	2600.00
22008	.62	.04	.06	444.48
22011	.79	.06	.07	1281.90
22009	.53	.04	.07	1281.90
22007	.64	.04	.06	1882.79
22005	.58	.03	.05	507.29
22004	.56	.03	.05	236.93
22012	.66	.04	.06	253.07
22020	.64	.04	.07	681.57
22888	.74	.02	.03	2832.87
22001	.59	.03	.05	3096.64
22006	.61	.04	.07	1653.75
23005	.69	.04	.06	105.84
23001	.64	.05	.08	1177.76
23007	.75	.05	.07	792.54
23008	1.04	.11	.11	990.80
23004	.72	.04	.05	1296.56
23003	.48	.04	.07	287.54
24007	.63	.04	.07	2718.76
24008	.99	.09	.09	547.68
24010	1.02	.03	.03	604.78
24012	1.09	.10	.09	420.88
24014	.79	.05	.06	3555.84
24004	1.04	.11	.10	634.77
24003	.91	.12	.13	420.88
24002	1.09	.14	.13	420.88
24005	1.09	.07	.07	420.88
24001	1.11	.11	.09	764.61
25020	.74	.06	.08	365.58
25018	.69	.06	.09	444.48
25021	.63	.03	.04	40.63
25014	.75	.04	.06	1096.88
25012	.76	.07	.09	244.91
25006	.91	.12	.13	126.43
25010	.69	.05	.07	287.54

ID.NO	MEAN	SDV	CVR	VOL
25008	.76	.04	.05	590.15
25030	.73	.04	.05	747.49
25025	.76	.02	.03	590.15
25024	1.18	.10	.08	533.99
25029	.64	.05	.07	236.93
25026	.59	.03	.06	398.14
25003	.59	.02	.03	185.83
26001	.88	.04	.04	5912.22
26002	2.07	.29	.14	4957.22
27300	.84	.06	.07	2024.59
27024	.93	.09	.10	1075.08
27030	.95	.05	.05	2967.03
27025	.76	.06	.08	835.69
27027	.62	.06	.09	131.70
27026	.91	.07	.08	1433.56
27017	1.14	.04	.03	244.91
27013	.76	.05	.06	835.69
27019	.69	.03	.05	2641.09
27020	.80	.07	.09	681.57
27021	.73	.04	.05	2759.14
27018	.68	.07	.10	590.15
27004	.92	.04	.04	1786.02
27009	.66	.06	.10	747.49
27003	.97	.06	.07	817.52
27011	1.17	.07	.06	520.52
27014	.84	.07	.09	799.62
27022	.96	.08	.08	2300.31
27008	.63	.08	.12	81.27
27023	.58	.05	.09	111.48
27101	1.22	.08	.06	305.89
27102	.94	.07	.08	2125.24
27006	.66	.04	.07	747.49
27001	.63	.04	.07	334.85
27015	.66	.04	.07	730.63
27016	.66	.02	.03	261.42
28053	.51	.16	.32	22.40
28002	.62	.13	.21	77.72
28088	.73	.07	.09	63.41
28032	.93	.23	.24	15.72
28045	.48	.03	.06	63.41
28062	.72	.03	.04	121.31
28038	.64	.09	.14	85.20
28050	.72	.04	.08	85.20
28030	.73	.05	.06	214.01
28009	.53	.04	.08	10.65
28006	.68	.04	.06	799.62
28046	.69	.09	.13	296.62
28060	.59	.05	.09	116.32
28002	.57	.09	.15	60.19
28999	.72	.06	.12	85.20
28007	.64	.06	.10	507.29
28039	.54	.05	.09	697.67
28031	.79	.10	.13	160.24
28012	.62	.06	.09	131.70
28017	.75	.10	.14	236.93
28064	.54	.05	.10	51.18
28025	.71	.05	.08	315.35

