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CARBON TURNOVER AND ACCUMULATION BY CORAL REEFS

University of Hawaii PH.D. 1979

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CARBON TURNOVER AND ACCUMULATION
BY CORAL REEFS

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION
OF THE UNIVERSITY OF HAWAII IN PARTIAL
FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN OCEANOGRAPHY

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By

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ABSTRACT

Previously developed methodology involving the high-precision measurement of changes in oxygen and various parameters of the CO_2 system in sea water has been used to monitor community metabolism in four Pacific coral reef systems. One Tree Is. and Lizard Is. in the Australian Great Barrier Reef, and Kaneohe Bay in Oahu, Hawaii, were each studied intensively over periods exceeding one year. Johnston Is. in the Central Pacific was studied briefly, because of its potential nonconformity to some of the findings from the other sites. There is great operational uniformity in coral reef metabolism apparently regardless of considerable variability in small-scale morphology and community structure. Seasonal variation of metabolism is great, probably at all latitudes at which coral reefs are found. Unperturbed systems are in autotrophic balance (zero gain, i.e. virtually all organic material produced is consumed) over a full year although there may be substantial organic gains or losses within the year. In this balanced system there is a predictable zonation of activity associated with biomass zonation. Much of the carbon fixed is redistributed downwind, mostly as detritus, but nearly all such material remains within the system (i.e., there are internal source areas and sink areas). The inorganic carbon cycle is at least 75% gain (i.e., 25% or less of the carbonate formed is likely to redissolve) in contrast to the balanced organic cycle. As with organic production, there is significant redistribution of inorganic carbonates (sediments) away from, and mostly downwind from, the site of fixation. High metabolic activity is entirely related to perimeters, from the main seaward perimeter to the narrow perimeters of lagoon patch reefs. This high activity is very uniform in rate, but its lateral extent appears related to upwind open water fetch. There is a pronounced relationship between gross photosynthesis and calcification in all functional reef areas. Standards are proposed for coral reef performance. A present-day reef-flat is likely to exhibit the characteristics: gross diel photosynthesis (P) of 7 gC $m^{-2}d^{-1}$, an autotrophic self-sufficiency (P/R) of unity, and a net gain in carbonates (G) equivalent to 4 $kgCaCO_3\ m^{-2}y^{-1}$. However, this operational status is found to be only a compromise between an "ultimate" mode of approximately P = 20, G = 10 and attenuation by a low activity sand/rubble mode of P = 1, G = 0.5. It is suggested that the "ultimate" mode, still found in small or specialized areas today, may have been of more general importance during a rising sea level. It is stressed that algal pavements (P = 5, G = 4) are a specialized feature of a standing sea level. By deduction only, the physical energy regime (waves, turbulence, etc.) is invoked as the factor controlling most operational parameters of coral reef metabolism. Several perturbations influencing standard performance are discussed. High nutrient levels in the absence of plankton response will elevate primary production and directly suppress calcification even without marked changes in community structure. Nutrient input resulting in a marked plankton response (Kaneohe Bay sewage impact) will result in a decline in photosynthesis, a massive increase in heterotrophic feeding (indicated by increasing R and a P/R as low as 0.4) and an eventual total degradation of the community. This latter shift involves a loss of structural maintenance (reduced

calcification), and eventually active erosion (pronounced carbonate dissolution by boring infauna). The final perturbation considered is terrigenous sedimentation, which is found to cause a simple loss of calcifying reef status. Photosynthesis declines but P/R increases. Calcification falls to zero but active dissolution does not occur. This response is analogous to the normal response in any reef system in the downstream sediment sink zones (algal and sea grass flats).

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GENERAL INTRODUCTION

The elucidation of carbon flux through coral reef systems at an operational level has received only limited attention. This dissertation emphasizes the considerable and somewhat unexpected uniformity which has been found in the carbon flux of several systems from different latitudes and with very differing biological makeup. A number of hypotheses of "standard" performance are put forward. However, attention is also drawn to those aspects of community metabolism which do not appear to conform to standards.

The beginnings of many of the ideas put forward date back to 1961 to the earliest coral reef study in which I was involved (Kinsey and Kinsey 1967). Some of these earlier studies are reconsidered, and in many cases further unpublished data are brought forward.

The methodology used throughout the several studies reported is consistent, giving the intercomparisons an advantage usually lacking in comparisons of data from different workers.

Data are considered from four principal sites: One Tree Is. and Lizard Is. in the Australian Great Barrier Reef, Kaneohe Bay on the island of Oahu in Hawaii, and Johnston Is. in the central North Pacific.

All concepts developed use the ubiquitous carbon flux as the definitive parameter. Specifically, the carbon dioxide fluxes are determined using both CO_2 and O_2 related techniques, and expressed in terms of: community gross photosynthesis (P) which is an estimate of all CO_2 fixed by all photosynthetic organisms in the reef community; community gross respiration (R) which is an estimate of all CO_2

released by all decomposition and respiration processes within the community (including the respiration of the autotrophs themselves); community gain in fixed inorganic carbonates (G) which is an estimate of the net precipitation of carbonates. From these three parameters a considerable amount can be inferred concerning fluxes of organic material, changes in standing crop, and general community and reef growth phenomena.

Section 1 of the Results and Discussion considers the detailed data from each of the principal sites individually. Many of the results and conclusions may appear to be of rather marginal statistical significance. The strength of the conclusions becomes apparent when the considerable consistency of trends exhibited between the various sites is considered. Section 2 draws attention to these trends and formulates a number of operational hypotheses for "standard" coral reef performance. Section 3 considers the aberrations from the hypothetical standards so far developed, which can result from environmental perturbations.

Section 1 is very detailed and may tend to labor some small points at considerable length. This approach has been deliberate to allow Section 2 and Section 3 to develop freely, unencumbered by the need to discuss fine detail. Certainly most of the inferential and more generally applicable content of the dissertation is contained in the relatively compact Sections 2 and 3. However, it is desirable that careful consideration be given to the detailed results in Section 1 as there are many aspects of the metabolic performance of the coral reefs studied, which are specific and are nowhere summarized in the later sections.

The data and the concepts developed in this dissertation should prove of considerable value in elucidating coral reef development and growth (physiographic accumulation) through time. Some of the preliminary data from some sites have already been considered in that light (Smith and Kinsey 1976; Davies and Kinsey 1977; Kinsey and Davies 1979a, 1979b). However, it is outside the scope of the dissertation to develop hypotheses of Holocene or future reef growth based on the "standards" of inorganic carbon ($CaCO_3$) accumulation presented here.

Most community metabolism studies done on coral reefs have investigated carbon flux either indirectly (O_2 flux) or directly (CO_2, DOC, and POC fluxes). However, most of these have been concerned with the organic or photosynthesis/respiration cycle and only a few have measured by direct chemical methods the flux through the inorganic "$CaCO_3$" cycle. Thus, there is now a fair body of knowledge on the overall trophic state of coral reefs but relatively less on the accumulation of carbonates based on CO_2 flux measurements. There is of course a considerable body of knowledge on the accumulation of carbonates based on stratigraphic and physiographic considerations. Much of this latter knowledge has been summarized by Adey (1978). Notwithstanding the number of metabolic studies carried out, the data only loosely suggest consistent trends. This scatter is probably accentuated by several factors: (a) methodology varies considerably, (b) data handling and interpretation vary considerably, and (c) it is often difficult or nearly impossible to determine the relationships of communities and zonation because of inconsistencies in descriptive terminology. The remainder of this Introduction will summarize the available data from published coral reef metabolic studies. Additionally, Sournia (1977a) has produced an excellent general review concerning coral reef primary productivity. The review covers at length the kinds of information included in the subsequent tables (except calcification), and discusses in detail the methodology used by various authors.

Table 1 summarizes metabolic data available from the published literature for reef-flats or other shallow high activity areas. In addition to P, R and G, values for the diel excess production ($E = P - |R|$) and the ratio of gross photosynthesis to respiration (P/R) are tabulated. Detailed discussion of all these variables is included in the Methods section and in Table 5. Units used are gC $m^{-2}d^{-1}$ for CO_2 flux through the organic cycle, and kg$CaCO_3$ $m^{-2}y^{-1}$ for CO_2 flux through the inorganic cycle. These mixed units are used to conform with the most common units in the coral reef literature. Values in Table 1 cover a reasonably wide range. However, considering the very loose degree of similarity in the communities and zones represented, and the frequently large differences in methods used, there is probably a surprising degree of consistency. While the mean value for gross diel photosynthesis (P) and the mean value for gross diel respiration (R) are equal at 7.9 gC $m^{-2}d^{-1}$ suggesting an overall tendency towards a P/R of 1, it is apparent that there is considerable variation

Table 1

Published Values for Community Metabolism in Reef-Flat Environments

Reference	Location	P*	-R	E	P/R	G
		(gC $m^{-2}d^{-1}$)				($kgCaCO_3$ $m^{-2}y^{-1}$)
Sargent and Austin (1949, 1954)	Rongelap atoll	4	3.5	+0.5	1.1	
Odum and Odum (1955)	Enewetak atoll	10	10	0	1.0	
Kohn and Helfrich (1957)	Kauai (Hawaii)	7.9	6.6	+1.3	1.2	
Odum *et al.* (1959)	Puerto Rico (various)	5-16	5-19		0.8-1.6	
Goreau *et al.* (1960)	Puerto Rico				0.7	
Emery (1962)**	Guam	4.5	7	-2.5	0.7	
Gordon and Kelly** (1962)	Oahu (Hawaii)	14	24	-10	0.6	
Jones (1963)	Florida			+0.8-2.0		
Ramachandran Nair and Gopinadha Pillai (1972)	Indian Ocean (various)	4-9				
Qasim *et al.* (1972)	Laccadives	6.2	2.5	+3.7	2.5	
Kinsey (1972)	One Tree Is. (Australia)					4.6
Smith (1973)	Enewetak II Enewetak III	6 11.6	6 6.0	0 +5.6	1 1.9	4 4
Smith and Marsh (1973)	Enewetak II Enewetak III	6 10.4	6 6.0	0 +4.4	1 1.7	
Kinsey and Domm (1974)	One Tree Is. (Australia)	7.5	6.8	+0.7	1.1	
Marsh (1974)	Guam	7.2	6.6	+0.6	1.1	
LIMER Team (1976)	Lizard Is. (Australia)					4
Sournia (1976a)	Moorea (Tahiti)	7.2	8.4	-1.2	0.9	
Kinsey (1977)	One Tree Is. Lizard Is.	7.2	7.4	-0.2	1.0	4.6 3.7
Mean		7.9	7.9		1.17	4.2
S.D.		2.7	5.0		0.49	0.4
n		(16)	(15)		(16)	(6)

Note: Data reported as published. Conversion to g C made if necessary but other corrections not applied.

* For explanation of variables see Table 5.

** My interpretation of unclear or non-specific results.

(or simply lack of agreement) in the autotrophic self-sufficiency (P/R) as determined for the individual systems (mean P/R = 1.17).

The values in Table 1 for the diel gain in carbonates (G) are very consistent. This consistency may, in part, reflect that the data originate from only two authors (Kinsey and Smith). This consistency was used by Smith and Kinsey (1976) to suggest the possibility of worldwide uniformity in the calcification rate of shallow reef-flat areas ($G = 4$ kgCaCO$_3$ m^{-2}y^{-1}). Consistency in ecosystem performance is not a novel concept, and has been stressed by a number of authors (including Ryther (1969) in the consideration of oceanic systems). The further development of this theme and related concepts is the primary purpose of this dissertation.

There has been a tendency for the high values obtained for gross community metabolism of reef-flats to be misquoted as representing the activity of "coral reefs". This is most unfortunate, as it has allowed coral reefs commonly to be considered as one of the world's most active natural ecosystems. It is very doubtful that this elevated status is justified. Table 2 gives the few metabolic rates available for complete reef systems (i.e., a reef system in which the only sources and sinks are the open sea or the atmosphere, and not other adjacent reef areas). It is apparent that overall activity is just as variable as that in Table 1, but at a level more in keeping with that of most other natural ecosystems (Odum 1971). Presumably the large open atolls such as Enewetak would be much less active than the shallow systems reported, because of the lower proportion of shallow patch reefs and reef-flats. The one point that seems totally consistent in these

Table 2

Published Values for Community Metabolism of "Complete" Reef Ecosystems**

Reference	Location	P*	-R	E	P/R	G
		(gC $m^{-2}d^{-1}$)				$kgCaCO_3\ m^{-2}y^{-1}$
Smith and Pesret (1974)	Fanning Is.			0.0	1	1
Smith and Jokiel (1975)	Canton Is.	6.0	5.9	0.06	1	0.5
Sournia and Richard (1976a)	Takapoto (Tuamotos)	4	4	0.0	1	
Kinsey (1977)	One Tree Is. (Australia)	2.3	2.3	-0.06	1	1.5
Kinsey and Davies (1979b)	Lizard Is. (Australia)	3.2	3.2	0.0	1	1.8

* For explanation of variables see Table 5.

** It should be stressed that all the systems included here are relatively shallow with considerable lagoon patch reef development. It seems reasonable to anticipate that the large open atolls such as Enewetak will exhibit much lower overall activity.

Note: The Bahama Banks data of Broecker and Takahashi (1966) have not been included as they represent an Atlantic system not clearly conforming to a reasonable definition of a coral reef.

total "ecosystem" data is that E is very close to zero (P/R = 1). Thus the somewhat variable P/R value of reef-flats indicated in Table 1 may nevertheless be a component of a balanced ecosystem. The dissertation will pursue at considerable length the implied concepts of sources, sinks and overall self-containment.

Table 3 demonstrates that plankton metabolism in the water overlying reef communities has been found to be variable over two orders of magnitude. However, at its highest it is still an order of magnitude lower than the activity of the total system. Thus total system metabolism studies give data which are a reasonable approximation to the activities of the benthic community. It will be seen in Chapter 3B that such proportionally low values for planktonic activity are not always found. The majority of the studies covered by Table 3 do not include data for plankton respiration. Based on the one study (Kinsey 1978) where both P and R data are available, it seems that respiration may exceed photosynthesis in the water column over reef systems. The logical interpretation is that the elevated R is contributed by zooplankton and detritus (decomposing), both of local reef origin. It is an appreciable deficiency of the ^{14}C method that it can give rather misleading results in a heterotrophic situation such as this.

It should be stressed that most of the results in the three tables above are based on studies involving relatively few data taken in many cases during only one brief expedition. There is therefore little reason for confidence in many of the implied findings except for the fact that certain trends seem to be consistent. I believe it to be

Table 3

Published Values for Planktonic Metabolism in the Water Overlying Reef Systems

Reference	Location	P*	-R	P/R
		$(gC\ m^{-2}d^{-1})$		
		O_2 based estimations		
Sargent and Austin (1949)	Rongelap Atoll	0.2		
Jones (1963)	Florida	0.04-0.06		
Motoda (1969)	Palau	0.08		
Johannes *et al.* (1972)	Enewetak Atoll		0.003-0.03	
Kinsey (1978)	One Tree Is. (Australia	0-0.06	0.1-0.3	0-0.3
		^{14}C estimations**		
Gordon *et al.* (1971)	Fanning Is.	0.5		
Sournia and Richard (1975a)	Moorea (Tahiti)	0.004-0.03		
Sournia and Richard (1976b)	Vairao (Tahiti)	0.1-0.4		
Sournia and Richard (1975b)	Tuamotos	0.1-0.3		
Sournia and Richard (1976a)	Takapoto (Tuamotos)	0.02		
Sournia (1977)	Gulf of Elat	0.003-0.01		
LIMER Team (1976)	Lizard Is. (Australia)	0.1		

* For explanation of variables see Table 5.

** ^{14}C estimates tend to lie somewhere between gross and net primary production. The tabulated values are therefore a low estimate for P.

important that consistent trends in otherwise doubtful data be taken seriously. It is with this motivation that the detailed investigation reported here was undertaken.

METHODS

GENERAL DISCUSSION

The methodology used throughout the various investigations covered by this dissertation has been consistent. There have been a few improvements in the precision of the instrumentation since the earliest work. However, this advantage has been frequently offset in the more recent studies, as the sites were subjected to smaller anomalies in water chemistry than those encountered in the earliest studies at One Tree Is. Of course, each new site requires some changes in technique or approach to suit differences in water flow regime, tidal flux, or morphological characteristics of the reef being studied. These changes have never been sufficient to change the nature of the information obtained from the investigations of community metabolism.

The approaches used have involved the monitoring of changes with time of the O_2 and CO_2 content of the water overlying the reef system, or isolated components of the system. The broad concepts used have been largely influenced by the methodology developed by H. T. Odum (Odum 1956; Odum and Hoskin 1958). All basic methodology used in the present work has been detailed at length in <u>Coral Reefs</u>: <u>Research Methods</u> (Stoddart and Johannes, eds., 1978 UNESCO). The most relevant papers are: Kinsey; Smith and Kinsey; Smith; Marsh and Smith (all 1978). The methods are all directed at the determination of a rate of CO_2 exchange for the community being considered. However, it is important to remember that CO_2 exchange in a coral reef community may result from calcification/dissolution processes as well as from photosynthesis/respiration processes. In general, I have favored the measurement of O_2 exchange as an indicator of CO_2 exchange through the "organic" cycle (photosynthesis/respiration). I have exclusively used alkalinity anomalies to derive estimates of CO_2 exchange through the "inorganic" cycle (calcification/dissolution). In some situations I have used the difference between total CO_2 anomaly (calculated from pH, alkalinity, S‰, temperature data: Strickland and Parsons 1968; Smith and Kinsey 1978; Smith and Key 1975; Park 1969) and CO_2 anomaly due to the inorganic cycle, to give an alternative estimate of CO_2 exchange through the organic cycle. Each of these concepts will be further outlined below.

All O_2 measurements were made using polarographic electrode systems (Kinsey 1978), usually with electrically driven underwater impellers to ensure optimum water flow past the membrane (Kinsey 1978). The rate of change of O_2 concentration estimated from a time series of such measurements was corrected for atmospheric exchange across the water/air interface using experimentally determined diffusion coefficients (Kinsey and Domm 1974; Kinsey 1978). Where vertical stratification in oxygen concentration was noted, measurements were made at appropriate depths and an integrated oxygen concentration calculated (Kinsey 1978). In this case, the diffusion correction was calculated as a function of the surface concentration only. The empirical relationship between oxygen flux and CO_2 flux for total communities is usually accepted as being:

$$\text{photosynthesis} \qquad CO_2 + H_2O \rightarrow (CH_2O) + O_2$$

$$\text{respiration} \qquad (CH_2O) + O_2 \rightarrow CO_2 + H_2O$$

However, in most communities the photosynthetic quotient (PQ = $\Delta O_2/\Delta CO_2$ in photosynthesis) and the respiratory quotient (RQ = $\Delta CO_2/\Delta O_2$ in respiration) are not exactly equal to one, as implied by the equations above. Therefore, it is necessary to apply values for these quotients in the conversion of O_2 anomalies to their equivalent flux in CO_2. The determination of these values will be discussed in detail in the second part of the Methods.

The organic cycle does not have any effect on the total alkalinity of sea water, regardless of whether one considers the processes to be represented by:

$$CO_2 + H_2O \longrightarrow CH_2O + O_2$$

<u>or</u>

$$HCO_3^- + H^+ \longrightarrow CH_2O + O_2$$

This is because total alkalinity (TA) is given by:

$$TA = [HCO_3^-] + 2[CO_3^{--}] + [OH^-] + [H_2BO_3^-] + \text{(other weak anions)} - [H^+] \quad \text{(where all proton donors or acceptors are included)}$$

On the other hand, there is a stoichiometric change in total alkalinity of 2 meq for every mM CO_2 flux through the inorganic cycle. This is because the removal of any cation such as Ca^{++} from solution <u>must</u> be balanced by an equivalent reduction in the total negative change. This balance can normally only be achieved by a shift in the distribution of such species as HCO_3^- and CO_3^{--}--i.e., components of the total alkalinity. The stoichiometry of these relationships is discussed extensively by Smith and Key (1975), Smith and Kinsey (1978), and Brewer and Goldman (1976). It is true that shifts in certain nutrient species such as NH_4^+ NO_3^- and HPO_4^{--} will cause interference in the accuracy of the calculation of calcification from the anomaly in total alkalinity (Brewer and Goldman (1976). However, it has been established (Kinsey 1978a) that this interference typically will reduce the precision of calcification estimates for coral reefs by less than 5%. Consequently, all CO_2 fluxes through the inorganic calcification/dissolution cycles reported in this dissertation have been based on ΔTA using the relationship:

$$\Delta CaCO_3 \quad = \quad \Delta TA/2 \quad \text{(on a molar basis)}$$

Total alkalinity was determined using a modification (Smith and Kinsey 1978) of the direct acid/pH method of Anderson and Robinson (1946).

Because CO_2 flux through the inorganic cycle has a stoichiometric effect on total alkalinity and because CO_2 flux through the organic cycle has none, it is possible to determine the latter flux knowing the <u>total</u> CO_2 flux and the ΔTA.

$$\text{i.e.}\quad \Delta CO_2 \text{ (organic)} = \Delta\Sigma CO_2 - \Delta CO_2 \text{ (inorganic)}$$
$$\text{or}\quad \Delta CO_2 \text{ (organic)} = \Delta\Sigma CO_2 - \Delta TA/2$$

This alternative to the O_2 based procedure for determining CO_2 flux through the organic cycle has been used in some work reported here. Particularly, sufficient such estimations have been made to ensure the calculation of a reliable value for metabolic quotients RQ and PQ. As indicated earlier, ΣCO_2 was derived indirectly from the well known relationships between TA, pH, temperature, and S‰. Specifically, the approach used was that of Smith and Kinsey (1978). Atmospheric exchange of CO_2 across the air/sea interface is much less of a problem than with O_2 (Smith and Kinsey 1978) and such exchange has been disregarded in the direct CO_2 based data reported in this dissertation.