ID.NO	MEAN	SDV	CVR	VOL
28888	.62	.07	.12	131.70
28049	.87	.07	.09	365.58
28027	.72	.06	.09	121.31
28063	.44	.05	.12	48.39
28005	.65	.09	.14	154.23
28014	.65	.04	.06	89.25
28059	.73	.14	.19	221.48
28995	.68	.06	.09	179.19
28015	.58	.10	.17	172.72
28051	.70	.04	.05	57.08
28052	.65	.10	.15	244.91
28037	.72	.20	.27	25.84
28004	.42	.04	.09	142.67
28044	.59	.03	.05	33.74
28016	.65	.09	.13	154.23
28001	1.13	.52	.47	29.62
28021	.70	.08	.12	57.08
28019	.83	.09	.11	315.35
28042	.62	.06	.09	214.01
28026	.54	.05	.09	547.68
28029	.48	.05	.10	35.94
28061	.55	.04	.08	420.88
28024	.75	.11	.15	137.11
28023	.68	.08	.11	420.88
28034	.57	.03	.06	1331.20
28011	.61	.07	.12	296.62
28040	.82	.12	.15	730.63
28010	.44	.04	.09	77.72
28041	.74	.10	.13	365.58
28056	.85	.10	.12	102.19
28013	.83	.08	.10	507.29
29036	.77	.05	.07	619.65
29038	1.18	.13	.11	930.57
29051	1.49	.09	.06	547.68
29004	.35	.03	.07	728.94
29006	.79	.08	.10	665.72
29034	1.26	.09	.07	2678.78
29002	1.05	.08	.07	81.27
29026	1.17	.04	.04	1474.62
29003	.80	.07	.09	287.54
29001	.78	.07	.09	2125.24
29051	1.75	.05	.03	891.80
31008	1.06	.08	.07	1596.73
31004	1.49	.10	.07	2924.65
31001	1.06	.09	.08	1075.08
31010	1.23	.14	.11	2484.75
31002	1.55	.12	.08	3320.95
31020	.94	.11	.12	269.94
31003	.93	.04	.05	2091.33
31007	1.50	.12	.08	561.60
32008	1.05	.08	.07	650.12
32002	1.00	.11	.11	3508.00
32011	.94	.09	.10	728.94
32010	.45	.06	.13	29.62
32015	.62	.02	.04	1075.08
32006	.79	.07	.09	2229.17
32007	1.10	.09	.08	2522.78

ID.NO	MEAN	SDV	CVR	VOL
32012	1.06	.20	.18	199.59
32002	.90	.04	.05	2561.19
32003	.65	.04	.07	2924.65
33010	.65	.03	.04	2372.95
33011	.84	.06	.07	2639.20
33046	.71	.06	.08	325.00
33017	1.40	.21	.15	891.80
33013	.82	.12	.14	38.24
33028	.69	.11	.16	106.77
33015	.66	.03	.04	160.24
33001	.83	.07	.09	507.29
33002	.65	.04	.06	1991.76
33005	.64	.04	.06	148.37
33014	.73	.08	.11	126.43
33006	.74	.10	.13	355.14
33007	.94	.08	.09	728.94
33016	.69	.02	.04	2372.95
34004	.61	.04	.07	296.62
34008	1.15	.10	.08	253.07
34009	.61	.05	.07	126.43
34007	.62	.06	.09	131.70
34001	.73	.02	.03	990.80
34017	.77	.06	.07	409.41
34014	1.28	.19	.15	148.37
34021	1.00	.11	.11	561.60
34006	.76	.04	.05	387.08
36003	1.20	.09	.07	2300.31
36004	1.39	.12	.09	2409.83
36001	1.42	.13	.09	3801.55
37018	.80	.10	.12	456.60
37006	1.02	.06	.06	344.89
37005	.88	.05	.06	1281.90
37007	.95	.07	.07	4897.50
37004	1.22	.16	.13	590.15
38011	.78	.03	.04	33.74
38004	.83	.03	.04	40.63
38009	.77	.11	.14	148.37
38007	.85	.15	.17	199.59
38013	1.27	.07	.05	142.67
38002	.90	.15	.17	51.18
38001	.92	.07	.07	253.07
38016	.72	.02	.02	25.84
38005	.77	.07	.09	148.37
38012	.98	.14	.14	305.89
38010	1.14	.18	.16	481.50
38015	.84	.07	.09	520.52
38018	.85	.09	.11	344.89
38014	.73	.13	.18	63.41
38017	.95	.12	.13	142.67
38020	.98	.07	.07	1257.72
38003	1.04	.09	.08	185.83
38006	.97	.12	.12	63.41
38019	.73	.06	.08	344.89