The majority of the studies reported here involved the monitoring of the water overlying general reef zones, and no enclosure of the system was used. The assumption is made that lateral variability in the water mass over relatively great distances is very small relative to temporal changes at a designated point or within a designated water mass, and therefore reasonable turbulent mixing of the water mass horizontally will do nothing to confuse the findings. The reliability of this assumption has been repeatedly established (Kinsey 1972, Kinsey 1978). However, situations do arise where heterogeneity is sufficiently extreme to invalidate the "open" flow or standing-water respirometry techniques. Such cases will be discussed in Chapter 1C. All work at Heron and One Tree Is. used a standing-water approach. This technique involves working during the very protracted periods (3-5 h) of slack low water caused by the isolation of the lagoon water mass from the ocean below about mid-tide. Monitoring in standing water at single fixed sites is used and very high precision, highly discriminatory data are obtained. At all other sites a flow technique was used. The technique is necessarily less discriminatory as the underlying community must, by definition, be continuously changing. Flow respirometry can be used under essentially all tidal conditions but is nevertheless simpler near low water. The monitors are moved with the water mass as it moves across the reef being studied. It is not necessary that the currents be unidirectional but it is necessary (as already discussed) that reasonable horizontal homogeneity of the water mass exists and preferably that only random and slow lateral mixing occur. It is nearly impossible to monitor changes in a water mass undergoing appreciable shear. In the flow techniques, the water mass is marked with dye (fluorescein) in the day or with lighted drogues at night.

The monitoring of water chemistry leads to the estimation of a number of instantaneous metabolic rates for the total community (including plankton). Table 4 summarizes the rate variables which will be used in this dissertation. y is converted to y_{max} (the standardized noontime rate) using the approach outlined by Kinsey (1978). This approach is based on the fact that typical reef communities exhibit typical forms for the diurnal photosynthesis curves. Thus, from a value of y obtained between about 0900 and 1500, it is reasonable to predict y_{max}, having first established a set of standard curves (Kinsey 1978). c_d is not similarly converted to a maximized rate as (a) the diurnal curve for calcification has a much flatter, broader plateau making the conversion of little value, and (b) the lower precision of calcification data does not justify such handling. In deriving values for p or p_{max}, the conventional assumption is made that r is a constant throughout the 24 h. This assumption has been found fairly valid throughout the night (Kinsey 1977, 1978). While the maintenance of the same value for r throughout the hours of daylight might be reasonably contested, there seems little real evidence for appreciable photorespiration in tropical marine algal communities. The units used in Table 4 and throughout the dissertation are in g C

Table 4

Hourly Metabolic Rate Variables and Their Units

Variable	Definition	Units
r	hourly respiration rate (measured at night)	gC $m^{-2}h^{-1}$
y	hourly rate of net photosynthesis (magnitude varies through day)	gC $m^{-2}h^{-1}$
y_{max}	peak hourly rate of net photosynthesis (this coincides with true noon)	gC $m^{-2}h^{-1}$
p	hourly rate of gross photosynthesis ($= y + \lvert r \rvert$)	gC $m^{-2}h^{-1}$
p_{max}	peak hourly rate of gross photosynthesis ($= y_{max} + \lvert r \rvert$)	gC $m^{-2}h^{-1}$
c_n	nighttime rate of net calcification (assumes the possibility of both precipitation and dissolution occurring simultaneously)	gC $m^{-2}h^{-1}$
c_d	daytime rate of net calcification (assumes the possibility of both precipitation and dissolution occurring simultaneously)	gC $m^{-2}h^{-1}$

Note: All the above variables are parameters of the total community. Thus "net photosynthesis" refers to the instantaneous difference between the rate of gross photosynthesis and the respiration of the total community.

rather than m mole CO_2, etc. This choice was quite deliberate as the majority of primary production literature has chosen to use such units.

The standardized hourly metabolic rates are converted to more useful diel parameters. These are listed in Table 5. The approach used to determine diel gross photosynthesis (P) from the noontime rate of peak hourly gross photosynthesis (p_{max}) involves the use of standard formulas based on the same standard curves referred to above (Kinsey 1978). For example, in late December, $P = 11.0\ p_{max}$ at One Tree Is., and $P = 10.7\ p_{max}$ at Lizard Is. Similarly, in late June, $P = 8\ p_{max}$ at One Tree Is., and $P = 9\ p_{max}$ at Lizard Is. Using annual mean values for the hourly rates, $P = 10.0\ p_{max}$ at One Tree Is., and $P = 10.2\ p_{max}$ at Lizard Is. This standard curve approach to using a discontinuous series of hourly rate data in the derivation of diel metabolism is discussed in detail by Kinsey (1978). Equivalent approaches have been developed for the calculation of G from c_d and c_n where the mean value of c_d is used rather than $c_{d_{max}}$ (as indicated in the previous paragraph). Because common useage of calcification rates tends to be in terms of annual gains rather than diel gains, most values of G in this dissertation will be in kg $CaCO_3\ m^{-2}y^{-1}$. Generally this unit is used only where G has been based on data obtained over most of the year. Seasonal calcification data are generally presented in the same units used for photosynthesis and respiration, gC $m^{-2}h^{-1}$.

Plankton metabolism reported has been determined either in 2 liter samples held _in situ_ in polyester (_very_ low diffusion exchange) bags, or in a 250 liter Plexiglas hemisphere sealed with a flat piece of Plexiglas across its diameter (uppermost). In the case of the plastic

Table 5

Diel Metabolic Rate Variables and Their Units

Variable	Definition	Units
R	Diel respiration = 24 r (assumes no photorespiration)	$gC\ m^{-2}d^{-1}$
P	Diel gross photosynthesis (calculated from p_{max} using the standard curve approach, Kinsey 1978)	$gC\ m^{-2}d^{-1}$
E	Diel net production, or gain (= P-|R|)	$gC\ m^{-2}d^{-1}$
P/R	Ratio of autotrophic self-sufficiency	-
G	Diel net production of carbonates (= approx. 11 c_d + 13 c_n**)	$gC\ m^{-2}d^{-1}$ or $kgCaCO_3\ m^{-2}y^{-1}$*

* Inconsistent unit used where data are based on long term means, to conform to common useage in the literature.

** The approach used here is analogous to the standard curve approach used to determine P (Kinsey 1978). Using annual means, G = 11 c_d + 13 c_n at One Tree Is., G = 11.5 c_d + 12.5 c_n at Lizard Is., etc. Where G is to be calculated for a particular time of the year, the formula varies with day length.

bags (used exclusively at One Tree Is.) the respiration was generally measured at night, but in a few cases black bags were used during the daylight hours. Monitoring in bags involved opening one of a series of replicates about every half hour and measuring the change of oxygen level, pH, etc., relative to a known starting point. The contents of each bag was measured only once. In the case of the large hemisphere (used exclusively at Kaneohe Bay), monitoring was continuous (enclosed electrodes) for 0_2 and temperature, and hourly for pH and other parameters. As wall effects are minimal in such a large container, it was found feasible to monitor one sample for 24 hours. Bag samples were rarely held more than 2-4 hours as metabolism became "non-linear" after that time.

The determination of metabolism for discrete environments (mostly relevant to Chapter 2B) was carried out inside plastic "fences" which isolated the water mass laterally, but allowed relatively normal exchange with the atmosphere (Kinsey 1972, 1973, 1978). Typically, these fences were 3-5 m in diameter and were placed around chosen communities on the reef-flat at times when the water depth was 50-100 cm.

NEW DEVELOPMENTS

One aspect of the methodology used here requires reexamination. A table of mean values for the metabolic quotients RQ ($\Delta CO_2/\Delta O_2$) and PQ^{-1} ($\Delta CO_2/\Delta O_2$) has already been published (Kinsey 1978). The application of such constants to the correction of oxygen data in the determination of true photosynthesis and respiration was also discussed at length in the same paper. However, there are now many more values available from both the original site (One Tree Is.) and a number of other sites, and it is desirable to examine the general applicability of those values already published. The previously published values for application to typical shallow reef-flat coral zones were RQ = 1.05, PQ^{-1} = 0.90 (n = 8). Similarly, values of RQ = 0.9 and PQ^{-1} = 0.9 (n = 16) appeared to apply where the community was a reef-flat coral outcrop isolated from the influence of the surrounding sand/rubble bottom. By considering the relative areas and metabolic rates, it could be determined that the sand/rubble bottom had metabolic quotients of RQ = 3, PQ^{-1} = 0.9. Thus, in that early work it seemed that a PQ^{-1} of 0.9 had general applicability in a shallow reef system with or without the dominance of corals and other hard substratum organisms. On the other hand, RQ was apparently quite variable with the high values indicating the contribution of CO_2 produced by essentially anaerobic decomposition associated with the sand/rubble bottom. The surprisingly anaerobic nature of some coral reef sediments within only millimeters of the surface has been emphasized by the work of Skyring and Chambers (1976).

Most coral reef studies reported have either assumed the empirical values of RQ = PQ = 1 for the metabolic quotients (Odum and Odum 1955; Kohn and Helfrich 1957; Smith and Marsh 1973) or have avoided the problem by reporting only oxygen anomalies, or CO_2 anomalies measured directly (Smith 1973). Studies on marine plankton frequently use the values recommended by Strickland and Parsons (1968) of RQ = 1, PQ^{-1} = 0.8.

By far the majority of reliable metabolic rate data reported in this dissertation are based on O_2 anomalies rather than CO_2 anomalies.

This deliberate preference was because of the much higher precision associated with O_2 estimation notwithstanding the problems of interface diffusion. It is therefore important that a meaningful conversion from metabolic rates based on O_2 to metabolic rates based on real CO_2 exchange can be made. To do this (Kinsey 1978), the oxygen anomaly, corrected for atmospheric diffusion exchange, is converted to an equimolar CO_2 equivalent and then corrected by multiplying by the relevant metabolic quotient.

Table 6 summarizes those values of the metabolic quotients available from the sites used in the various studies reported in this dissertation. Site details are given in Section 1 of the Results and Discussion. Values are presented in order of decreasing dominance by corals; through dominance by corals and coralline algae; mixed substratum communities with relatively high content of foliose and filamentous algae; low standing crop areas on sand and rubble; to algal flats of various kinds. The final group of data represent areas in Kaneohe Bay, Hawaii under stress from high organic input. This input, dominated by diatoms, is driven by the sewage nutrient input to the SE end of the bay. Many of the data in Table 6 have quite high standard deviations but certain trends are evident. Considering first the PQ^{-1} values, it can be seen that all values obtained for areas with high coral or coralline algae cover (A,B,C) are close to 0.9. Data for sites with larger proportions of non-calcifying algae (D,E) tend toward higher values of 1 to 1.1. When non-calcifying plants become the only dominant primary producers (F), values obtained seem very variable. However, there is some suggestion of the highest values being

Table 6

Values* for the Metabolic Quotients in Reef Communities ($\Delta CO_2/\Delta O_2$)

Community	RQ	PQ^{-1}
A. Isolated coral outcrops (One Tree Is.)		
Acropora pulchra	0.85(0.15)n=10	0.87(0.17)n=10
Porites andrewsi	0.90(0.19)n=18	0.93(0.13)n=11
Leptoria phrygia	0.83(0.05)n= 4	0.87(0.09)n= 9
B. Seaward coral slopes		
Lizard Is. pinnacle P1	0.80(0.10)n= 3	0.91(0.20)n= 4
C. Coral/coralline algae dominated reef-flats		
Lizard Is. seaward flat A	0.93(0.30)n= 5	0.95(0.60)n=24
K'Bay central, coral zone	0.87(0.14)n= 6	0.92(0.26)n=18
One Tree coral/sand zone DK13	1.03(0.13)n=30	0.91(0.10)n=30
D. Reef-flat and lagoon reefs with higher foliose or filamentous algae content		
Lizard Is. lagoon reef-flat, D1,2	1.22(0.71)n=10	1.08(0.38)n=13
K'Bay barrier reef-flat, K	--	0.95(0.51)n= 9
Lagoon reticulum, One Tree, DK22	1.10(0.30)n= 6	0.98(0.25)n= 8
E. Low standing crop sand flats--corals and algae		
One Tree sand flat, DK17	1.50(0.50)n= 4	0.99(0.45)n= 6
K'Bay central	--	1.05(0.40)n=10
K'Bay Coconut Is.	--	1.09(0.46)n=16
F. Algal flats		
K'Bay Central (red algae)	1.08(0.69)n= 3	0.91(0.21)n=11
K'Bay Coconut Is. (red algae)	--	1.09(0.66)n=14
K'Bay NW (mixed, some seagrass)	1.36(0.64)n=11	1.28(0.65)n=24
Lizard lagoon (mixed, some seagrass)	3.30(1.20)n= 6	1.84(0.31)n= 3
H. Areas dominated by filter feeding and organic input		
K'Bay Coconut Is., "coral" zone	1.12(0.86)n= 5	1.12(0.68)n=16
K'Bay Lilipuna reef	1.61(1.14)n= 8	1.63(0.54)n= 8
K'Bay SE reef-flat	1.08(0.58)n= 7	1.86(1.54)n=13

* Value in parentheses is the standard deviation. n is the number of determinations used to calculate the mean values tabulated.

associated with sites having a seagrass component. I am not aware of any logical explanation for this overall trend. All the sites so far mentioned are established in later sections of this dissertation to be marginally or considerably autotrophic. The sites under H are considerably heterotrophic and, in common with the most highly autotrophic sites in F, exhibit elevated values for PQ^{-1}. Why both these biotic categories fix more moles of CO_2 than the number of moles of O_2 they release, whereas all the high calcifying areas produce equivalently more O_2, is not clear. It should be stressed that the CO_2 incorporated into calcification is not included in the derivation of these metabolic quotients (see first part of Methods). In fact, there is some suggestion (Smith and Kinsey 1978) of an underestimation of calcification using the alkalinity method, indicating that the ΔCO_2 (organic) estimates calculated by difference (ΔCO_2 organic = $\Delta \Sigma CO_2 - \Delta CO_2$ inorganic) should tend to be high--i.e., PQ^{-1} might be expected to be a little higher in high calcification zones as a result of this possible experimental error, not low as they are found to be.

There is some similarity in the trends for RQ in Table 6 to those described above for PQ^{-1}. Thus zones dominated by corals approximate 0.9 whereas the inclusion of increasing amounts of non-calcifying algae seems to be associated with higher values. A more realistic association is probably between increased proportions of loose or unlithified consolidated sediments and the higher values. The highly heterotrophic areas (H) also exhibit values higher than 1. However, these values are not high enough to suggest that anaerobic decomposition plays a major role. This finding is perhaps surprising in view of the substantial component of anaerobic processes at sites such as the Lizard lagoon algal flat (RQ = 3.3), and the rubble bottom in the coral zone at One Tree Is. (RQ = 3.0). Both the latter two sites and the three highly heterotrophic sites under H are receiving a high input of organic particulates, but the difference may be that the biota of the heterotrophic sites is dominated by presumably efficient and aerobic filter feeders and detritivores, whereas the biota of the turbulent reef-flats previously mentioned is dominated by algae, and the decomposition processes are probably dominated by microheterotrophs.

Because of the considerable variability found in the values obtained for both RQ and PQ^{-1}, the calculated values for metabolic rates used throughout this dissertation have used the mean metabolic quotients obtained for the particular site.

RESULTS AND DISCUSSION

The subject matter of the dissertation is presented in three Sections covering (1) the individual studies of several relatively normal coral reefs, (2) the general operational hypotheses of coral reef performance derived from the first Section, and (3) the consideration of the effects of several perturbations on coral reef performance. Each Section consists of several Chapters designated A, B, C, etc.

SECTION 1

REGIONAL BASELINE STUDIES

This most detailed section of the dissertation will present the findings of four studies made of very different coral reefs. The amount of work done at each of these sites varies considerably as does the nature of the investigations. Consequently, while every attempt is made to adopt a uniform approach to presentation, there are areas of considerable difference. Some comparisons are made between sites throughout the section, but detailed comparative arguments are mostly kept for inclusion in Section 2.

A. SOUTHERN REGION, GREAT BARRIER REEF

General Information

All of the work serving as the starting point for this study of the flux of carbon through coral reef systems was done at the southern extremity of the Australian Great Barrier Reef. However, while ambient conditions south of this area have not been conducive to the development of complete surface reef structures, it should not be assumed that the discrete reefs which constitute the "barrier" near this southern limit are substandard in any respect. Their morphology and stage of Holocene development is apparently equivalent to that found elsewhere in the Barrier Reef system, and general species diversity, etc., is little below that of more northerly areas. These characteristics have no doubt been maintained by the persistence of the East Australia Current which maintains steady larval input from the north essentially right down the length of the Great Barrier Reef.

A number of periods of research have been used (Table 7) over nine years in this area with by far the principal effort being at One Tree Island. Some more specialized work (Kinsey 1973) was done at Heron Island, 12 miles away. Both reef systems are little, if at all, modified by man over most of their area though Heron Is. has had a small tourist facility in operation for about 30 years. Because that island is located at the western (leeward) extremity of its reef and allows very poor access to the enclosed lagoonal system of the remainder of the reef, human interference has been very minimal. One Tree Is. has been used virtually only for research, and only since 1965. It is located at the windward extremity of its enclosed lagoonal

Table 7

Field-work Timetable for One Tree Island and Heron Island

Year	Period	Site
1967	Sept./Oct. (3 weeks)	One Tree
1968	Sept./Oct. (5 weeks)	One Tree
1969	Nov./Dec. (3 weeks)	One Tree
1970	Aug./Oct. (12 weeks)	Heron
1971/72	July/Jan. (7 months)	One Tree
1972	Apr./Dec. (9 months)	One Tree
1973/74	July/Feb. (8 months)	One Tree
1975	Feb./Mar. (4 weeks)	One Tree

system (Fig. 1), and allows very good access to all parts of the reef. The enclosing algal rim of the main level at One Tree Is. (Fig. 1) is almost exactly at Mean Water Level (MWL). As the enclosure is absolute, the resulting tidal pattern within the small atoll-like lagoon is essentially a half sine-wave (Fig. 2). This means that the entire system is subjected to standing water for about 5 hours on each tidal cycle. Heron Is. reef experiences a somewhat similar cycle but is at less than MWL. At One Tree Is., all low tides can be seen to be essentially identical. This has resulted in a very uniform (within 2 cm) flat top to all lagoonal formations. Another phenomenon of great importance occurs with occasional small neap tides where no significant rise occurs on one of the high tides. At such times the lagoon is subjected to standing water for about 18 hours. Therefore there is the possibility of this stress causing a control on such things as the standing-crop/oxygen-availability relationship (see later). The situation is further aggravated by the fact that all such tides seem to occur at night and in the months of September, October, and November (Spring). An indication of frequency is given by: 1 in 1967, 4 in 1968, 3 in 1969, and 0 in 1970.

Table 8 gives general information about the weather, tides, flushing rate, location and reef type for One Tree Is. It can be seen that the location is continental shelf and exposed, tides are large, weather and winds marginally tropical, and flushing time short compared with the periods of weeks or months associated with most Pacific atoll systems (Smith and Pesret 1974; Smith and Jokiel 1975; Von Arx 1954).

Figure 1. One Tree Is. and its extensive shallow lagoonal reef. The perimeter fully enclosed the main level at MWL so that all low tides are at this constant level and only the top half of the "sine wave" for each tidal cycle is experienced. The lower level lagoon is still well above LWS and is about 0.5 m lower than the main level. This part of the reef apparently represents Holocene accretion.

░ cays

▨ heavily consolidated algal pavement

◎ intertidal rubble banks

▩ outer reef-flat coral zone

▥ lagoon areas with reticulated patch reefs

⊞ open lagoon with submerged pinnacles

This reef is fully exposed to the open sea. The main N/S transect is shown, and the location of the most commonly used sites indicated. "F" is the site used for all fertilization studies. The actual reef crest is at DK10. The algal pavement slopes away, seaward of this crest, and terminates abruptly with a spur and groove zone leading into the steep seaward slope. See Table 9 for site details.