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1021	3	10	1
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2008	1	4	1
2003	1	6	1
2001	4	3	1
2002	1	5	1
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3045	2	6	2
3024	7	12	2
3001	1	6	2
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5007	2	7	2
5003	3	4	2
5011	3	4	2
5009	3	7	2
5010	3	5	2
6010	2	12	1
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7008	3	8	3
7004	4	7	3
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7009	3	11	3

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8612	5	6	1
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9011	2	11	3
9001	2	13	3
9017	3	14	3
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11044	3	6	2
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11032	3	11	2
11045	3	14	2
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11046	2	9	2
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13005	3	9	3
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15011	1	4	2
15028	1	10	2
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15018	3	6	2
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15057	1	6	3
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16008	3	6	2
16201	3	7	2
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17004	3	10	3
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20943	2	9	2
20935	4	6	2

ID.NO	SPP	AGE	DPTH
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21212	3	11	1
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ID.NO	SPP	AGE	DPTH
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28032	4	2	1
28045	2	6	1
28062	2	5	1
28038	2	5	1
28050	2	7	1
28030	4	6	1
28009	4	3	1
28006	4	10	1
28046	2	7	1
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28002	4	5	1
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28007	4	9	1
28039	2	12	1
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28012	1	6	1
28017	1	6	1
28064	1	5	1
28888	1	7	1

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28027	1	5	1
28063	1	6	1
28005	1	6	1
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28059	1	6	1
28995	1	6	1
28015	1	7	1
28051	1	4	1
28052	1	7	1
28037	6	3	1
28004	1	9	1
28044	1	4	1
28016	1	6	1
28001	3	2	1
28021	1	4	1
28019	1	6	1
28042	2	7	1
28026	1	11	1
28029	1	5	1
28061	1	10	1
28024	3	5	1
28023	3	8	1
28034	2	14	1
28011	3	8	1
28040	3	8	1
28010	3	7	1
28041	3	7	1
28056	3	4	1
28013	3	7	1
29036	1	8	1
29038	1	6	1
29051	2	4	1
29004	2	16	1
29006	2	8	1
29034	2	8	1
29002	2	3	1
29026	2	15	1
29003	2	6	1
29001	3	12	1
29051	2	4	1
31008	3	8	2
31004	2	7	2
31001	3	7	2
31010	3	8	2
31002	3	7	2
31020	2	5	2
31003	2	10	2
31007	3	4	2
32008	4	6	2
32002	4	11	2
32011	4	6	2
32010	2	5	2
32015	8	12	2
32006	8	12	2
32007	8	9	2

ID.NO	SPP	AGE	DPTH
32012	3	4	2
32002	4	11	2
32003	4	16	2
33010	5	15	2
33011	5	12	2
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33017	5	5	2
33013	7	3	2
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36001	2	8	2
37018	1	7	2
37006	3	5	2
37005	3	9	2
37007	3	13	2
37004	3	5	2
38011	4	3	1
38004	2	3	1
38009	2	5	1
38007	4	5	1
38013	4	3	1
38002	2	3	1
38001	2	5	1
38016	2	3	1
38005	2	5	1
38012	4	5	1
38010	2	5	1
38015	2	7	1
38018	1	6	1
38014	2	4	1
38017	2	4	1
38020	4	8	1
38003	2	4	1
38006	4	3	1
38019	2	7	1