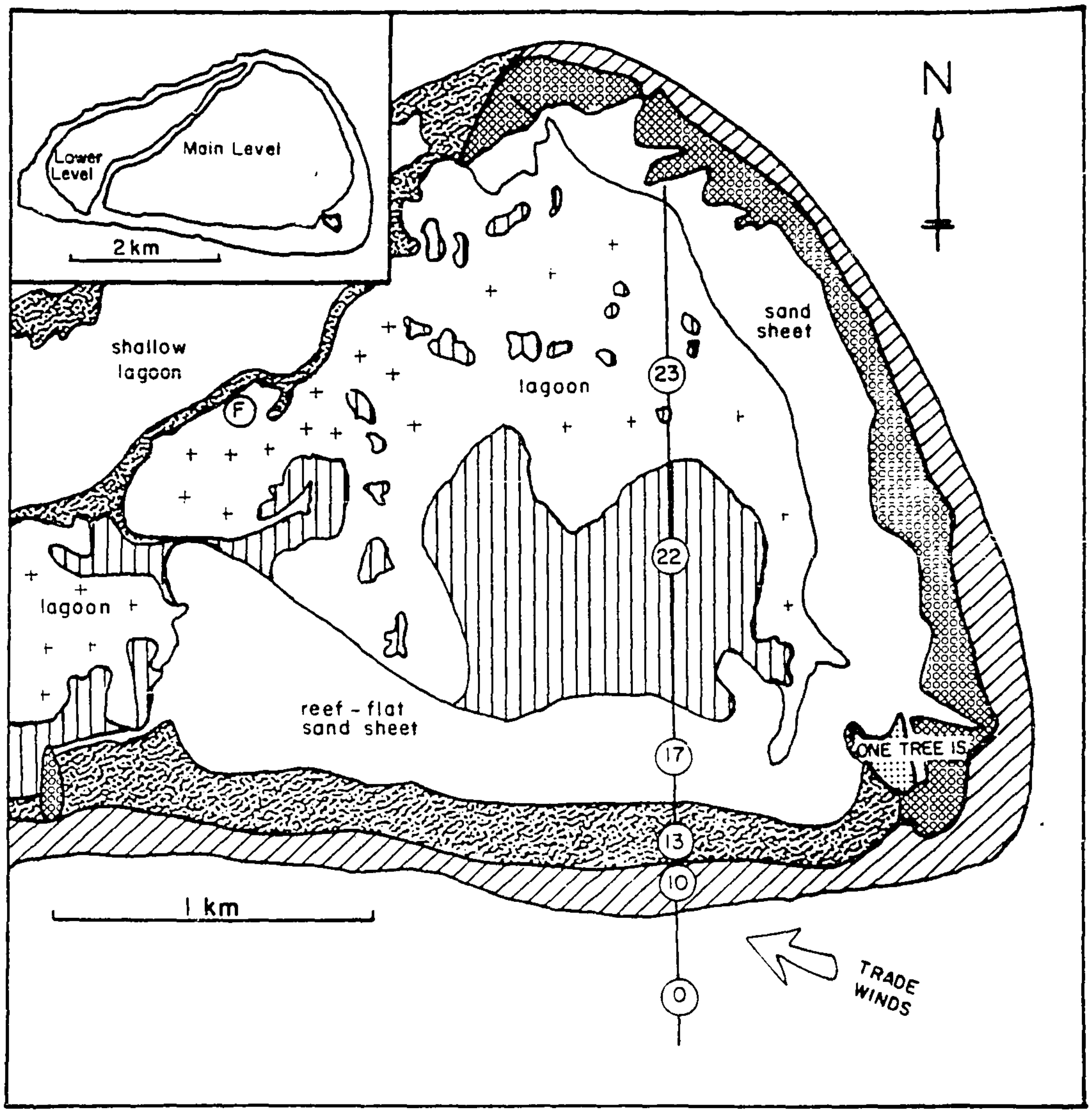

Lower Level
Main Level
2 km
N
shallow lagoon
lagoon
sand sheet
lagoon
reef - flat sand sheet
F
23
22
17
13
10
0
ONE TREE IS.
1 km
TRADE WINDS

Figure 2. Tidal profiles within the lagoon at One Tree Island. Plotted points and solid lines are actual measured water level during three separate tidal cycles. In each case the plot is begun from the point when the first detectable rise occurred. The solid arrow is the time of predicted high tide. The open arrow is the time of actual top of the tide. The dashed lines indicate the theoretical pattern of the ebb tide calculated from the actual time of the top of the tide, but assuming that the reef was not enclosed by its rim at MWL.

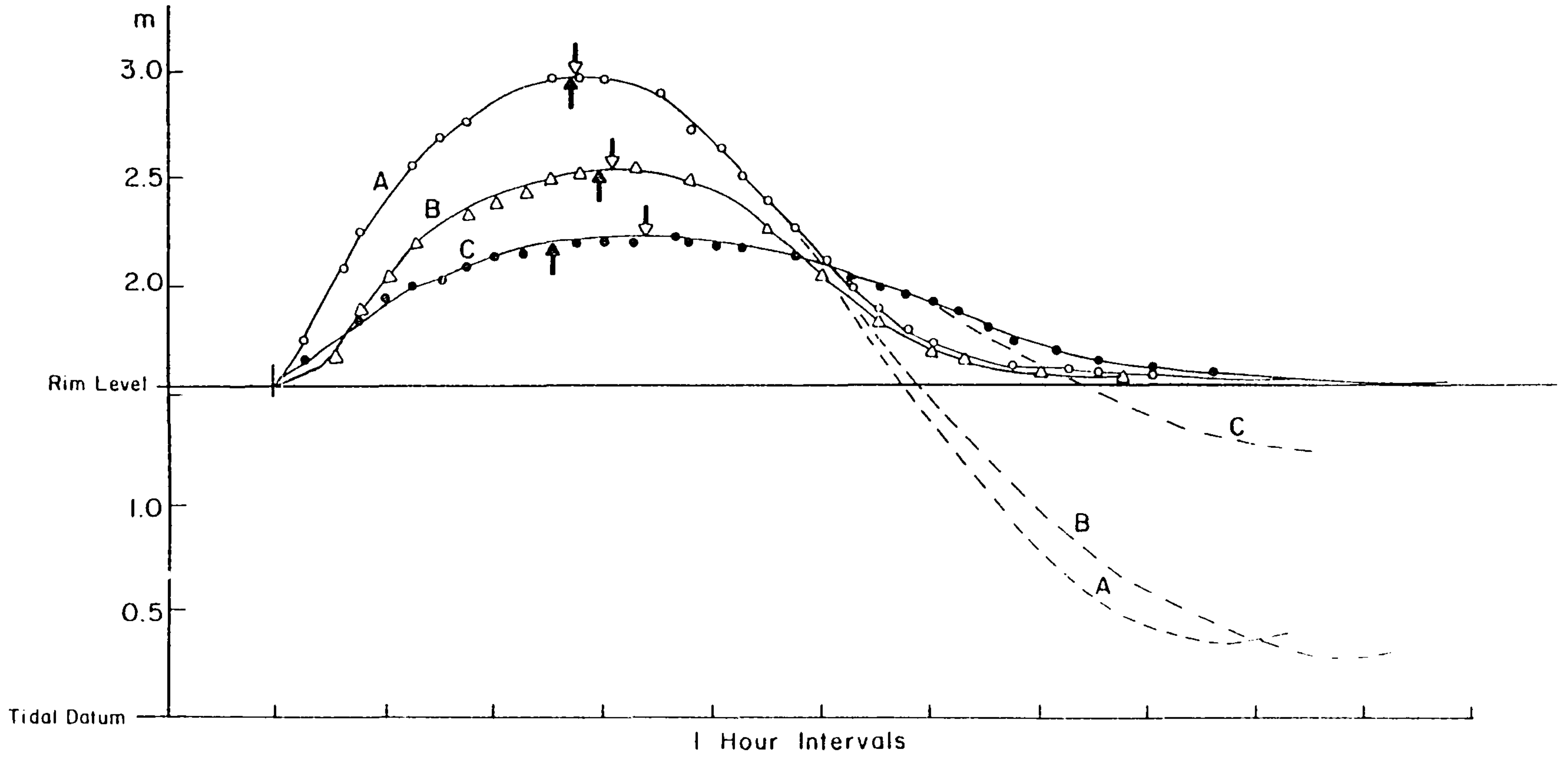

m
3.0
2.5
2.0
Rim Level
1.0
0.5
Tidal Datum
A
B
C
C
B
A
1 Hour Intervals

Table 8

One Tree Island
Geographic, Meterological and Tidal Information

Location:	23° 30'S, 152° 6'E, 90 km off Australian east coast, on the continental shelf (25-55 m) 10 km inside the 200 m line of the continental slope. Close to southern extremity of Great Barrier Reef Province.
Reef Type:	Discrete platform (4.7 km by 2.7 km) with shallow fully enclosed (below mean water level) lagoon containing elaborate reticulated patch reef structure. Not associated with any exposed terrigenous structure. Fully exposed to open sea.
Weather:	Strongly seasonal, marginal SE trades strongest in winter. Summer has frequent calms. Precipitation erratic and throughout year (100-130 cm). Wind E-S 55% mostly winter (10-20 knot) E-N 22% mostly summer (7-10 knot) S-W 14% mostly winter (7-15 knot) near calm 9% mostly summer
Tides:	Semidiurnal Larger spring range 2.9 m Smaller neap range 0.8 m Only top 50% of tide is experienced inside reef because of complete enclosure at mean water level.
Currents:	Strong local tidal currents outside reef. Water flow through lagoon has a pronounced wind driven component but ebb flow frequently opposes wind. Net flow is downwind.
Flushing:	Approximately 4 days (Davies et al. 1976).

Table 9 and Figure 1 summarize the particulars and location of the various sites used along a single transect of 2265 m. This transect was chosen to be a representative windward/leeward cross section of the reef. Because of the full exposure of this reef to the ocean, the algal pavement (DK8, DK11) is wide, heavily cemented, and generally intertidal as it is mostly on a seaward dip from the actual reef crest. However, the reef-flat coral zone (DK13) is flamboyantly developed, probably because of the constancy of the low tide level lagoonward of the reef crest. These 0.8 m high generally viable coral outcrops with their associated epiphytic algae, Porolithon overgrowth, and fauna cover the 35% of the area referred to as "hard bottom". The remaining 65% is unconsolidated coarse sediments. These sediments are similar to those of the prograding sand sheet (DK17) behind the coral zone where few coral outcrops remain. However, in the DK17 area there is a more extensive surface film of filamentous algae. The formations of the lagoon reticulum (DK22) are somewhat similar to those of the reef-flat (DK13). The principal differences are (a) there is a greater percentage of loose sediment bottom at DK22, (b) the formations are much higher at 2.5 m, (c) the reefs form a directionally random reticulum rather than "windrows" as is the case at DK13, and (d) there is a conspicuously higher component of foliose and filamentous algae. The open lagoon (DK23) formations are mostly submerged and poorly developed pinnacles with an occasional discrete patch reef. The patch reefs and the wider reefs of the lagoon reticulum themselves show zonal structure, with a perimeter hard substratum zone and an unconsolidated coarse

Table 9

Site Summary Along Main South/North Transect
One Tree Island (windward to leeward)

Zone Description	Zone Extent (m)	Fixed Monitoring Sites Designation	Distance from Outer Limit of Zone (m)	Low Tide* Depth (m)	Hard Bottom (%)
Seaward slopes above 5 m	60	DK4	40	3.5	100
Algal pavement	165	DK8	50	0.1	100
Algal pavement	165	DK11	140	0.3	100
Reef-flat coral zone	200	DK13	75	0.8	35**
Reef-flat sand & rubble	240	DK17	120	0.5	<5**
Lagoon: reticulum	750	DK22	500	2.5	10**
Lagoon: open	850	DK23	240	4.8	5-10***

* All low tides are identical because of total enclosure of lagoon at mean water level--i.e., above the outside low water level.

** This area is made up of reef outcrops growing to the low tide level.

*** Some of this is discrete patch reefs, some is deeply submerged coral.

sediment central area. These perimeter zones are typically 2-10 m wide, as compared with the overall reef perimeter width of 350-400 m (i.e., the algal pavement plus the active coral zone).

Here, and elsewhere in this dissertation, the term "perimeter zone" will be used to describe areas of algal pavement and areas of predominant hard substrate coral activity forming the outer boundary or edge of larger formations. In modern reefs this perimeter zone is essentially always a shallow water (<1 m at low tide) structure. The sand flats frequently lying lagoonward of the coral zone are not included as part of the reef perimeter as they represent the progradation of sediments generated by the perimeter and are not functionally part of the active perimeter zone. The total width of active perimeter has great relevance to many of the concepts to be developed in later chapters in Section 2.

Water Properties

Table 10 shows certain properties of the ocean water adjacent to One Tree Is. for most months of the year. It can be seen that variations are only moderate with clear seasonality in temperature (21.5° in mid-winter; 26° in mid-summer) and in pH (8.3^{+} in mid-winter; 8.2 in mid-summer). In general terms the water mass is very uniform with few effects evident from precipitation or biological activity.

Table 11 shows the diel and seasonal temperature trends within the reef system. Not surprisingly the summer temperatures tend to be greater than or about equal to (at night) the ocean temperature. Winter temperatures tend to be about equal to or less than (at night) the ocean temperature. Diel range over the reef-flat varies from 4°C

Table 10

Properties of the Open Water off One Tree Island

Month		Temperature (°C)	pH	Alkalinity (meq l^{-1})	Salinity (‰)
January	(1972)	26.0	8.22	-	
February	(1975)	25.6	8.20	2.30	
March					
April					
May	(1972)	23.5	8.25	2.31	
June	(1972)	21.8	8.29	2.33	
July	(1972)	21.5	8.31	2.36	
August	(1972)	21.6	8.28	2.34	35.7
September	(1972)	22.3	8.27	2.34	35.6
October	(1972)	23.2	8.24	2.34	35.6
November	(1972)	23.7	8.23	2.34	
December	(1972)	25.0	8.23	2.34	

Little variation occurs day to day.

Those months where several years data are available suggest small variations in pH and alkalinity year to year, e.g. pH 8.29 ± 0.02 in Sept., Alk. 2.35 ± 0.02 in Sept., though one significant discrepancy has been recorded so far--viz.

December	(1969)	25.7	8.19	2.28

Oxygen content of the water always falls in the range 96-101% of saturation with respect to air at atmospheric pressure.

Table 11

Lagoon Water Temperatures (°C), One Tree Island

Month	Outer reef-flat (0.8 m at low tide)		Central areas (2-4 m deep at low tide)	
	Daytime	Nighttime	Daytime	Nighttime
January			26-28	25-26.5
February			26-28	25-26
March				
April	27	23		
May			23-24	22-23.5
June	22	18	21.5-22	21-21.5
July			19.5-22	19-21
August			20-22.5	20-22
September	25	20	21-23.5	21-23
October			22.5-26	22-24.5
November			24-27	24-27
December	33	25	27-28.5	25.5-27

Under severe weather conditions temperatures may move a degree or two either side of the ranges quoted. Similar anomalies will also occur on some extreme neap tides when negligible high tide flushing occurs.

In areas with 0.1-0.2 m of water cover at low tide, nighttime winter temperatures will follow atmospheric temperature (as low as 15°).

in the cool months to as much as 8° C in the summer. Diel range in the lagoon is from only 0.5° C in winter to about 1° C in summer. Total annual range is about 15° C over the reef-flat and about 12° C in the lagoon, compared with only 4.5° C in the ocean. Greater extremes are experienced by very shallow areas of the reef crest and tide pools on the seaward slope of the algal pavement.

Extremes of a number of water composition variables are indicated in Table 12. The effects of the biological activity of the reef are very obvious in all variables, with pH and oxygen showing obvious response to respiration and photosynthesis, while alkalinity shows obvious response to the calcifying activity of the reef. It seems highly significant that the nighttime alkalinity is considerably elevated above that of the open ocean (Table 10). This implies that net dissolution of carbonates is a general phenomenon in the dark on the One Tree Is. reef. As indicated in a footnote, salinity stress is not a feature of any site on this reef.

The range of oxygen concentration in Table 12 seems quite extreme and perhaps approaching levels that might be expected to cause physiological limitation. However, I believe it to be highly significant that much <u>more</u> extreme levels occur on the occasions with no tidal rise. On such occasions at night, the oxygen saturation falls to about 14% if there is minimal wind (Kinsey 1973). 14% seems to have particular relevance as similar levels have been found (Kinsey 1973) to be normal in some areas of Heron Is. reef every calm night. Heron reef, because of its lower level relative to MWL, <u>never</u> experiences a lack of tidal rise. The tentative hypothesis which can be made from

Table 12

Typical Diel* Variations in Low Tide Water Properties Over Main Transect at One Tree Island, October 1968 (Kinsey 1972)

	O_2			
Site	% Saturation	mg l^{-1}	pH	Alkalinity (meq l^{-1})
DK8 outer pavement	40-200	3.0-13.0	7.92-8.81	2.55-2.20
Outer limit of reef-flat	39-180	2.9-12.0	8.07-8.51	2.50-2.25
DK13 reef-flat coral zone	44-165	3.3-11.0	8.10-8.43	2.45-2.30
DK17 reef-flat sand zone	74-138	5.5-9.0	8.17-8.42	2.40-2.35
DK22 lagoon reticulum	83-120	5.9-8.2	8.26-8.36	2.47-2.36
DK23 open lagoon	92-108	6.5-7.5	8.29-8.34	2.43-2.36

* Ranges indicate typical values found near the end of a low tide standing water period which had occurred totally in the dark - left value, and totally in the sunlight - right value.

** Extreme neaps giving essentially no high tide influx occur a few times each year. When this is at night, oxygen saturation typically drops to 14% (0.95 mg l^{-1}), and pH to 7.80 at DK13. However, normal nighttime values at Heron Island in an equivalent site, never subjected to a non-influx of tidal water, reach O_2 of less than 20% (1.4 mg l^{-1}), with pH = 7.85, every calm weather night.

Salinity not detected outside the range 35.0‰ to 36.1‰.

these findings is that the standing crop and community composition which such a reef-flat can support is that which will ensure that the oxygen content will never fall below a level of about 15% of air saturation. Of course this does not imply that all reef-flats will have standing crop controlled in this way, as many have such a vigorous and continuous flow of new water across their communities that no such oxygen stress is possible. I have little further data to support this hypothesis and it therefore remains as an interesting but entirely speculative notion.

Metabolic and Calcification Data

The remainder of this chapter is devoted to a presentation and discussion of the community metabolism data obtained from the main transect sites at One Tree Is. A strong case exists (Kinsey 1977) for accepting that year to year variations in metabolic rates for any one site and at any specific time of the year are very small. Consequently, in the discussion which follows, no distinction will be made for the year in which the estimations were made.

Table 13 summarizes all carbon flux data obtained from the principal reef-flat site at One Tree Is. (DK13). Over the several years of this study, 128 estimates of net photosynthesis (y), 81 of respiration (r), 92 of daytime net calcification (c_d), and 60 of nighttime net calcification (c_n) have been made. This includes only "useable" estimates and not those in which experimental problems caused the rejection of the outcome. The monthly groupings presented have operational logic as the field data fall into such groups. All values for y have been converted to the noontime equivalent, y_{max},

Table 13

Summary of the Seasonal Means of Hourly Metabolic Rate Data*
for the Reef-Flat Coral Zone, Site DK13, at One Tree Island

Months	Metabolic Variable	Estim. Mean Hourly Rate ($gC\ m^{-2}h^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
June/July	y_{max}	0.23	0.02	31	2
	r	-0.22	0.02	23	2
	p_{max}	0.45			
	c_d	0.18	0.09	23	10
	c_n	-0.02	0.02	19	23
Sept./Oct.	y_{max}	0.41	0.02	47	1
	r	-0.31	0.02	24	1
	p_{max}	0.72			
	c_d	0.16	0.05	41	5
	c_n	-0.02	0.01	19	11
Nov./Dec./Jan.	y_{max}	0.47	0.02	35	1
	r	-0.33	0.03	25	2
	p_{max}	0.82			
	c_d	0.16	0.09	19	13
	c_n	-0.03	0.02	17	16
Mar./Apr.	y_{max}	0.51	0.02	15	1
	r	-0.39	0.03	9	3
	p_{max}	0.95			
	c_d	0.18	0.13	9	24
	c_n	-0.02	0.01	5	22

y_{max} : peak hourly rate of net photosynthesis
r : hourly respiration rate
p_{max} : $y_{max} + |r|$ = peak hourly rate of gross photosynthesis**
c_d : daytime rate of net calcification
c_n : nighttime rate of net calcification

* Rates are corrected for atmospheric diffusion and the metabolic quotients where applicable.

** In each case only the mean values of y_{max} and $|r|$ have been summed. This is because individual values of y_{max} and r were rarely determined on the same day.

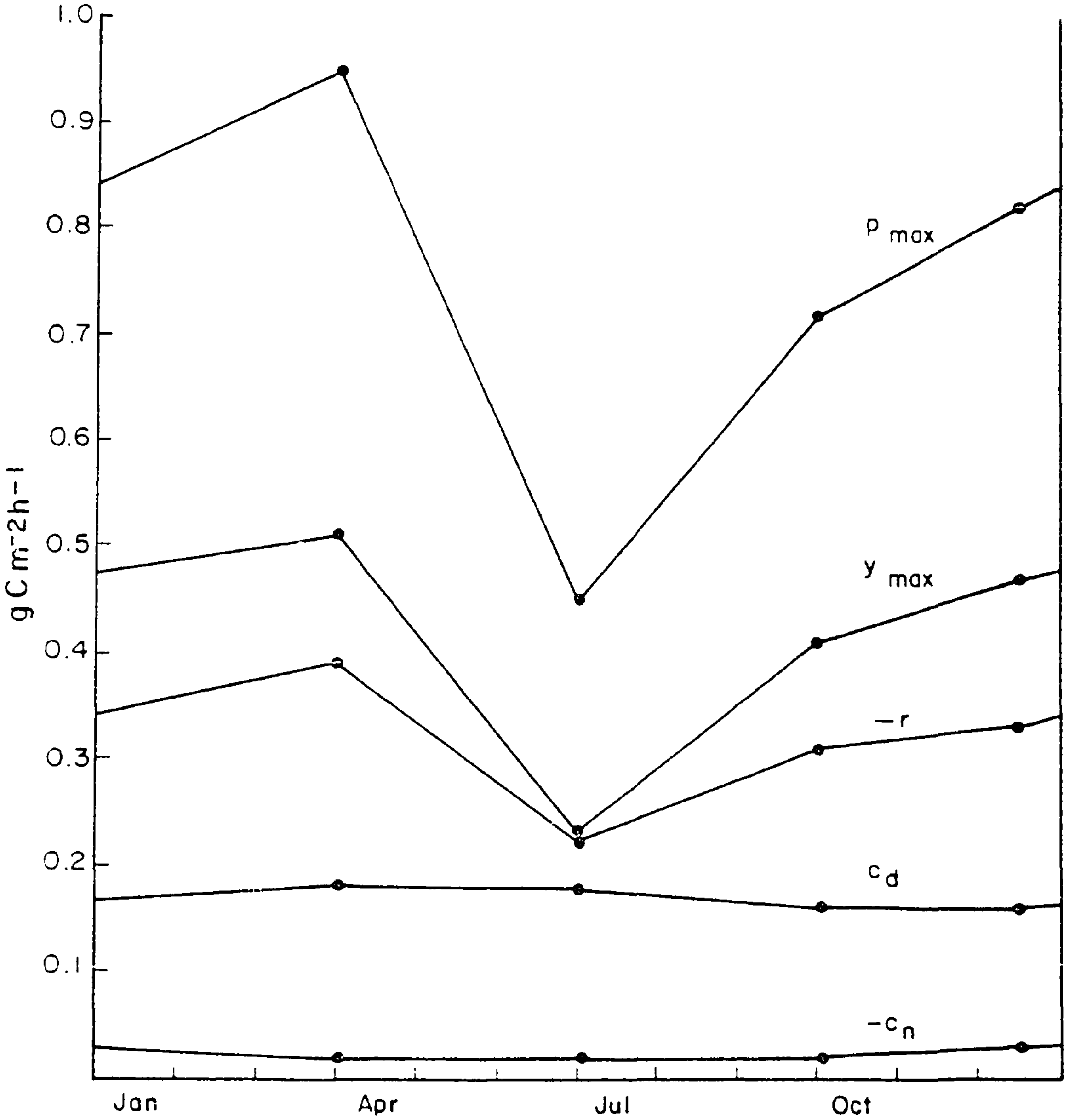
using the procedures outline elsewhere. Because of the "noisier" nature of calcification data, c_d represents the means of the estimates regardless of the time of day. However, nearly all estimations of c_d are from the period of the day for which photosynthesis is within 10% of maximum rate. To obtain p_{max}, the mean y_{max} is added to the mean $|r|$. As individual values of r rarely come from the same 24 hour period as the values for y_{max}, there is little point in determining individual values for p_{max}, and in fact such a derivation would be entirely arbitrary. It can be seen that all tabulated values for y_{max} and r have standard errors 1, 2 or 3% making them very reliable estimates. Values for c_d and c_n have standard errors between 10 and 25% making them more questionable; however, the consistency of these calcification estimates greatly enhances their usefulness.

Seasonality of Metabolism and Calcification

Figure 3 summarizes the seasonal trends in the hourly metabolic rates from Table 13. It is obvious that both respiration and photosynthesis exhibit marked seasonality with a minimum value in winter and a maximum value not in summer, but in fall. It should be stressed that this is notwithstanding the fact that the temperature maximum occurs in January (mid-summer). By comparison with the seasonality in the organic carbon cycle, calcification rates show essentially no seasonality. The slight inverse trend is not statistically significant.

Table 13 and Fig. 3 clearly demonstrate that active dissolution (negative calcification) is a normal feature of this coral dominated reef-flat (c_n always <0), and probably represents the loss of at least

Figure 3. Hourly metabolic rates as a function of the time of year for the reef-flat coral zone, site DK13 at One Tree Is. (based on data in Table 13).


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
g C m-2h-1
Jan
Apr
Jul
Oct
p max
y max
−r
c d
−c n

a quarter of the total carbonates fixed. It is also apparent that the amount of carbon fixed in calcification varies from 40% of the amount fixed by photosynthesis during an hour of daylight in winter to only 20% during an hour of daylight in fall. Similarly the amount of carbon released by respiration (and decomposition) during an hour of darkness varies from 50% of that fixed at the noon hour during winter to 40% for most of the remainder of the year.

The diel integration of the hourly rates discussed above is presented in Table 14. The weighted mean for the whole year is based on the reasoning that the months for which data are not available exhibited metabolic rates intermediate between those for the time periods on either side of the missing month. On the integrated basis, seasonality is even more pronounced as must inevitably be the case with the inclusion of day length in the calculation. There is now marginal seasonality evident in calcification though this is inevitable from the formula used to calculate G for different day lengths. Several important new conclusions can be drawn from Table 14 and from Fig. 4 which summarize those data:

(1) It is obvious that calcification represents a high gain process (75% gain if we assume c_n applies throughout the whole 24 hr) whereas the photosynthesis/respiration cycle varies from only 14% gain down to a 32% loss. In absolute terms, calcification involves a gain (G) of close to 1.5 gC $m^{-2}d^{-1}$ throughout the year (4.6 kgCaCO$_3$ $m^{-2}y^{-1}$). Gain in organics (E) varies from 1.1 gC $m^{-2}d^{-1}$ in mid-summer, to a loss of 1.7 gC $m^{-2}d^{-1}$ in winter.

Table 14

Seasonal Trends in Diel Community Metabolism
of the Reef-Flat Coral Zone, Site DK13, at One Tree Island

Months	P	-R	E	P/R	G
	($gC\ m^{-2}d^{-1}$)				($gC\ m^{-2}d^{-1}$)
June/July	3.6	5.3	-1.7	0.68	1.3
Sept./Oct.	7.2	7.4	-0.2	0.97	1.5
Nov./Dec./Jan.	9.0	7.9	1.1	1.14	1.6
Mar./Apr.	9.0	9.4	-0.4	0.96	1.7
Weighted mean	7.2	7.4	-0.2	0.97	1.5*

Even the smallest differences between P and R are about equal to sum of the standard errors (see Table 13). All differences between values of P or R for consecutive time periods are significant, except the identical values for P = 9.0. Differences for consecutive values of G are not individually significant because of the variance in estimates of c_d and c_n. However, the trend is obvious because of the day-length component used in the derivation of G.

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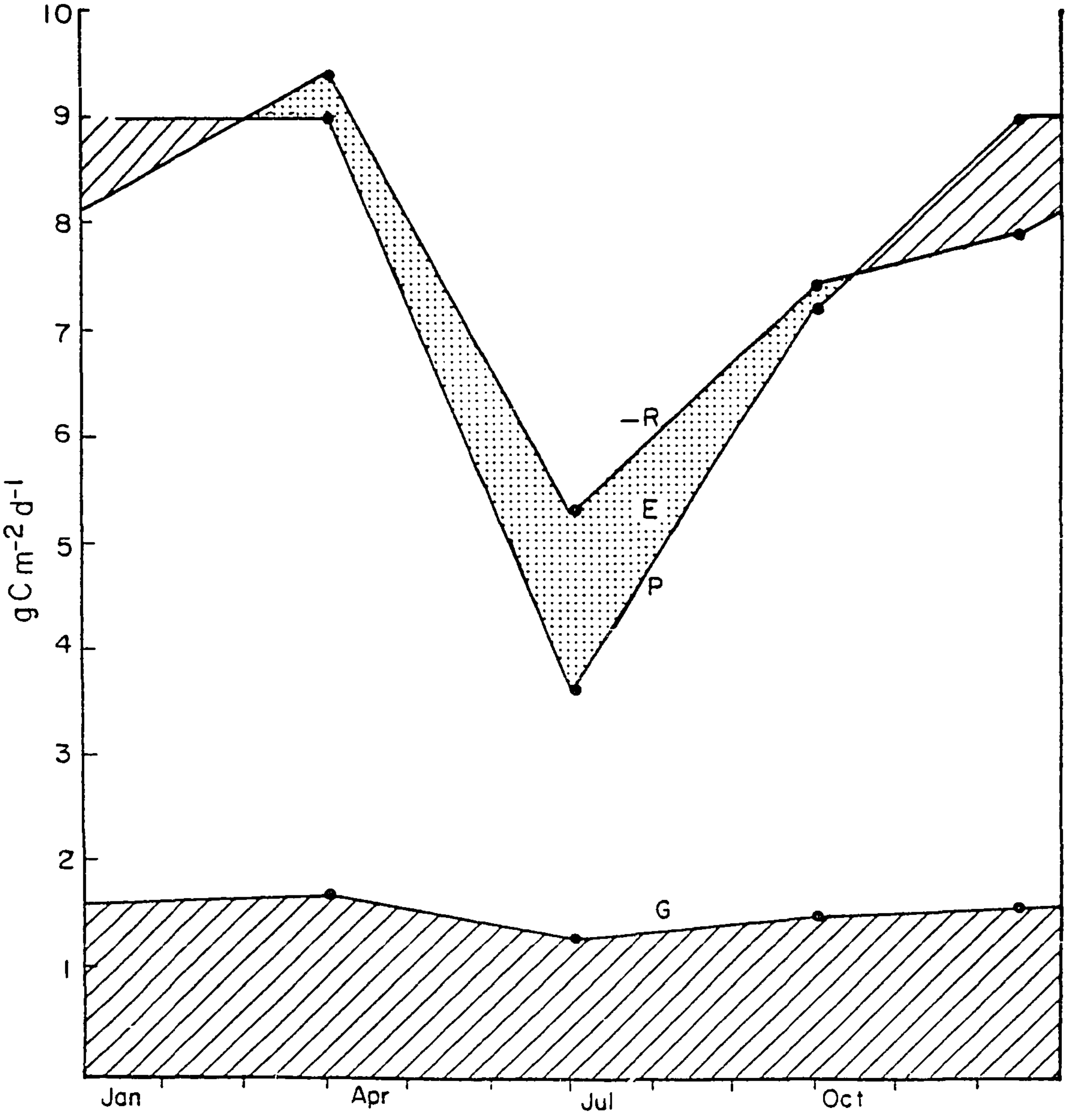
* = 4.6 $kgCaCO_3\ m^{-2}y^{-1}$

Figure 4. Daily metabolic rates as a function of the time of year for the reef-flat coral zone, site DK13 at One Tree Is. (see Table 14). The cross hatched areas represent net gain and the stippled area net loss.


10
9
8
7
6
5
4
3
2
1
g C m-2 d-1
-R
E
P
G
Jan
Apr
Jul
Oct

(2) Expressed differently, the autotrophic self-sufficiency (P/R) varies from 70% in winter to 114% in summer, with an overall weighted mean of 97%.

(3) In terms of total carbon flux, photosynthesis (P) and respiration (R) are processing from approximately 3½ times (winter) to 5½ times (fall) as much carbon as calcification.

(4) The results obtained for this reef-flat coral zone are in good general agreement with most of those obtained by other workers (Table 1) for similar areas on other reefs. It is obvious that the agreement may be a lot better if the comparisons could be made on a careful, seasonal basis. Most other reports have ignored seasonality and assumed that the estimates reported represented the general case. There is striking similarity in all parameters between this One Tree Is. reef-flat in spring (<u>or</u> the annual mean), and the reef-flats reported by Kohn and Helfrich (1975), Smith and Marsh (1973), Marsh (1974), and Sournia (1976). The significance of this similarity and its importance in predicting coral reef performance and response to perturbation will be discussed in a later chapter (2E).

A number of points of interpretation also need to be discussed:

(1) A positive net gain in carbonates does not necessarily mean that the material fixed accumulates at the site of its fixation. Thus all 4.6 $kgCaCO_3\ m^{-2}y^{-1}$ formed at this site may be redistributed (and probably is) as mobile sediments when viewed in a long-term time frame.

(2) Gain or loss of organics (E) can be interpreted in more than one way. It is probable that the average loss of 0.2 $gC\ m^{-2}d^{-1}$ (estimated over the whole year) represents the need for organic input

--i.e., plankton and/or detrital input exceeding export. However, the more dramatic loss of 1.7 gC $m^{-2}d^{-1}$ in winter and the gains of 1.1 gC $m^{-2}d^{-1}$ in summer more probably reflect transition phases of seasonal standing crop shifts--i.e., at One Tree Is. standing crop increases in summer and decreases in winter. This is entirely compatible with visible seasonal changes in the more labile foliose algae near this southern end of the Barrier Reef. This subject will be discussed more in the chapter on sources and sinks (2A).

Zonation of Metabolism and Calcification

Table 15 summarizes all carbon flux data obtained from the principal sites of the main transect at One Tree Is. during the whole duration of the study. For each site, data are presented in the form of annual means derived from all seasonal data available, and weighted proportionally for any missing months as covered in connection with the discussion on seasonality at DK13 (Tables 13 and 14). This whole process makes it very complex to estimate a meaningful standard deviation. The procedure used has been to take the mean of the standard deviations for any time periods in which the rate data themselves were averaged as per Table 13. Thus the relatively complex regression which relates these variables to season is taken into account, albeit simplistically, rather than giving a standard deviation for all data which would unfairly reduce the precision of the estimation of mean annual rate.

It is obvious that the reef-flat coral zone received far more attention than any other site reported in Table 15. However, the only estimates with very low reliability are the majority of nighttime

Table 15

Summary of the Annual Weighted Means* of Hourly Metabolic Rate Data** for Sites Along the Main Transect at One Tree Island

Zone	Site	Metabolic Variable	Estim. Mean Hourly Rate ($gC\,m^{-2}h^{-1}$)	Standard Deviation***	No. of Estim. (n)	Standard Error (%)
Algal pavement	DK8	y_{max}	0.18	0.05	4	14
		r	-0.02	0.01	4	25
		p_{max}	0.20			
		c_d	0.12	0.08	4	33
		c_n	0.00	0.01	3	>100
Reef-flat coral zone	DK13	y_{max}	0.41	0.02	128	<1
		r	-0.31	0.03	81	1
		p_{max}	0.72			
		c_d	0.16	0.09	92	6
		c_n	-0.02	0.02	60	13
Reef-flat sand and rubble	DK17	y_{max}	0.03	0.01	10	11
		r	-0.06	0.02	5	15
		p_{max}	0.09			
		c_d	0.01	0.01	7	38
		c_n	0.00	0.00	4	0
Lagoon: reticulum	DK22	y_{max}	0.18	0.01	35	1
		r	-0.13	0.01	18	2
		p_{max}	0.31			
		c_d	0.06	0.03	21	11
		c_n	-0.01	0.01	10	32
Lagoon: open	DK23	y_{max}	0.07	0.01	9	5
		r	-0.07	0.01	4	7
		p_{max}	0.14			
		c_d	0.02	0.01	4	25
		c_n	0.00	0.02	3	>100

y_{max} : peak hourly rate of net photosynthesis
r : hourly respiration rate
p_{max} : $y_{max} + |r|$ = peak hourly rate of gross photosynthesis
c_d : daytime rate of net calcification
c_n : nighttime rate of net calcification

* Each mean is determined from monthly means (where available) giving equal weight to each month of the year. Where no data available, the month is assumed to have a rate midway between those of adjacent months (see Table 13).

** Rates corrected for atmospheric diffusion and the metabolic quotients where applicable.

*** Standard deviation used is the mean of those from any month for which data are available (see Table 13).

calcification values. Most interzonal differences are of considerable magnitude which gives them a high level of significance. Even a marginal case such as c_d for DK8 and DK13 has a 70% chance of the means being different (t test), and c_d for DK17 and DK23 has a 90% chance of the means being different.

The negative calcification (or dissolution) at DK13 has already been mentioned. Over the year this represents the loss of about 25% of all carbonates formed. It is interesting to note that the only other site for which this phenomenon was noted, was the other site substantially dominated by the same kind of coral/<u>Porolithon</u> outcrops over a sand/rubble bottom: i.e., DK22. This site is apparently losing a very similar amount by dissolution--30%. All other sites approximated zero calcification at night, though there is little statistical significance in this observation. At least it is appropriate to note that all sites had negligible to slightly negative rates of calcification at night. Similarly, all sites exhibited significant positive calcification rates during the day.

The relationship between photosynthesis and calcification was noted previously in connection with the seasonality of metabolism. It is interesting to examine this relationship with respect to zonation and using the annual means of metabolic rates. The one area totally dominated by algae and particularly encrusting corallines, the algal pavement (DK8), has a calcification rate during the day which is 60% of the rate of gross photosynthesis ($c_d/p_{max} = 0.6$). The two areas with coral/<u>Porolithon</u> dominance, the reef-flat coral zone (DK13) and the lagoon reticulum (DK22), are calcifying at 20%

of the rate of gross photosynthesis. The remaining two areas dominated largely by sediments, the reef-flat sand and rubble zone (DK17) and the deep open lagoon (DK23), are calcifying at the lowest proportional rates: 11% of gross photosynthesis at DK17 and 14% of gross photosynthesis at DK23. While these differences seem highly relevant to the biotic makeup of the zones, it is perhaps even more interesting to note that all areas except the algal pavement actually fall within the relatively narrow range of 11-22%. This is considering that the absolute range of calcification among the sites is eightfold. It does suggest a "generic" relationship between calcification and photosynthesis in all coral reef communities. This concept will be investigated further in Chapter 2E.

Table 16 and Fig. 5 summarize the diel rates calculated from the hourly rates covered in Table 15. Here the calcification rates have been expressed in the common usage form of $\mathrm{kgCaCO_3\ m^{-2}y^{-1}}$ for easier comparisons with other published data. This means, however, that direct proportionality comparisons between P and G require conversion to equivalent carbon units. Of course these comparisons would result in essentially the same information which has already been discussed for comparisons between the daytime hourly rates p_{max} and c_d, as both have been shown to be strictly daytime functions (at least at One Tree Is.).

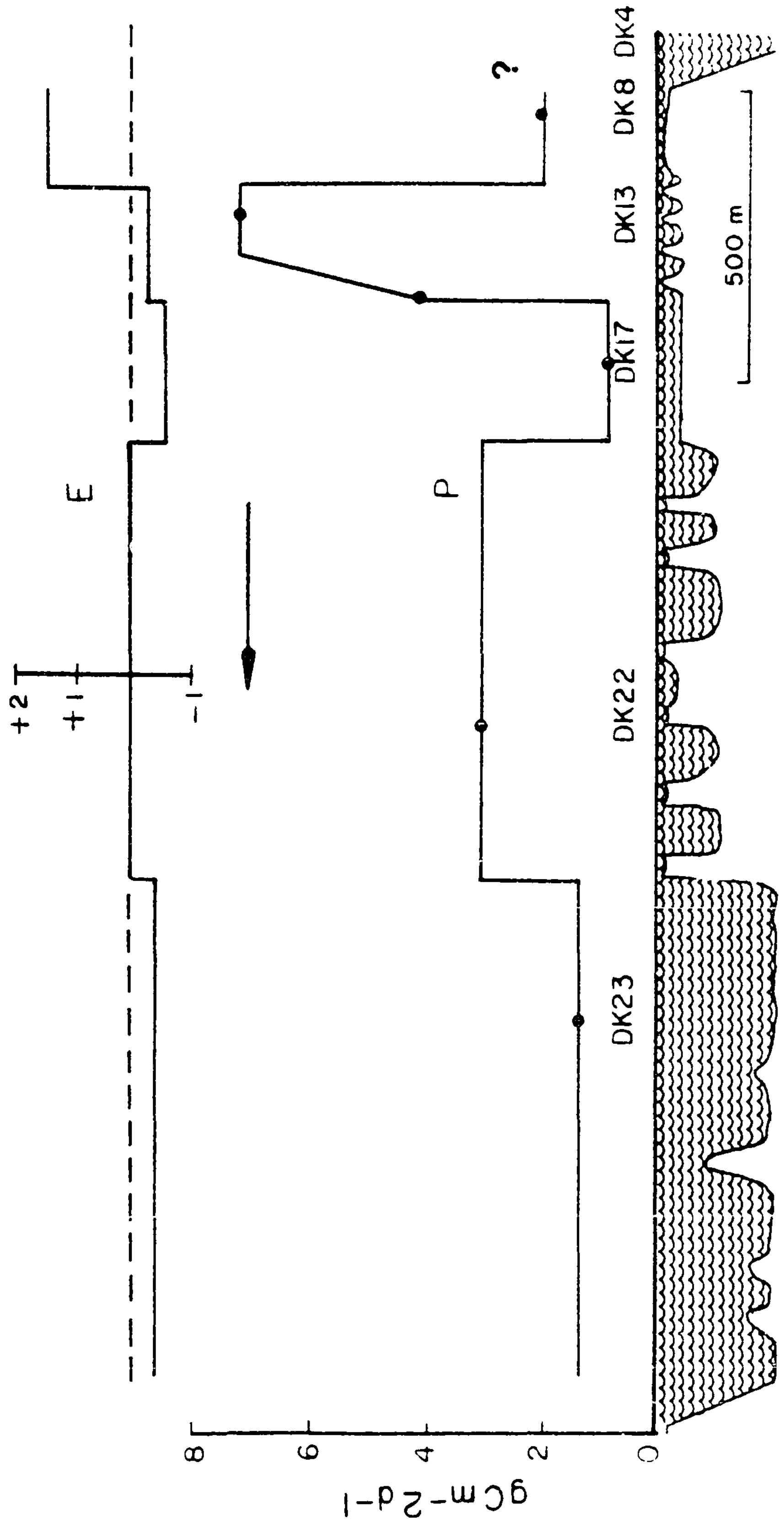
It can be seen from both Table 16 and Fig. 5 that P varies considerably across this fairly typical reef and <u>only</u> the reef-flat coral zone is in the range typified by most published values for coral reef productivity (Table 1). This stresses the point made in

Table 16

Zonation of Community Metabolism Along the Main Transect at One Tree Island, Based on Annual Mean Rates

Zone	Site	P	-R	E	P/R	G
		(gC $m^{-2}d^{-1}$)				($kgCaCO_3\ m^{-2}y^{-1}$)
Seaward slopes	DK4	no data				
Algal pavement	DK8	2.0	0.5	1.5	4	4.0
Reef-flat coral zone	DK13	7.2	7.4	-0.2	0.97	4.6
Reef-flat sand and rubble	DK17	0.9	1.4	-0.5	0.6	0.4
Lagoon: reticulum	DK22	3.1	3.1	0	1.0	1.5
Lagoon: open	DK23	1.4	1.7	-0.3	0.8	0.5
Weighted mean for transect from outer edge of pavement to leeward extremity of lagoon (see Fig. 1)		2.30	2.35	-0.05	0.98	1.5

Figure 5. Primary production along the main transect at One Tree Is. Plots of both gross diel photosynthesis (P) and net gain (E) are shown. The arrow indicates dominant water flow, and hence probable direction of movement for any suspended algal detritus from the algal pavement (DK17). A representation of the vertical section along the transect is also given. The depth of the deepest areas in the lagoon, near DK23, is about 4.5 m. Data points are weighted annual means. The sharp cut-off assumed for each zone is compatible with the abrupt changes in morphology and standing crop which actually occur. However, estimates were all made at the site of the actual plotted points.


gCm-2d-1
0
2
4
6
8
E
P
+2
+1
-1
?
DK23
DK22
DK17
DK13
DK8
DK4
500 m

the introduction, that the high activity zones of the reef-flat have, perhaps undeservedly, become synonymous with "coral reef" in discussions of reef productivity. However, Sournia (1976a, 1976b, 1977) has drawn attention to the existence of areas of lower activity, and of course the "total system" productivity work of Smith and Pesret (1974) and Smith and Jokiel (1975) has stressed the importance of considering a complete reef system as being somewhat more than just a reef-flat. It is obvious from Fig. 5 that the reef-flat outer zone is outstandingly the site of dominant activity but that it represents a relatively small part of the whole. The other area of significant activity is the somewhat biotically related lagoon reticulum which has nearly half the photosynthetic activity per unit area but is much more extensive.