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1003	950	3	5
1005	950	3	5
1042	950	3	5
1030	950	3	5
1047	950	3	5
1027	950	3	5
1034	950	3	5
1021	950	3	5
2005	1065	1	4
2088	1065	1	4
2008	1065	1	4
2003	1065	1	4
2001	1065	1	4
2002	1065	1	4
3048	1465	1	4
3051	1465	1	4
3045	1465	1	4
3024	1465	1	4
3001	1465	1	4
3006	1465	1	4
3041	1465	1	4
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3004	1465	1	4
3044	1465	1	4
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3003	1465	1	4
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4023	1466	2	4
4022	1466	2	4
4042	1466	2	4
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5004	1472	2	4
5001	1472	2	4
5002	1472	2	4
5005	1472	2	4
5006	1472	2	4
5007	1472	2	4
5003	1472	2	4
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5009	1472	2	4
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7005	1502	2	2
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8045	1503	2	2
8043	1503	2	2
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8614	1503	2	3
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11038	1573	2	4
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11034	1573	2	4
11020	1573	2	4
11412	1573	2	4
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11044	1573	2	4
11041	1573	2	4
11032	1573	2	4
11045	1573	2	4
11431	1573	2	4
11046	1573	2	4
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11048	1573	2	4
11051	1573	2	4
11371	1573	2	4
11317	1573	2	4
11410	1573	2	4
11049	1573	2	4
12007	1587	2	4
12011	1587	2	4
13001	1638	2	4
13003	1638	2	4
13005	1638	2	4
13004	1638	2	4
14010	1632	3	5
15002	1806	2	1
15019	1806	2	1
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15007	1806	2	1
15021	1806	2	1
15010	1806	2	1
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15011	1806	2	1
15028	1806	2	1
15001	1806	2	1
15018	1806	2	1
15053	1806	2	4
15057	1806	2	4
15023	1806	2	4
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15016	1806	2	3
15015	1806	2	3
15017	1806	2	3
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16009	1856	3	4
16001	1856	3	4
16008	1856	3	4
16201	1856	3	4
16101	1856	3	4
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16102	1856	3	4
17003	1870	2	4
17005	1870	2	4
17007	1870	2	4
17004	1870	2	4
18051	1871	2	3
19001	1872	3	3
19002	1872	3	3
20010	1873	2	4
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20901	1873	2	2
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20903	1873	2	2
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20905	1873	2	2
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20910	1873	2	2
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20916	1873	2	2
20943	1873	2	2
20935	1873	2	2

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20932	1873	2	2
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21001	1881	3	4
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21007	1881	3	4
21008	1881	3	4
21009	1881	3	4
21111	1881	3	4
21211	1881	3	4
21212	1881	3	4
21107	1881	3	4
21110	1881	3	4
21108	1881	3	4
21109	1881	3	4
21141	1881	3	4
22018	1886	1	4
22019	1886	1	4
22017	1886	1	4
22014	1886	1	4
22013	1886	1	4
22015	1886	1	4
22016	1886	1	4
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22020	1886	1	4
22888	1886	1	4
22001	1886	1	4
22006	1886	1	4
23005	1901	2	2
23001	1901	2	2
23007	1901	2	2
23008	1901	2	2
23004	1901	2	2
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24007	1902	3	4
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25026	1903	1	4
25003	1903	1	4
26001	1913	3	4
26002	1913	3	4
27300	1921	1	1
27024	1921	1	1
27030	1921	1	1
27025	1921	1	1
27027	1921	1	1
27026	1921	1	1
27017	1921	1	1
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27008	1921	1	1
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27006	1921	1	1
27001	1921	1	1
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27016	1921	1	1
28053	1953	2	3
28002	1953	2	3
28088	1953	2	3
28032	1953	2	3
28045	1953	2	3
28062	1953	2	3
28038	1953	2	3
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28009	1953	2	3
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28004	1953	2	3
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28010	1953	2	3
28041	1953	2	3
28056	1953	2	3
28013	1953	2	3
29036	1971	3	3
29038	1971	3	3
29051	1971	3	3
29004	1971	3	3
29006	1971	3	3
29034	1971	3	3
29002	1971	3	3
29026	1971	3	3
29003	1971	3	3
29001	1971	3	3
29051	1971	3	3
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31010	2054	2	4
31002	2054	2	4
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31003	2054	2	4
31007	2054	2	4
32008	2095	2	4
32002	2095	2	4
32011	2095	2	4
32010	2095	2	4
32015	2095	2	4
32006	2095	2	4
32007	2095	2	4
32012	2095	2	4
32002	2095	2	4
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38012	2343	2	3
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38018	2343	2	3
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38017	2343	2	3
38020	2343	2	3
38003	2343	2	3
38006	2343	2	3
38019	2343	2	3