Considering the distribution of excess production (E) across the reef, it can be seen that by far the most outstanding area is the algal pavement where most production is excess. There seems little doubt, in view of the direction of dominant water flow, that this excess is satisfying, at least in part, the mild deficits exhibited by the sediment dominated areas DK17 and DK23. The high activity outer reef-flat also has a small requirement for such input whereas the lagoon reticulum is self-sufficient. This whole subject of sources and sinks will be discussed more fully in Chapter 2A.

The distribution of calcification activity is the most strongly related to proximity to the reef edge. The two perimeter zones represented by DK8 and DK13 produce more than three times as much carbonates per year per unit area than any other part of the system.

The importance of perimeter zones has been alluded to previously and will be dealt with extensively in the various chapters of Section 2.

If the zonal information of Table 16 is integrated with respect to zonal extent (i.e., the curve in Fig. 5 is integrated), the results obtained should tell a great deal about the complete system. Integration of the entire area of the One Tree Is. reef would be more reliable than the linear transect approach reported here. However, available data are insufficient to justify this alternative. All other reef systems in this dissertation will be handled similarly. Table 17 summarizes the results of the transect integration. It should be stressed that the simple square form of the curve integrated (Fig. 5) is justified as the zones represented have a very uniform morphology and distribution of biota, with very sharp zonal delineation. The only zone exhibiting an attenuation of characteristics is the reef-flat coral zone in which the windrows taper to give progressively lower percent bottom cover lagoonward of the halfway mark. It can be seen from both Fig. 5 and Table 17 that this has been taken into account. Table 17 puts the whole system into perspective. It is obvious that the zones of greatest significance in primary production are the lagoon reticulum at 2 kgC d^{-1} followed by equal contributions of 1 kgC d^{-1} from the high activity reef-flat coral zone and the low activity main open lagoon. Only three areas seem consequential in the discussion of imports or exports. The algal pavement is a major exporter of 0.25 kgC d^{-1}. The sediment areas represented by DK17 and DK23 are the importers of 0.11 kgC d^{-1} and 0.26 kgC d^{-1} respectively. This leaves the whole transect with

Table 17

Integration of Community Metabolism
Along the 1 m Wide Main Transect at One Tree Island

Zone	Length (m)	P	E	G
		(gC $m^{-1} d^{-1}$)		(kgCaCO$_3$ $m^{-1} y^{-1}$)
Seaward slopes	60	no data		
Algal pavement	165	330	250	660
Reef-flat coral zone	200	1080*	-30*	690*
Reef-flat sand and rubble	240	200	-110	100
Lagoon: reticulum	750	2330	0	1130
Lagoon: open	850	1190	-260	430
Total transect	2265			
Transect with available data	2205	5130	-150	3010

* These estimates have taken into account the reduced activity associated with the inner end of the coral zone, caused by the tapering of the windrows.

the probably significant deficit of an average of 150 gC d^{-1}. This could be satisfied by the net import of plankton or the input of excess production from the unmonitored outer slopes. This will be discussed further in 2A. The other unmonitored areas, the leeward reef-flat and leeward slopes, are unlikely to be important in this overall mass balance as they serve only as an outflow area for the rest of the system and could, at best, only act as a sink for exported material from the lagoon.

The creation of carbonates by the total system is dominated by the lagoon reticulum and by the combined contributions of both parts of the perimeter zone (algal pavement plus reef-flat coral zone). Each of these complexes is contributing similar total quantities but the ultimate fate of their accumulated sediments is probably rather different. The reef perimeter carbonates, with the present near-constant sea level, are almost certainly prograding away from the site of their creation to form the reef-flat sand sheet (DK17, etc.). This sand sheet in turn is slowly encroaching on, and burying the lagoon reticulum. On the other hand, the carbonates formed by the reticulum itself are mostly accumulated where they are formed, because of the lower energy of the environment and the deeper water. Thus this accumulation is also contributing to the burial of the reticulum, though more or less evenly, rather than by encroachment from the edge as is the case with the sediments originating from the reef perimeter. The obvious corollary of these processes is that the role of the reticulum in all metabolic reef processes is being quantitatively diminished with time, unlike that of the present-day perimeter which is probably in a state of approximate dynamic equilibrium. This presupposes that the reticulum type formation is not itself growing into the open lagoon. In general there does not seem much evidence to support this possibility (Davies and Kinsey 1977; Davies et al. 1976).

Planktonic Contribution

In all the discussion so far of the primary production and respiration of the One Tree Is. system, the rates have referred to total community effects with no reference to the proportional contributions of the benthic and planktonic communities. In fact, it has been generally assumed that planktonic communities contribute only very marginally to the total (Introduction; Table 3). Here the distinction should be stressed between a deficit or excess in the total community metabolism (E) for which the explanation may be the mass input or export of particulate carbon as plankton or detritus, and the actual instantaneous contribution to the photosynthesis or respiration of that plankton or detritus. The former (E) can be very large (e.g., DK8 or DK17 in Table 16) but its contribution to planktonic metabolism may be quite small while still in suspension, as the material concerned in such mass transport is commonly fresh algal detritus of relatively low metabolic rate. At One Tree Is. a number of attempts have been made to determine the planktonic metabolism. These all utilized the plastic bag technique described elsewhere (Kinsey 1978). Unlike the situation when dealing with the benthic community, the amount of biologically active material in suspension obviously can vary with the weather and tide. This makes sampling more complex. As all community data reported here for One Tree Is. utilized the slack low-tide period, all water samples for plankton metabolism were also taken at low tide. The results of this work are summarized in Table 18. It can be seen that planktonic metabolism is quite low but not totally insignificant. It is heavily dominated by a decomposition/respiration component, and primary production is typically very low. This is a very important observation, as most published data for reef plankton have been concerned with estimating primary production (Table 3) and have generally used ^{14}C methods not giving information on the decomposition/respiration of planktonic material. Primary production in One Tree Is. lagoon water typically has been found to approximate zero (i.e., significantly less than 0.1 gC $m^{-3}d^{-1}$). However, over the reef-flat there is typically a detectable 0.1 gC $m^{-3}d^{-1}$. I am inclined to favor that this is the detection of activity from incoming detrital particles rather than phytoplankton. Sournia (see Introduction) has found much higher primary production in some lagoon waters but this appears to be a function of long residence time which does not occur at One Tree Is. The respiration of lagoon water at One Tree Is. is variable but averages 0.1 gC $m^{-3}d^{-1}$ in the main lagoon areas, and 0.3 gC $m^{-3}d^{-1}$ over the reef-flat. The high values for both P and R mentioned in Table 18 for patch reef centers are an interesting reflection of the more intense localized activity which can occur within the system, but are of very marginal consequence to the consideration of total zonal metabolism. Applying the values from Table 18 to the diel

Table 18

Metabolic Activity of the Water Mass in the One Tree Island Area: Summary of Trends

(gC $m^{-3}d^{-1}$)

R	total estimates (n = 38)				
	minimum level found	=	0.08	(n=3)	in lagoon
	windward slopes	=	0.18	(n=2)	± 0.02
	reef-flat (DK13, DK17)	=	0.3	(n=8)	± 0.1
	lagoon (DK22, DK23)	=	0.1[*]	(n=8)	± 0.1
	patch reef centres	=	0.4	(n=20)	± 0.2
P	total estimates (n = 36)				
	typically, for windward slopes and lagoon and patch reef centres	=	0.0	(n=27)	± 0.01
	all values for reef-flat	=	0.1	(n=4)	± 0.05
	occasional patch reef centres	=	0.3	(n=5)	± 0.2

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[*] Lagoon values are only set showing clear response to wind, with calm values approx. 0.1 and windy weather values approx. 0.2.

metabolism data of Table 16, a number of minor but interesting changes in interpretation can be considered:

(1) The reef-flat coral zone changes from P = 7.2, R = 7.4 to P = 7.1, R = 6.9. Thus it seems likely that the benthic community may be a minor exporter of organic matter over the year, even though the zone, complete with its suspended planktonic material, is a slight net consumer.

(2) The reef-flat sand and rubble zone changes from P = 0.9, R = 1.4 to P = 0.8, R = 1.1 which is considerably closer to self-sufficiency though the area is a net consumer whether the total community or just the benthic community is considered.

(3) The lagoon reticulum changes from P = 3.1, R = 3.1 to P = 3.1, R = 2.8 suggesting a slight net export by the benthic community but more interestingly gives a P/R = 1.1 which, considered together with the finding in (1), suggests that the coral dominated areas will prove to be exporting communities. This seems very relevant as these two areas have a lot in common biologically.

(4) The open lagoon remains a significant net consumer, and there is inadequate information to speculate on the situation in the water over the algal pavement.

Most of the more significant and relevant conclusions reached in this chapter will be used in the integrating discussions of Section 2.

B. NORTHERN REGION, GREAT BARRIER REEF

General Information

After the development of all basic methodology and the acquisition of most data at One Tree Is., attention was shifted to Lizard Is. in the Northern Region of the Great Barrier Reef (14°40'S). The system differs from One Tree Is. reef in a number of respects. Lizard Is. is associated with high granitic islands, it is inside the main Great Barrier Reef structure, and of course it is well within the usually accepted optimum latitudes and ocean temperatures for coral reef development. The main bulk of the reef has developed as a triangle of inter-island reefs (Fig. 6) between three high islands. However, terrigenous sediments are not a major component of the present-day reef surface (P. J. Davies, pers. comm.). The location inside the Barrier Reef itself has led to another important difference from One Tree Is. as algal pavements are less well developed and much narrower. The apparently more optimum latitude of Lizard Is. has not led to much greater diversity than at One Tree Is. because One Tree Is. reef already has a community structure the diversity of which is guaranteed by biotic input from the north with the southerly flowing currents. Perhaps the most conspicuous biotic differences are the very extensive occurrence of soft corals at Lizard Is. while they are relatively sparse at One Tree Is., and the presence of small sea grasses on the sand flats at Lizard Is. while they are totally absent at One Tree Is. Measured diversity of fishes and corals is higher at Lizard Is. but this is certainly not visually apparent (F. H. Talbot, pers. comm.).

Figure 6. The Lizard Island complex of three main high granitic islands with their system of inter-island reefs and 10 m deep open lagoon with a bare sediment floor. All areas are fully tidal and the extensive reef-flats are at about LWS. The reef-flats do have zonation with some algal pavement development but this has not been indicated separately because it is less well defined than at One Tree Is. The entire width of the seaward reef-flat exhibits a slight lagoonward dip. The various transects and sites used for experimental work are indicated (see also Table 21).

◝ high granitic islands

▨ reef-flat with significant coral and/or coralline algal development

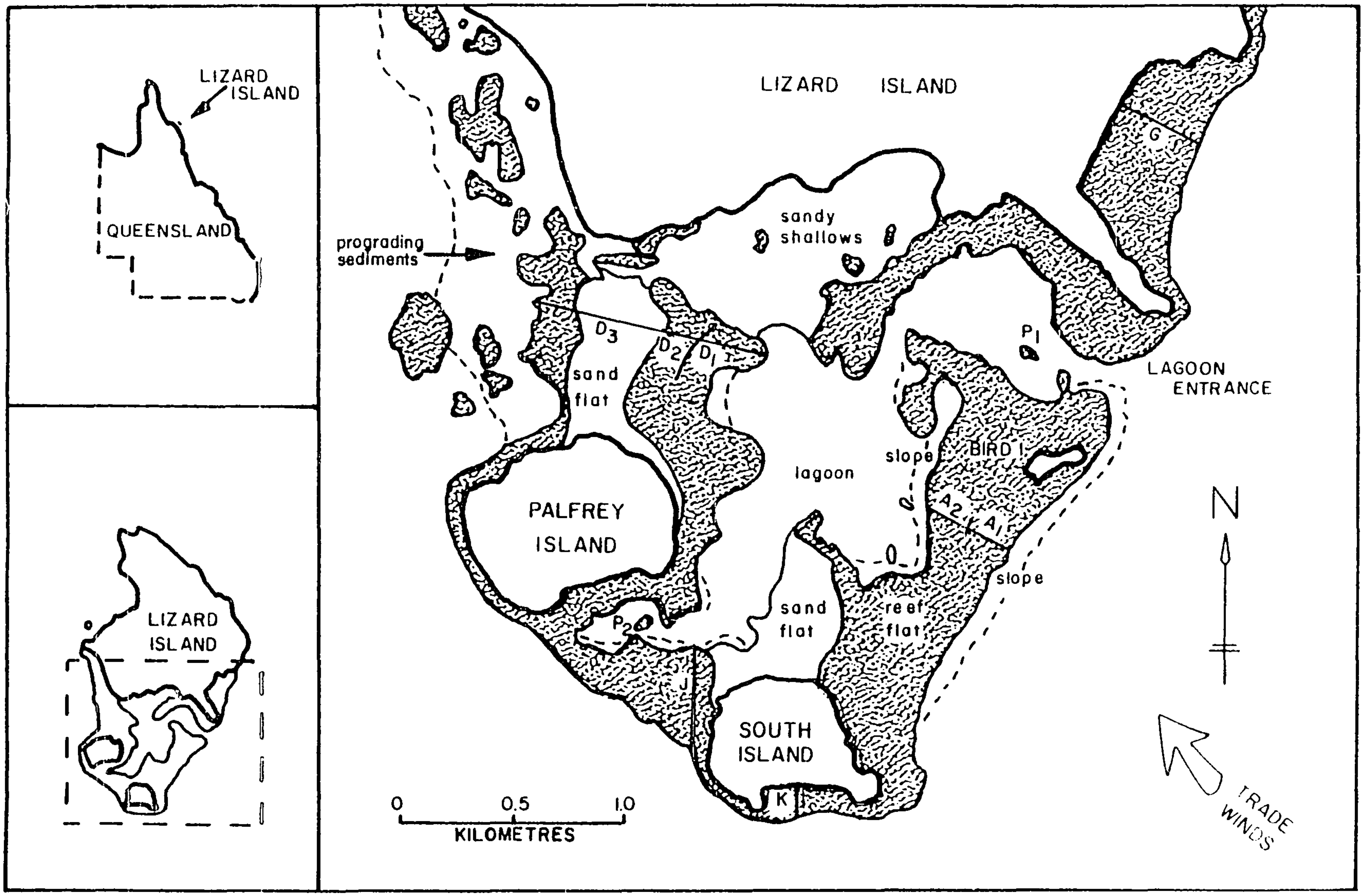
LIZARD ISLAND
QUEENSLAND
LIZARD ISLAND
LIZARD ISLAND
sandy shallows
prograding sediments
G
D_3
D_2
D_1
P_1
LAGOON ENTRANCE
sand flat
lagoon
slope
BIRD I.
PALFREY ISLAND
A_2
A_1
N
slope
sand flat
reef flat
P_2
J
SOUTH ISLAND
K
0
0.5
1.0
KILOMETRES
TRADE WINDS

Table 19 indicates the periods of research activity on the Lizard Is. system. While only two years are represented, maximum effort was made to cover most months of the year in view of the pronounced seasonality found for the metabolic patterns in the One Tree Is. system.

In common with the southern site, Lizard Is. has had very little human interference and essentially no impact on the reef system can be detected. There is now a very small guest house and the Research Station of the Australian Museum, both located on the main island, but as these are both very recent, there has been little time for contemporary human impact. It is the better part of a century since any other extended use has been made of the island, and very little exploitation of reef itself has ever occurred.

Fig. 6 shows the configuration of the system. It is obvious that the lagoon has a fully open entrance and as such the lagoonal system is exposed to the full tidal range. Thus the reef-flats are at, or marginally below, Low Water Springs (LWS). The standing water, fixed site, low tide monitoring approach so appropriate at One Tree Is. was found to be unsuitable at Lizard Is. as there is insufficient water over the reef-flats on most low tides. Also there is less of a three dimensional aspect to the reef-flat formations so that it is not possible to monitor the water mass between the coral formations in the way that was so successful at One Tree Is. Because of these considerations, all community metabolism was measured in a flowing system, usually towards the middle of the tidal rise or fall.

Table 19

Field-work Timetable for Lizard Island

Year	Period	
1974	Dec. (3 weeks)	
1975/76	Apr./Jan. (10 months)	
1975	Sept./Oct. (2 weeks)	LIMER expedition
1976	July/Dec. (6 months)	

General information about location, reef type, weather, tides, etc., is given in Table 20. It can be seen that the reef is even smaller than the One Tree Is. reef, is located inside the main Barrier Reef, has a simple lagoon with little patch reef structure, is in a strong and consistent trade wind belt but experiences only locally generated wind waves, has large but very variable tides, has reef-flat and lagoon currents which are all downwind regardless of tide, and experiences extremely rapid flushing with only a few hours residence time. Most of these characteristics are appreciably different from the equivalent characteristics of the One Tree Is. system (Table 8).

Table 21 and Fig. 6 summarize the sites used in this study. Transect A is a seaward reef-flat with a reasonably consolidated algal pavement (A1) gradually giving way to coral/algal zone (A2) of small heads on a partially consolidated pavement interspersed with loose rubble bottom. The whole transect is near horizontal with a slight dip towards the lagoon. There is no seaward dip of the algal pavement as described for One Tree Is. and the pavement is not nearly so massive a structure as that at One Tree Is. The lighter construction is presumably because of the lack of heavy ocean swell reaching this reef. As mentioned earlier, the coral heads on these reef-flats lack the defined flat-topped windrows of the fully enclosed, constant low-tide-level environment at the southern site. There is generally much less relief in the reef-flat and there is essentially no extensive loose sandy areas between the coral outcrops. Because of the presence of the deep (10 m) lagoon, a prograding sand sheet has not developed leeward of Transect A. Presumably all sediment movement

Table 20

Lizard Island
Geographic, Meterological and Tidal Information

Location:	14°40'S, 145°30'E, 30 km off Australian east coast, on the shallow (10-30 m) continental shelf and 16 km inside the main Great Barrier Reef structure and in its Northern Region.
Reef Type:	Small (2 km x 2 km) inter-island system joining three granitic islands arranged in a triangle. Small open fully tidal lagoon with very little patch reef structure. Exposed to only local wind waves because of proximity of main barrier reef.
Weather:	Moderate seasonality. Strongly under the influence of SE trades all the year but with unstable stormy weather in summer. Typical wind 15-30 knot ESE. Precipitation summer and fall (200 cm).
Tides:	Semidiurnal--frequently very asymmetrical. Larger spring range 2.6 m Smaller neap range 0.3 m
Currents:	Totally dominated by wind and straight down wind. Ebb flow rarely reverses except during calms.
Flushing:	Extremely rapid--surface water typically only 4-5 hr (Limer Team 1976). Some holdup may occur at lower levels in lagoon (10 m).

Table 21

Site Summary
Lizard Island*

Description	Zone Extent (m)	Designation	Water Depth at LWS (m)	Hard Bottom (%)
Seaward slopes above 5 m	20	-	0-5	100
Seaward pinnacle (nearly all coral)	90	P1	0.2	100
Seaward reef-flat	450	Transect A	0-0.6	Variable
- Algal pavement	200	A1	0-0.2	100
- Coral/algal (small to large heads on discontinuous pavement)	250	A2	0.2-0.6	40
Lagoon	1000	-	10	0
Lagoon reef-flat	1000	-		
Total exper. transect	830	Transect D	0-0.2	Variable
- Perimeter zone (coral)	42	D1 (outer)	0	100
- Coral/algal	270	D1 (total)	0-0.2	30-10
- Small heads	200	D2	0.2	10
- Sand/algal flat (some sea grasses)	360	D3	0.2	0
Leeward coral/algal	180	-		

---

* Information presented in the order representing seaward/windward towards leeward. The pinnacle P1 is not strictly seaward of the reef crest but is in the open lagoon entrance.

has been directly into the lagoon causing general infilling. The lagoon itself lacks any significant reef development with the exception of two large pinnacles (P1 and P2) of outstandingly spectacular coral development very analogous to that occurring on the upper 5 m of the outer seaward slopes of the whole Lizard Is. system. P1 is located near the lagoon entrance and is exposed to a reasonable amount of wave action. That pinnacle has been used in the study, as a reasonable compromise, to represent the seaward slopes. This is because of the difficulty of working on, or even getting to the outer reef face in normal strong trade wind weather. Transect D is a large reef-flat which should probably correctly be visualized as a lagoon reef even though it does lead eventually to a leeward reef-flat without any intervening lagoon. D1 and D2 form that part of the reef-flat which can reasonably be called a "coral" zone, though the proportion of live corals in the community is much lower than found in the DK13 area at One Tree Is. There is virtually no true algal pavement on Transect D, in common with most lagoon reefs. However, the outer 40 m (D1 outer) is a coral/Porolithon zone of essentially continuous hard uneven substrate but again with a rather low content of living corals. D2 has been distinguished from D1 because of the much sparser distribution of coral heads and the introduction of a high component of foliose algae. D3 is a sand-flat which appears to have resulted from infilling approximately analogous to that occurring at DK17 at One Tree Is., but no longer actively prograding because it has totally filled up to the leeward reef-flat. The sand flat has extensive mixed small algae and some seagrass cover. The lack of present-day mobility in this sand sheet has no doubt been at least partially responsible for the more extensive plant community development here than is found on the sand-flat at One Tree Is.

Considering again the concept of "perimeter zones", it is clear that the whole of Transect A comes into this category. Similarly D1 is a true perimeter zone. D2 is probably best visualized as transitional. This concept will be discussed more in Section 2.

Water Properties

Table 22 summarizes some properties of the water entering the Lizard Is. system. Unlike the situation at One Tree Is. (Table 10), this water is already inside the Barrier Reef and has probably had longer recent exposure to other coral reef environments. The total annual range in water temperature is about 3-4° C, only slightly less than the 4.5°C range at One Tree Is. The mean temperature is about 27° C, about 3.5° C higher than that at One Tree Is. However, year-to-year variability seems likely to be high (up to 2° C in any month). pH exhibits much the same seasonality, ranging from 8.25 in winter to 8.10 in spring. Summer and fall values were not obtained. Overall, the pH range is marginally lower than the range at One Tree Is. Alkalinity was somewhat variable and lower than at One Tree Is., consistent with the slightly lower salinity (Table 12).

Table 23 indicates diel and seasonal extremes of a number of variables in the water over the shallow reef-flats. All variables are less extreme than those measured at One Tree Is. (Table 12) as would be expected in a system which essentially never experiences standing water conditions. Further, there is no analogy here to the great

Table 22

Properties of the Water Entering Lizard Island Reef System*

Month		Temperature (° C)	pH	Alkalinity (meq l^{-1})
January	(1976)	27.1		
February				
March				
April	(1975)	28.0		
May				
June	(1975)	25.3	8.23	2.30
July	(1975)	25.5	8.26	2.30
	(1976)	24.0		2.31
August	(1975)	25.9	8.24	2.30
	(1976)	23.5	8.13	2.33
September	(1975)	25.5	8.13	2.25
October	(1975)	26.7	8.17	2.31
	(1976)	26.5	8.10	2.25
November	(1976)	28.5		
December	(1974)	28.2		
	(1975)	27.6		2.17

Oxygen is always in the range 95-105% of saturation.

Salinity is typically 35.1-35.2‰ but few estimates were obtained.

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* It should be stressed that this water comes off the shallow continental shelf and is already inside the main Great Barrier Reef.

Table 23

Typical Low Tide Diel Extremes in Water Properties Over Shallow Transects A and D at Lizard Island

Temperature (°C)	O_2		pH	Alkalinity
	% Saturation	mg l^{-1}		(meq l^{-1})
28-29 (summer) 24-26 (winter)	75-130	4.9-8.3	8.05-8.28	2.34-2.23

Ranges indicate values found near low tide at night (left value) and in sunshine (right value).

extremes occurring a few times a year at One Tree Is., when there is no effective tidal rise inside the reef crest. Alkalinity values appear to fall slightly to either side of the range in the incoming water. This finding is consistent with the influence of net calcification in the daytime, and net dissolution at night. The same phenommenon (more dramatically demonstrated) was noted for One Tree Is. (Tables 10 and 12).

Metabolic and Calcification Data

The remainder of this chapter presents and discusses the findings of the metabolic studies at Lizard Is. A general premise, when research was shifted from the southern limit of the Great Barrier Reef to the northern end, was that the higher and presumably more optimal temperatures would result in higher metabolic rates and less seasonality. It will be seen in the following results that both aspects of this premise were essentially incorrect, though there are some differences which I believe to be of consequence.

Table 24 summarizes all carbon flux data from the seaward reef-flat (Transect A). This site is chosen for the examination of seasonality in detail as it most closely resembles the One Tree Is. reef-flat which was used in the seasonality discussion in the previous chapter. The monthly groupings are slightly different to those chosen for One Tree Is. because of timetabling differences only. All net-photosynthesis rates (y) have been normalized to the noontime equivalent (y_{max}). However, c_d has not been normalized from the measured values as the precision of this measurement does not justify such minor correction. All rates for c_d were made within the period when

Table 24

Summary of the Seasonal Means of Hourly Metabolic Rate Data* for the Complete Seaward Reef-Flat (Transect A including pavement area) at Lizard Island

Months	Metabolic Variable	Estim. Mean Hourly Rate (gC $m^{-2}h^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
June	y_{max}	0.29	0.11	4	19
	r	-0.16	0.09	3	32
	p_{max}	0.45			
	c_d	-			-
	c_n	-			-
July/Aug.	y_{max}	0.41	0.12	15	8
	r	-0.29	0.09	2	20
	p_{max}	0.70			
	c_d	0.08	0.12	18	35
	c_n	-			-
Sept./Oct.	y_{max}	0.41	0.16	16	10
	r	-0.28	0.10	8	13
	p_{max}	0.69			
	c_d	0.10	0.06	38	10
	c_n	-0.01	0.08	9	>100
Nov./Dec./Jan.	y_{max}	0.42	0.20	9	16
	r	-0.49	0.01	4	1
	p_{max}	0.91			
	c_d	0.12	0.09	24	15
	c_n	-0.03	0.05	7	63
April	y_{max}	0.31	0.17	11	17
	r	-0.33	0.21	2	41
	p_{max}	0.64			
	c_d	-			-
	c_n	-			-

y_{max} : peak hourly rate of net photosynthesis
r : hourly respiration rate
p_{max} : $y_{max} + |r|$ = peak hourly rate of gross photosynthesis**
c_d : daytime rate of net calcification
c_n : nighttime rate of net calcification

* Rates are corrected for atmospheric diffusion and the metabolic quotients where applicable.

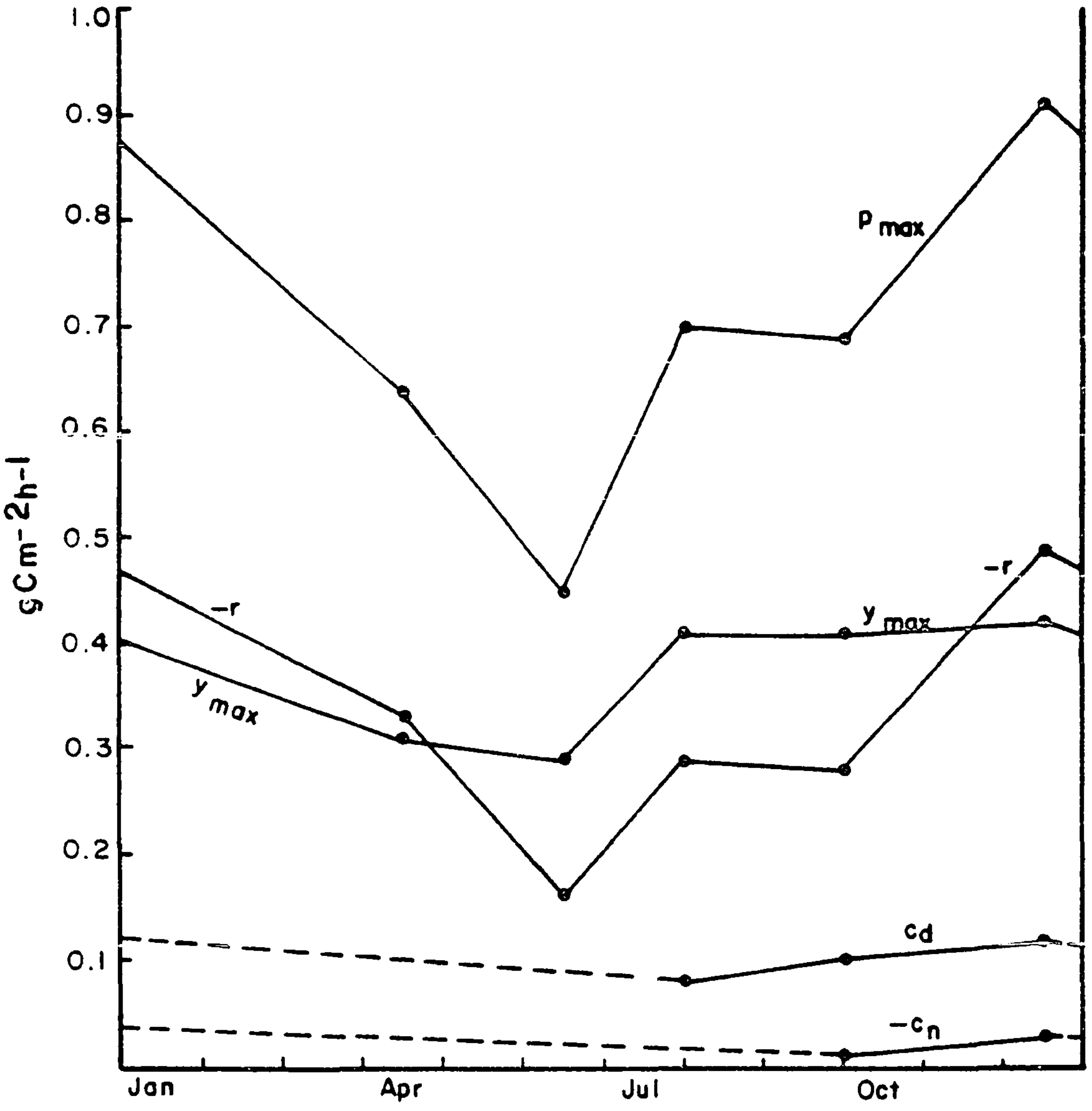
** In each case only the mean values of y_{max} and $|r|$ have been summed. This is because individual values of y_{max} and $|r|$ were rarely determined on the same day.

photosynthesis was ± 10% of maximum. Many of the general comments relevant to the interpretation of this table are the same as those made in the previous chapter, and will not be repeated here. It can be seen that all standard errors are considerably higher than those in Table 13 for One Tree Is. Consequently, the null hypothesis should be that these rates are the same as those from One Tree Is. and we are looking for suggestions of pronounced difference.

Seasonality of Metabolism and Calcification

Fig. 7 summarizes the seasonal trends presented in Table 24. It is obvious that considerable seasonality exists in both respiration and photosynthesis. In general the proportional increase from winter to summer is about the same factor of 2 which was found for One Tree Is. (Table 13). Actually, respiration rates at Lizard Is. seem a little more seasonal even though temperatures are generally 3.5° higher at Lizard I. It is also obvious that metabolic rates are remarkably similar at the two sites. The one point of marked dissimilarity is the significant summer/fall changes in metabolism. One Tree Is. experienced a significant increase in hourly rates from summer into fall regardless of a falling temperature. A slow buildup of standing crop was suggested as the explanation, possibly because of excessive losses brought about by the marginal conditions of winter. On the other hand, Lizard Is. exhibits a statistically significant ($p = 0.1$) fall in both respiration and photosynthesis from summer into fall. The relevance of this finding will be discussed further, later in this chapter.

Figure 7. Hourly metabolic rates as a function of the time of year for the seaward reef-flat, Transect A, at Lizard Is. (see Table 24). This transect includes both algal pavement and coral/algal zones. Calcification rates have been simply extrapolated from December to July (c_d) or September (c_n).


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
gCm-2h-1
Jan
Apr
Jul
Oct
p max
-r
y max
-r
y max
cd
-cn

The values available suggest that nighttime net dissolution of carbonates occurs, as it does on the reef-flat coral zone at One Tree Is. Daytime calcification rates are at least 30% lower than those at One Tree ($p = 0.01$) which is interesting in view of the extremely similar respiration and photosynthesis occurring. The amount of carbon fixed in calcification varies from 20% of the amount fixed by photosynthesis during an hour of daylight in winter, to only 13% during an hour of daylight in summer. Both values are much lower than the 40% and 20% found for the coral dominated reef-flat at One Tree Is. The significance of this discrepancy will be discussed more later. The suggestion of some seasonality in calcification rates is of doubtful statistical significance, particularly in view of the virtual lack of seasonality in hourly calcification rates at One Tree Is. Assuming c_n to approximate the rate of *gross* dissolution (i.e., assuming *no* calcification occurs at night) and therefore to apply for 24 h of the day, it can be seen that about one-third ($24\,|c_n|/11.5[c_d + |c_n|] = 1/3$) of the total carbonates formed undergoes dissolution. This is reasonably compatible with the finding that one quarter underwent dissolution on the coral zone of the reef-flat at One Tree Is.

The amount of carbon released by respiration (and decomposition) during an hour of darkness varies (Table 24) from 40% of the amount fixed by photosynthesis during the noon hour in winter and spring, to 50% during summer and fall. There is a clear and reasonably significant reversal of the trend found at One Tree Is. and this reversal also will be discussed in more detail later.

The diel integration of the hourly rates discussed above is presented in Table 25. The weighted mean for the whole year is based on the reasoning that the months for which data are not available exhibited rates intermediate between those for the time periods either side of the missing month. Fig. 8 summarizes the data in Table 25. Seasonality can now be seen to be even more marked than in the hourly rates because of the day length effect. There are three dramatically different aspects of the metabolic performance in this Lizard Is. reef-flat compared with that in the equivalent zone at One Tree Is. (Table 14 and Fig. 4):

(1) There is a pronounced drop in both diel respiration and gross photosynthesis between summer and fall.

(2) There is marked photosynthetic insufficiency in summer ($E = -2.1$) and continuing into fall ($E = -1.4$) whereas in winter the system is producing a marginal excess ($E = 0.3$), a situation which continues through spring.

(3) Gain in carbonates (G) is significantly lower than at One Tree Is. ($G = 1.0$ and $G = 1.5$).

All other general conclusions reached in the previous chapter still apply. The range of autotrophic self-sufficiency (P/R), from 108% in winter to 82% in summer and fall, is a similar range to that at One Tree Is. but represents a complete seasonal reversal (see also (1) and (2) above). Why is this difference found? The most reasonable hypothesis is that One Tree Is. is experiencing optimum conditions in summer and hence this is the time of algal blooms and other optimizing of standing crop (with growth continuing into fall).

Table 25

Seasonal Trends in Diel Community Metabolism of the Complete Seaward Reef-Flat (Transect A including pavement area) at Lizard Island

Months	P	-R	E	P/R	G
	(gC $m^{-2}d^{-1}$)				(gC $m^{-2}d^{-1}$)
June	4.1	3.8	0.3	1.08	
	*	*			
July/August	6.5	7.0	-0.5	0.93	0.8**
Sept./October	7.2	6.7	0.5	1.07	1.0
	*	*			
Nov./Dec./Jan.	9.7 *	11.8	-2.1	0.82	1.1
	*	*			
April	6.5	7.9	-1.4	0.82	
Weighted mean***	7.4	8.3	-0.9	0.89	1.0‡

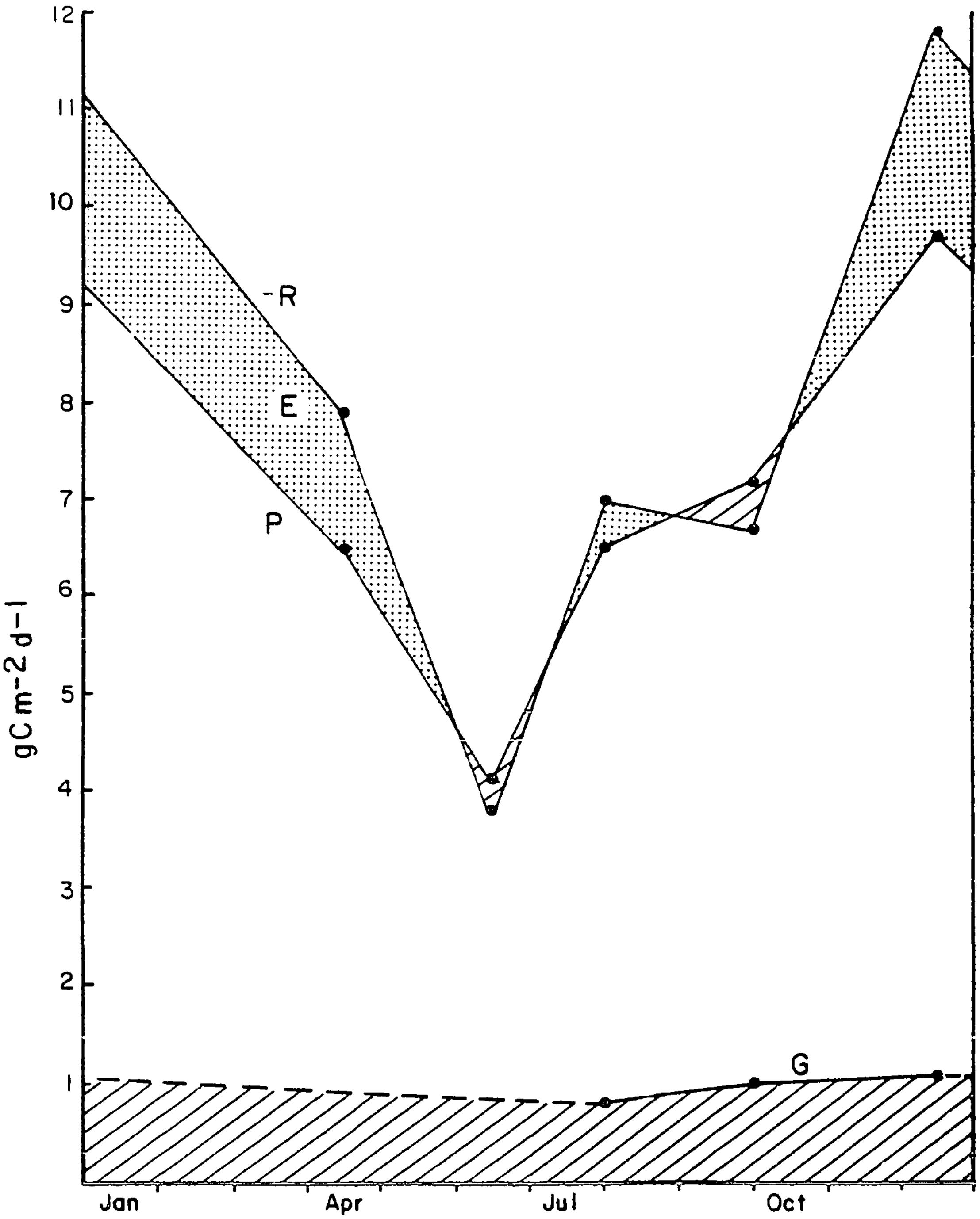
* Differences between these adjacent values of P or R, or between values of P <u>and</u> R, are significant at the 0.1 level or better (t test). The remainder of individual differences are therefore less significant. The overall trends, however, seem very clear.

** A value of 0.01 has been assumed for c_n in the derivation of this value for G (see Table 24).

*** These values may differ slightly from values used in Table 26. This is because all estimations used for Table 26 are based on the more simplistic approach of taking the means of all data obtained throughout the study without specifically weighting for each individual month.

‡ = 3.0 kgCaCO$_3$ $m^{-2}y^{-1}$

Figure 8. Daily metabolic rates as a function of the time of year for the seaward reef-flat, Transect A, at Lizard Is. (see Table 25). The cross hatched areas represent net gain, and the stippled area net loss.


12
11
10
9
8
7
6
5
4
3
2
1
gC m-2 d-1
-R
E
P
G
Jan
Apr
Jul
Oct

In winter the One Tree Is. reef experiences marginal temperature, and possibly light conditions, and hence the summer bloom starts to decline rapidly. By contrast, Lizard Is. experiences something closer to optimum conditions in winter. Hence the maximum (though lower) gain situation occurs then, with blooms of benthic algae, etc. Summer represents excessive heat and light conditions, precipitating an early decay of the excess crop and hence the negative gain. With the declining crop, it is inevitable that high metabolic rates cannot be maintained through the fall months, hence metabolism drops much faster than the temperature. This explanation is apparently compatible with direct observations of blooms in the foliose algae at both sites, but no accurate standing crop data are available (Cribb 1966 for general discussion).

For purposes of direct comparison with the One Tree Is. conclusions in the previous chapter:

(1) Calcification is a high gain (70%) process at Lizard Is. (75% at One Tree Is.).

(2) Photosynthesis/respiration varies from 8% gain to an 18% loss with reversed seasonality (14% gain to 32% loss at One Tree Is.).

(3) In terms of total carbon flux, photosynthesis (P) and respiration (R) are processing approximately 4 times as much carbon as calcification in winter ($3\frac{1}{2}$ times at One Tree Is.) to 10 times as much carbon in summer ($5\frac{1}{2}$ times at One Tree Is. in fall).

The comments in the previous chapter concerning the interpretation of long and short-term gains and losses of fixed organic and inorganic carbon are equally appropriate here, and will not be repeated.

Overall, this site is not only in close general agreement with the metabolic performance at One Tree Is., but also with data for similar areas on other reefs (Table 1), particularly those of Kohn and Helfrich (1957), Smith and Marsh (1973), Marsh (1974), and Sournia (1976a). There are discrepancies between these various sites, particularly in the value determined for E, but it is obvious from this and the previous chapter that such discrepancies will be inevitable if seasonality is not taken into account. All the other studies referenced are based on data over a short period.

Zonation of Metabolism and Calcification

Table 26 summarizes the annual means of all carbon flux data for the whole, or major parts of Transect A, and also for the specific zones A1 and A2. In this and subsequent tables of other transects at Lizard Is., the means have not been carefully weighted for each month as was done for One Tree Is. zonal data (Table 15) because the general precision of the available data does not justify this detailed treatment. However, the overall means and standard deviations given for each data set do include data from most months in a reasonably uniform spread. Most comment on zonation within Transect A will be reserved for the discussion of Table 29, the diel rates. However, a few comments on the hourly rate data are desirable. While of very limited statistical significance, it can be seen that the negative rate for c_n indicating nighttime dissolution is a feature of A1, the algal pavement area with very little coral development. On the other hand, A2, the inner area of the reef-flat with a higher population of corals, actually exhibits slight positive net calcification at night.

Table 26

Summary of the Annual Means* of All Hourly Metabolic Rate Data** for the Seaward Reef-Flat, Transect A, at Lizard Island

Description	Metabolic Variable	Estim. Mean Hourly Rate ($gC\ m^{-2}h^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
General transect A data	y_{max}	0.39	0.18	50	6
	r	-0.35	0.17	14	13
	p_{max}	0.74			
	c_d	0.10	0.10	80	12
	c_n	-0.02	0.08	15	100
Outer pavement area: A1	y_{max}	0.41	0.16	27	7
	r	-0.28	0.23	5	36
	p_{max}	0.69			
	c_d	0.08	0.09	34	20
	c_n	-0.01	0.03	5	>100
Inner coral/algal area: A2	y_{max}	0.39	0.23	4	29
	r	-0.37	0.09	7	10
	p_{max}	0.76			
	c_d	0.12	0.13	15	27
	c_n	+0.01	0.05	6	>100

y_{max} : peak hourly rate of net photosynthesis
r : hourly respiration rate
p_{max} : $y_{max} + |r|$ = peak hourly rate of gross photosynthesis
c_d : daytime rate of net calcification
c_n : nighttime rate of net calcification

* Because of the generally less precise nature of data obtained at Lizard Is. compared with those from One Tree Is., means are not specifically weighted for each month. They are simple means of data which are well spread over the whole year except February and March. Standard deviations are also for the complete data set.

** Rates are corrected for atmospheric diffusion and the metabolic quotients where applicable.

This observation seems quite contrary to the findings at One Tree Is. where negative nighttime rates seem principally a feature of coral dominated zones. It is again stressed that there is little statistical significance to this observation. It was previously noted that carbon flux in calcification was low relative to that in photosynthesis in Transect A (14%) compared with the coral zone of the reef-flat at One Tree Is. (20%). It can be seen that the proportion does increase with increased coral cover (12% in A1; 16% in A2), but nowhere reaches the 20% level. Perhaps of greater interest is the fact that the outer pavement area (A1), which might be expected at least slightly to approach the biotic structure of the massive seaward algal pavement at One Tree Is., exhibits a totally different calcification to photosynthesis ratio (12% at Lizard Is.; 60% at One Tree Is.).

Table 27 summarizes the annual means of the various zones within Transect D, the lagoonal reef-flat leeward of the 1 km wide lagoon. Again most comment will be reserved for the discussion of the diel data. However, the calcification to photosynthesis ratio will again be considered in relation to the hourly data. It also seems important to note that nighttime dissolution is universal across this reef-flat, from the outer edge of coral/Porolithon community, to the leeward sand flat/algal/seagrass community. Calcification equals 16% of the rate of carbon flux through photosynthesis across the general perimeter area (D excluding D3) and 17% in the outer perimeter zone (D1). It falls to 14% in the inner reef-flat of small heads (D2). All of these are in good agreement with the 12-16% over Transect A. However, in

Table 27

Summary of the Annual Means* of All Hourly Metabolic Rate Data** for the Lagoonal Reef-Flat, Transect D, at Lizard Island

Description	Metabolic Variable	Estim. Mean Hourly Rate ($gC\ m^{-2}h^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
General transect D data (not including D3)	y_{max}	0.48	0.31	33	11
	r	-0.23	0.10	20	10
	p_{max}	0.70			
	c_d	0.11	0.10	44	14
	c_n	-0.02	0.08	21	87
Coral/algal zone: D1	y_{max}	0.45	0.31	22	15
	r	-0.24	0.09	9	12
	p_{max}	0.69			
	c_d	0.11	0.11	29	17
	c_n	-0.02	0.04	10	63
Zone of small heads: D2	y_{max}	0.27	0.10	5	16
	r	-0.23	0.10	4	21
	p_{max}	0.50			
	c_d	0.07	0.05	9	24
	c_n	-0.02	0.05	5	>100
Sand/algal flat: D3	y_{max}	0.24	0.11	7	17
	r	-0.18	0.06	7	13
	p_{max}	0.42			
	c_d	0.02	0.12	6	>100
	c_n	-0.01	0.04	7	>100

y_{max} : peak hourly rate of net photosynthesis
r : hourly respiration rate
p_{max} : $y_{max} + |r|$ = peak hourly rate of gross photosynthesis
c_d : daytime rate of net calcification
c_n : nighttime rate of net calcification

* Because of the generally less precise nature of data obtained at Lizard Is. compared with those from One Tree Is., means are not specifically weighted for each month. They are simple means of data which are well spread over the whole year except February and March. Standard deviations are also for the complete data set.

** Rates are corrected for atmospheric diffusion and the metabolic quotients where applicable.

the major leeward sand flat (D3) the ratio drops to 5%. This is much lower than the 11-22% found everywhere at One Tree Is. and suggests that this sand flat has developed a biota of a kind not found at all at One Tree Is. and of a kind responsible for essentially no role in reef-accretion except perhaps the binding of sediments.

Table 28 summarizes the annual means for metabolic data obtained for the seaward pinnacle (P1). This structure is believed to be a close simulation of the outer reef slopes of the Lizard Is. system and has an extremely high cover with live corals (Table 21). With respect to the dominant role of corals in the community structure, P1 can actually be compared with the outer reef-flat at One Tree Is. (DK13), though the percent cover at DK13 is much lower (Table 9). The calcification to photosynthesis ratio at P1 is 20% which makes the analogy to the One Tree Is. site even more interesting, as it also had a 20% ratio. However, there is a significant difference in the calcification regime of these two sites. The nighttime dissolution is very pronounced at P1. It is more extreme than the dissolution found for any other site at Lizard Is. or at One Tree Is. ($p = 0.001$). At P1, half of all carbonates produced undergo subsequent dissolution (based on the same type of calculation used previously:
$24 |c_n| / 11.5[c_d + |c_n|] = 1/2$).

Tables 29a and 29b and Fig. 9 summarize the diel rates calculated from the hourly rates in Tables 26, 27 and 28. The calcification rates have been expressed in the common usage form of $\mathrm{kgCaCO_3\ m^{-2} y^{-1}}$. Table 29a has been based on the numerous general data available for Transect A and outer Transect D. Table 29b has been based on the

Table 28

Summary of the Annual Means* of All Hourly Metabolic Rate Data** for the Seaward Pinnacle PI at Lizard Island

Description	Metabolic Variable	Estim. Mean Hourly Rate ($gC\ m^{-2}h^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
General transect: PI	y_{max}	0.68	0.26	17	9
	r	-0.23	0.18	10	24
	p_{max}	0.91			
	c_d	0.18	0.11	27	12
	c_n	-0.07	0.05	10	23

It is considered that this pinnacle is a close operational equivalent to the outer reef slope (above 5 m) which could not be monitored under most weather conditions.

y_{max} : peak hourly rate of net photosynthesis
r : hourly respiration rate
p_{max} : $y_{max} + |r|$ = peak hourly rate of gross photosynthesis
c_d : daytime rate of net calcification
c_n : nighttime rate of net calcification

* Because of the generally less precise nature of data obtained at Lizard Is. compared with those from One Tree Is., means are not specifically weighted for each month. They are simple means of data which are well spread over the whole year except February and March. Standard deviations are also for the complete data set.

** Rates are corrected for atmospheric diffusion and the metabolic quotients where applicable.

Table 29a

Zonation of Community Metabolism Along a Downwind Cross Section of the Reef System at Lizard Island, Based on Annual Mean Rates

--using general data for Transect A and Transect D (excluding D3)*

Zone	Designation	P	-R	E	P/R	G
		(gC $m^{-2}d^{-1}$)				(kgCaCO$_3$ $m^{-2}y^{-1}$)
"Outer slopes"** (actually pinnacle)	P1	9.3	5.5	3.8	1.7	3.6
Seaward reef-flat	A	7.5	8.4	-0.9	0.9	2.7
Lagoon		assumed very low				
Lagoon reef-flat	D1/D2	7.1	5.5	1.6	1.3	3.1
Sand/algal flats	D3	4.3	4.3	0	1.0	0.3
Weighted mean		3.7	3.5	0.2	1.06	1.2

* A large proportion of the data from Transect A and the outer half of Transect D (D1 and D2) are indefinitely designated and can not be assigned to the specific zones A1, A2, D1 or D2. In most cases they would include some of each of the pair of zones involved.

** The lagoon entrance pinnacle P1 is considered to be a close equivalent to the outer reef slope.

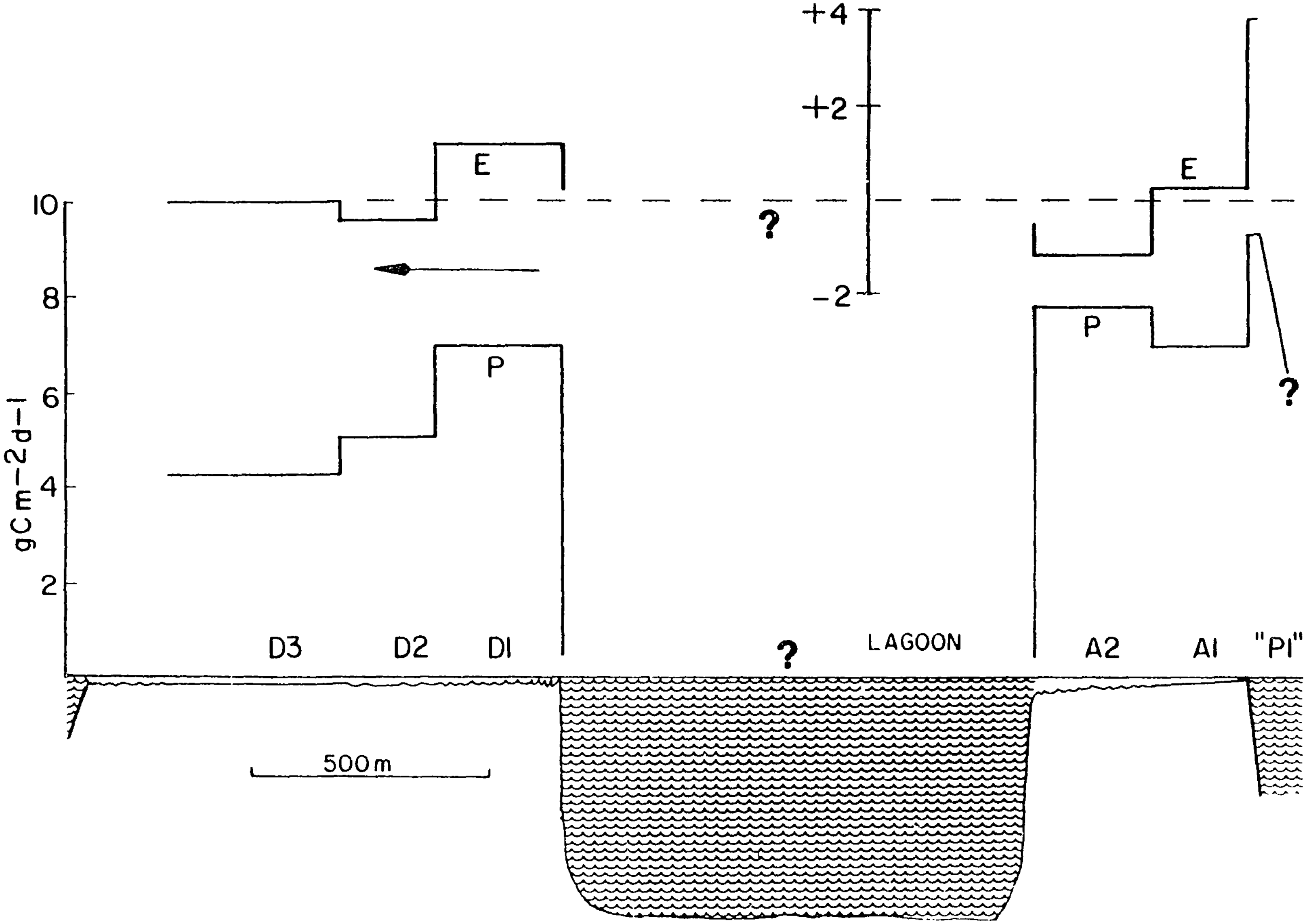
Table 29b

Zonation of Community Metabolism Along a Downwind Cross Section of the Reef System at Lizard Island, Based on Annual Mean Rates

--using individual zonal data for A1, A2, D1, and D2

Zone	Designation	P	-R	E	P/R	G
		(gC $m^{-2}d^{-1}$)				($kgCaCO_3\ m^{-2}y^{-1}$)
"Outer slopes" (actually pinnacle)	P1	9.3	5.5	3.8	1.7	3.6
Reef-flat pavement	A1	7.0	6.7	0.3	1.0	2.4
Reef-flat coral/algal	A2	7.8	8.9	-1.1	0.9	4.6
Lagoon		assumed very low				
Lagoon-flat coral/algal	D1	7.0	5.8	1.2	1.2	3.1
Lagoon-flat small heads	D2	5.1	5.5	-0.4	0.9	1.7
Sand/algal flats	D3	4.3	4.3	0	1.0	0.3
Weighted mean		3.5	3.4	0.1	1.01	1.3

Figure 9. Primary production along a downwind cross section of the reef system at Lizard Is., based on annual mean rates. Plots of both gross diel photosynthesis (P) and net gain (E) are shown. The arrow indicates dominant water flow, and hence the direction of movement for any suspended detrital material. A vertical section of the reef is also given. The depth of the lagoon is 10 m. Each value is plotted as a line extending across the full zone. The estimation was normally made in a flowing system across the full width of the zone, and not at a fixed site as was done for One Tree Is. (Fig. 5).


gCm-2d-1
10
8
6
4
2
+4
+2
-2
E
P
E
P
?
?
?
D3
D2
DI
LAGOON
A2
AI
"PI"
500m

more specific but less numerous and less precise (higher standard error) data for the individual zones within the transects. I am inclined to take more note of the Table 29b information as the higher precision of the Table 29a data is offset by the fact that many of these estimations were made in the central areas of the transects, and therefore tend to make inadequate allowance for the inner and outer extremities. It can be seen that the differences between the actual rates tabulated on the two different bases is only minor in any case. Overall, it is apparent that all shallow areas have somewhat consistent high rates of photosynthesis. This trend is much more marked than at One Tree Is. where the rates seem much more varied. However, this distinction may be very different in its implications than it seems, and this will be discussed in Chapter 2B. It is assumed that the lagoon production is very low and in fact is likely to not exceed the planktonic production rate of 0.1 gC $m^{-2}d^{-1}$ determined by the LIMER team (1976). Lagoon respiration is probably not likely to exceed the 0.1 gC $m^{-3}d^{-1}$ range already determined experimentally for One Tree Is. In a 10 m water column this could represent as much as R = 1 gC $m^{-2}d^{-1}$, though such a high level of consumption seems improbable. The level of production on the seaward pinnacle P1 is extremely high and is the highest so far reported in this study. It can be seen that substantial gain (E) over the year is clearly a feature of the outer perimeter zones, in keeping with the general observation made for One Tree Is. P1, A1, and D1 can all reasonably be considered as outer perimeter areas. The areas immediately behind these zones are net consumers ($E < 0$), supporting the general concept of consumption of imported detritus. The sand/algal flat in the lagoon (D3) is an autotrophically self-sufficient area, in keeping with its location in a low energy environment at a considerable distance downstream from the nearest perimeter zone. D3 represents the secondary colonization of a stabilized sand sheet. There is very little calcification activity associated with this community.

Calcification can be seen to be high, if a little inconsistent, across the outer slopes and entire seaward reef-flat. This finding would certainly seem consistent with what is known for One Tree Is. It is particularly interesting to stress that this relatively small range from 2.4 to 4.6 kg$CaCO_3$ $m^{-2}y^{-1}$ is notwithstanding the fact that coral cover varies from virtually 100% at P1 to only about 10-15% on A2 and essentially 0% on the pavement area of A1. Again, this observation is consistent with the findings at One Tree Is. where the level of carbonate production almost seems simplistically to be a function of proximity to the reef edge rather than of the biota present. The same high calcification rate (3.1 kg$CaCO_3$ $m^{-2}y^{-1}$) is a feature of the outer perimeter area (D1) of the lagoon reef but falls off rapidly behind that area.

Considering the weighted overall mean metabolism for the Lizard Is. system (Table 29b) compared with the same parameter for the One Tree Is. system (Table 16), it can be seen that these two small (2.5 km) reef transects are performing in a very similar manner. The Lizard Is. system has a slightly higher primary production ($P = 3.5$ versus $P = 2.3$). The extensive lagoon flat is responsible for this difference. The Lizard Is. system is producing slightly less carbonates (G = 1.3 versus G = 1.5). The lack of the extensive lagoonal patch reef structure is largely responsible for this difference. The slight apparent organic excess at Lizard Is. (E = 0.1 versus E = -0.05) can be explained largely by the inclusion of the outer reef slopes which were not included in the One Tree Is. study.

The integration of the diel data over the length of the transect is given in Table 30. It can be seen that, in total terms, all areas in this reef except the outer slope which is too narrow, and presumably the lagoon which is virtually devoid of any benthic primary producers, are contributing similar amounts to gross photosynthetic turnover. Similarly all areas including the outer slopes, but excluding the algal flat (D3), are making a quantitative impact on the balance of the system (E). In calcification, it can be seen that quantitative impact is spread broadly across the reef. The fate of these carbonates is a little different from that of those produced at One Tree Is. The probable fate of nearly all carbonates produced over the seaward reef-flat is to directly in-fill the deep lagoon. No patch reef structure is being buried as is occurring at One Tree Is., and there is no appreciable progradation of a sand sheet behind the reef-flat active zone because of the considerable depth of the lagoon. The carbonates produced by the lagoon reef-flat can no longer cause infilling behind the active area as this is already totally filled and stabilized (D3). It is probable that all these carbonates are transported over the shallow reefs and deposited as a prograding talus leeward of the main reef structure. This talus is, in fact, very obvious in an aerial view of the Lizard Is. system.

Table 30

Integration of Community Metabolism Along a 1 m Wide Cross Section of the Reef System at Lizard Island

Zone	Length	P	E	G
	(m)	$(\text{gC m}^{-1}\text{d}^{-1})$		$(\text{kgCaCO}_3\ \text{m}^{-1}\text{y}^{-1})$
"Outer slopes" (pinnacle P1)	20	190	80	70
Reef-flat pavement (A1)	200	1400	60	480
Reef-flat coral/ algal (A2)	250	1950	-280	1150
Lagoon	1000	assumed very low		
Lagoon-flat coral/ algal (D1)	270	1890	320	840
Lagoon-flat small heads (D2)	200	1020	-80	340
Sand/algal flats (D3)	360	1550	0	110
Total transect	2300	8000	100	2990

The near balance of P and R is encouraging to the acceptance of the findings of this study as it was to the acceptance of the One Tree Is. study. Unfortunately, there are some illogical aspects to the neat balance found. For instance, the transect A2 is consuming considerably more (E = -280) than the zones upstream of it are producing (E = 80 + 60). Similarly, the lagoon transect D1 is producing considerably more (E = 320) than is being consumed downstream of itself (E = -80). However, these discrepancies are of only limited statistical significance, and the system does seem to be closely approaching the concept of self-sufficiency for coral reefs.

Planktonic Contribution

No estimates of planktonic activity, other than the LIMER (1976) data already mentioned, have been made for the water over Lizard Is. reefs. However, in common with the One Tree Is. findings, and probably the situation on any other small rapidly flushed system, it is unlikely that planktonic photosynthesis or respiration plays a role of more than marginal quantitative impact.

C. HAWAIIAN ISLANDS

General Information

Metabolic studies of the reef-flat communities in Kaneohe Bay, Oahu, Hawaii were begun in September 1976, concurrently with the final period of research on Lizard Island. The Hawaii study was principally aimed at elucidating the response of shallow reef systems to a long-term, continuous, and chronic input of sewage to Kaneohe Bay. This work formed part of the EPA (Contract #R803983) and Marine Affairs Coordinator (State of Hawaii) funded program under Dr. Stephen V. Smith to examine all aspects of sewage impact in the bay, and subsequently, the effects of diverting sewage input from the bay.

Because most of the data in no sense relate to normal unperturbed reef systems, they will be presented and discussed largely in Chapter 3B. However, there were a number of aspects of the findings which are relevant to the baseline study, and these will be discussed in the present chapter. For the sake of consistency, all general information about Kaneohe Bay will also be included here, and only minimally repeated in the main results chapter.

Table 31 indicates the periods of research activity which will be included in this dissertation. These are all during the time when full sewage input was occurring in Kaneohe Bay. During the period of shutting down of sewage input (November 1977-May 1978) and into the early "recovery" period, further research was carried out. However, this work will not be included anywhere in this report. It can be seen that the total time devoted to research was similar to that at Lizard Is., though considerably less data were accumulated. Attention was

Table 31

Field-work Timetable for Kaneohe Bay

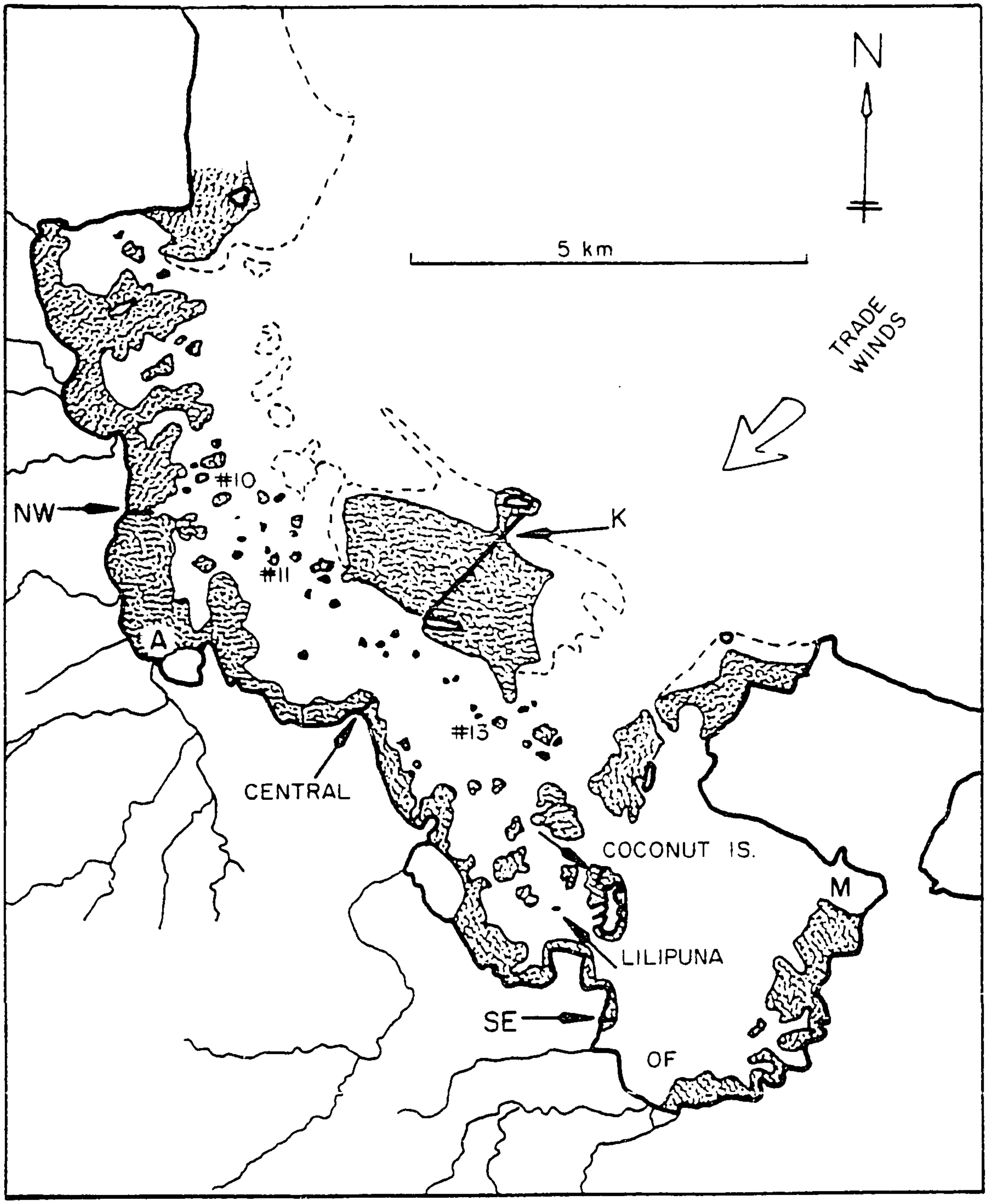
Year	Period	Sites
1976/7	Sept./Feb. (6 months)	EPA reef-flat sites
1977	Apr./Sept. (6 months)	EPA reef-flat sites
1977	Jan./Aug. (occasional only)	Special calcification sites
1977	Aug./Sept. (occasional only)	Barrier reef sites
1977	Oct./Nov. (occasional only)	Plankton experiments

given, independently of the EPA study, to a number of other sites in the bay.

By contrast with the two Australian reefs, Kaneohe Bay has been for a long time under a variety of human related stresses. Principal among these have been sewage input, sediment runoff in excess of that which would result from "natural" levels of erosion, and a nutrient input with streams, elevated somewhat above the natural very low level by the effects of agricultural fertilizers. Also in contrast with the Australian systems, this reef complex is immensely overshadowed by a volcanic (basaltic) terrigenous system. Freshwater runoff and sediment input from natural and quite rapid erosion of basic basaltic lavas have long been major factors influencing this reef system. Figure 10 shows the layout of the bay with its associated reefs. Freshwater input is dominated by streams in the NW area of the bay, with another significant component in the southern corner of the bay. Sewage input was dominated by the outfall from the Kaneohe municipal plant (O.F. in Fig. 10), with a major additional component (25% of the total) from the Marine base on Mokapu peninsula (M). A minor input (5%) also occurred in the NW sector at A in Figure 10. Most of the sewage has been domestic, with secondary treatment, and its impact, simplistically, has been that of a nutrient input (30000 mole day^{-1} total dissolved nitrogen, 3300 mole day^{-1} total dissolved phosphorus, and only 550 kg day^{-1} BOD loading). The nutrient input at the major point source at OF has served to operate a phytoplankton "chemostat" feeding a relatively steady stream of particulate phytoplankton carbon along the inshore areas of the bay toward the NW. The physiography,

Figure 10. Kaneohe Bay on the southeast coastline of the island of Oahu in Hawaii. An extensive system of short streams feeds fresh water into the bay with most inflow in the northwest sector and a significant inflow into the south end of the bay. Sewage outfalls are indicated OF, M, A with their proportional input in that order. The extensive fringing reefs and patch reefs are fully tidal and are mostly near LWS level except those northwest of the barrier structure. The 15 m deep lagoon has a muddy floor and there are no deeply submerged reefs. Most reef-flats exhibit zonation but this cannot be shown on this scale (see Tables 33 and 34). Most sites used for experimental work are indicated.

╲	shore-line
▨	reef-flats near LWS
⋮	submerged reefs


N
5 km
TRADE WINDS
#10
NW
K
#11
A
#13
CENTRAL
COCONUT IS.
M
LILIPUNA
SE
OF

meteorology, hydrography and inputs for Kaneohe Bay are discussed in detail by Smith et al. (1978) and will not be detailed further here.

Kaneohe Bay is fully tidal with most reef-flats a few centimeters to 0.5 m below L.W.S. Monitoring procedures were therefore carried out in the same format used at Lizard Is.--flow respirometry at intermediate water depth.

Table 32 summarizes general information on location, reef type, weather, tides, circulation, etc. It can be seen that the reef is not only associated with a large land mass, but is considerably more extensive than either of the Australian systems studied. The lagoon is deeper again (15 m) than that at Lizard Is. (10 m) and has no reef type benthos except on the patch reefs which are all surface level structures at this time (with the exception of some dredged areas). Oahu is only marginally in the NE trade winds and consequently wind is variable. While the latitude is similar to that at One Tree Is., it is interesting to note some marked differences in weather. Trade winds are dominant in summer with rainfall tending to be more in late winter and spring. One Tree Is. has trade winds only in winter, with rain throughout the year and summer storms. Tides are much smaller than those at either Australian site. Flushing time is much longer than at the Australian sites. Wave action on the shore-line fringing reefs is probably comparable to that on the lagoon reef-flats at Lizard Is., having been generated across a relatively open 1-2 km lagoon. Wave action on the barrier reef is variable and can be very heavy with total exposure to the open Pacific Ocean.

Table 32

Kaneohe Bay, Oahu
Geographic, Meterological and Tidal Information

Location: 21° 30'N, 158° 00'W, windward embayment on the island of Oahu, Hawaii, rising from an area approximately 4500 m deep, close to the center of the North Pacific subtropical gyre.

Reef Type: Series of land-associated reefs including a partial "barrier" reef structure, lagoonal patch reefs, and fringing reefs, covering an enclosed area 13 km by 3.5 km. Pronounced estuarine influences, and a sewage input gradient. Fully exposed to open sea, and fully tidal.

Weather: Moderate seasonality. Marginal NE trades, strongest in summer (averaging 18 knot). Precipitation erratic but most consistent in spring. Amount very regionally variable but totalling 120-150 cm y^{-1} over bay itself. Effects of run-off from high rainfall land area adjacent much more important.

Wind	NE	50%	any time of year, but strongest in summer
	E	32%	
	N,SE	6% each	
	S	6%	fall and winter

Tides: Semidiurnal becoming almost diurnal at times.
Larger spring range 1.0 m (1.23 X Honolulu tides, Kinsey unpublished)
Smaller neap range 0.1 m

Currents: Typically weak, largely tidal with localized superimposed wind driven flow. Dominant flow is toward NW end of bay and out. Small scale flow over reef-flats normally downwind.

Flushing: 13-14 days average residence time (Smith et al 1978).

The reef systems of Kaneohe Bay are enormously varied. Some of these variations appear to be stress related; others have no single evident correlation with either sewage, silt or freshwater stress. In a landward-seaward direction, reefs occur in three easily definable categories, (a) fringing reefs, (b) patch reefs, (c) barrier platform structures. Most of the patch reefs (northwest of the southern entrance channel) and probably all of the barrier reef show little obvious evidence of stress as recognizable SE/NW trends (longshore). On the other hand, the fringing reefs show marked variation from the SE to NW, and most of this is obvious stress related variation.

Table 33 and Fig. 10 summarize the sites used in the EPA sewage impact study. The SE, Central and NW sites are fringing reefs on the main Oahu shoreline. The Coconut Is. transect is a fringing type reef on a small high island in an inshore area of the bay, and the Lilipuna site is the complete top of a small inshore patch reef. The sites, from SE to Central, are in order of decreasing sewage impact. The NW site may have marginal sewage input from the northern source (A on Fig. 10), but has been principally influenced by heavy terrigenous sediment input. All sites except Lilipuna have a shoreline algal zone obviously influenced by the contact with land, and extending out varying distances according to the other factors influencing the site. There is little remaining of typical reef organisms at the SE site even though the platform is obviously of reef origin. The conspicuous standing crop dominance is by zoanthids and sponges. The Central site is the one most nearly approaching a pristine fringing reef and exhibits typical (for Hawaii) reef communities with well developed zonation.

Table 33

Site Summary EPA Reef-flat Transects, Kaneohe Bay*

Designation		Description	Extent (m)	Water Depth at LWS (m)	Hard Bottom (%)
Transect	Zone				
SE	total	unconsolidated and eroded reefal platform--fringing reef	118	1-0.4	<5
Lilipuna	total	scattered heads on eroding platform --patch reef	62	0.15	30
Coconut Is.	total	fringing reef on terrigenous island in bay	214	0-0.2	variable
	"coral"	substantially modified margin	30	0-0.2	100-20
	sand-flat	scattered small heads on sand	84	0.2	<5
	algal-flat	mostly foliose reds on sand	100	0.2	0
Central	total	fringing reef on central headland	189	0.05-0.30	variable
	"coral"	normal Hawaiian coral/algal margin	52	0.05	100
	sand-flat	scattered small to medium heads on sand	62	0.25	5
	algal-flat	heavy standing crop of foliose reds on sand	75	0.30	0
NW	total	reefal platform with unconsolidated sediments and mixed foliose algae (reds and greens)	286	1.3-0.4	0

* All information presented in the order representing outer or seaward edge towards the inner or leeward.

However, it does have a noticeably heavy crop of the massive benthic alga Dictyosphaeria on the outer flat and slopes. The NW site is a very wide, somewhat muddy flat. Like the SE site its identity as a coral reef flat has largely been lost but its present standing crop is dominated by mixed algae. The reef slope at this site does have a relatively well developed coral community. For a detailed analysis of the community structure at these three sites see Smith et al. (1978). The Coconut Is. site exhibits what could probably be described as a borderline reef community with reasonably normal zonation. Large populations of zoanthids are evident here and it seems at least possible that this reef is presently degenerating towards the situation found at the SE site. On the other hand, the Lilipuna patch reef is also a borderline reef where normal zonation has largely degenerated, but reef type organisms are still in fair evidence distributed more or less randomly over the narrow reef top. The strong dominance by zoanthids is not so obvious here, but there is a conspicuous buildup of sponges. This reef is directly in the normal path of the phytoplankton stream originating at the point of sewage input and moving up the coastline of the bay to this point (under normal trade wind conditions). The Coconut Is. site is not under this direct influence, but typically is bathed by the rather murky estuarine and sewage modified water of the South Sector. The transitional status of the Coconut Is. and the Lilipuna sites makes them extremely important in considering any trend exhibited between the relatively unmodified Central Bay site, and the totally modified SE site adjacent to the sewage outfall.

The SE, NW and Lilipuna sites are each reasonably homogeneous with respect to standing crop distribution. Consequently, the whole width of the flat has been treated as a single zone. Dependent on current, the monitoring has been made either across most of the width of the flat, or (more usually) along the flat at about the median position. As the Lilipuna patch reef is only 62 m across, its total diameter was always used.

The Central and Coconut Is. sites have three easily recognizable zones. From the outer edge: (a) Coral Zone - a zone of coral heads and miscellaneous reef organisms on a continuous hard substratum with considerable Porolithon encrustation (zoanthids also very common on the Coconut Is. site, and Dictyosphaeria on the Central site). (b) Sand Flats - a zone of scattered coral heads and algal covered boulders on a dominantly sand bottom. (c) Algal Flat - a zone free of scattered heads with relatively heavy cover of algae (mostly Hypnea/Acanthophora) over a sand substratum. While this crop was always obvious and heavy with a constant boundary position at the Central site, it varied considerably in all these aspects on Coconut Is. Here, most algae had disappeared by the beginning of June 1977, and rapidly bloomed again in fall 1978. It is not known whether this is a predictable seasonal cycle.

Each of these zones was monitored separately, either in succession if a strong shoreward current was flowing, or, more usually, simultaneously if periods of relatively slack water were used.

In addition to the EPA sites described above, a transect across the barrier reef was monitored for calcification. The various zones along this Transect K are summarized in Table 34. There is virtually no suggestion of either sewage or terrigenous sediment influences on this barrier system. However, it exhibits poor coral development, even near the outer edge of the very wide flat, and there is much evidence (Smith et al. 1973) that it is more appropriate to consider this structure as a relict dune beach structure with partial lithification and a present-day community which has not caused very extensive recent reef growth. As well as the barrier transect, a number of patch reefs in the outer part of the bay have been examined for calcification. These were chosen because of extremes in their community structure, not because they were particularly typical. #10 (Fig. 10) had two zones: 100% cover with Porites compressa, and 100% cover with viable Porolithon. #11 had 100% cover with Porites compressa in very shallow water. #13 had a sparse community in which the only apparent calcifier was Halimeda.

Water Properties

Table 35 summarizes some properties of the water entering the reef-flats of the EPA transects (Kinsey unpublished, and Smith et al. 1978). I have inadequate information to include the properties of water crossing the outer barrier reef. It can be seen that variability is appreciable and somewhat randomly related to season except for temperature. Even temperature is moderately inconsistent year-to-year. Salinity typically is not greatly variable but certainly reflects periods of local rainfall. At times not represented in Table 35, a substantial near-freshwater lens may develop in the bay after extreme storms (Banner 1968) and this has been known to cause major

Table 34

Site Summary
Barrier Reef Transect, Kaneohe Bay*

Zone Description	Zone Extent (m)	Designation	Water Depth at LWS (m)	Hard Bottom (%)
Seaward zone of large coral heads on sandy bottom	300	K1	2-0.9	10
Algal pavement with small foliose algae	200	K2 (outer)	0.4	90
Algal pavement with some sand and larger foliose algae	200	K2 (inner)	0.4	70
Algae over dead coral head--extensive blue-greens	400	K3 (outer)	0.25	20
Algal dominated on sandy rubble--mostly reds	800	K3 (inner)	0.25	0
Sea grass bed	100	K4	0.5	0
Total transect	2000	K		

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* All information presented in the order representing seaward/windward towards leeward. Zone widths indicated are only roughly estimated.

Table 35

Properties of the Water Entering the Reef-flats of the EPA Transects*

Month (1976) (1977)	Temperature (°C)	pH	Alkalinity (meq l^{-1})	Salinity (‰)
January	23.8			
	24.0	8.22	2.18	35.2
February	22.5			33.8
	24.0	8.13	2.26	35.0
March	23.1			34.0
	23.1			35.2
April	23.7			34.4
	24.0		2.06	34.3
May	24.7			34.5
	25.1		1.94	34.5
June	25.6			34.8
	27.1	8.22	2.16	34.5
July	25.7			35.0
	26.2	8.19	2.26	35.0
August	26.8			35.1
	27.2	8.24	2.20	35.0
September	27.7	8.17	2.24	35.0
	27.1	8.26	2.31	35.1
October	26.7	8.19	2.21	34.7
	26.7			35.3
November	23.8	8.24	2.31	35.1
	25.5			35.0
December	23.7			35.0
	24.5			34.8

* These values represent the general water mass near the reefs in the central bay. Somewhat more extreme values are sometimes encountered entering the SE and NW transects. However, differences are small.

Oxygen content always lies between 98 to 100% of saturation.

reef-flat benthos kills. Such an extreme event did not occur during the period of this research. The annual temperature range of 4-5° C is similar to that at Lizard Is. (3-4°) and One Tree Is. (4.5°). The mean temperature is about 25° C which is about 1.5° higher than at One Tree Is., regardless of the same latitude, and 2° less than at Lizard Is. However, it should be noted that the long-term mean for Kaneohe Bay is probably nearer to 24° C which is essentially in keeping with One Tree Is.

Table 36 summarizes low-tide diel and seasonal extremes of some variables in the water over the reef-flats. Ranges are a little more extreme than at Lizard Is. but much less extreme than at One Tree Is. because of the lack of low tide standing water conditions (except perhaps on a few extreme LWS tides). Alkalinity values are too scattered and affected by freshwater dilution for there to be any clear suggestion of values over the reef-flat being spread either side of incoming values. This finding was invoked for both One Tree Is. and Lizard Is. as evidence for net calcification in the day, and net dissolution at night being more or less ubiquitous phenomena. One characteristic which was much more obvious on the fringing reef sites in Kaneohe Bay than on any other site used in this dissertation was that of patchiness in the water composition. The water crossing these reef-flats frequently exhibited extreme horizontal variability though seldom any vertical stratification. This effect was much more extreme on days with a wind velocity of less than 10 knots (5 meters/sec). With zero wind velocity, the effect was so extreme, particularly at the SE site, as to make the monitoring of the water mass virtually meaningless--

Table 36

Typical Low Tide Diel Extremes in Water Properties
Over EPA Reef-flat Transects, Kaneohe Bay

Temperature (°C)	O_2		pH	Alkalinity (meq l^{-1})
	% Saturation	mg l^{-1}		
26-28 (summer) 22.5-24.5 (winter)	40-150	2.6-10	8.05-8.35	2.24-2.13

Ranges indicate values found near low tide at night (left value) and in sunshine (right value).

Salinity would be in conformity with that in the main lagoon (Kaneohe Bay) except at times of heavy precipitation. No work was done at such times.

e.g., O_2 content varying from 110% to 130% of saturation over only 3 meters, the related pH variation being 8.280 to 8.297. Considering that the 1/2-1 h time period used would result in changes, due to metabolic activity, of only 5-10% in O_2 and 0.005-0.01 in pH, it is obvious that there were constraints on the weather suitable for carrying out monitoring in the EPA study.

Metabolic and Calcification Data

The remainder of this chapter will present a few findings from Kaneohe Bay which have some bearing on the general baseline study of coral reef carbon flux. The remainder of the data, specific to the impact of sewage, will be presented in Chapter 3B. It might reasonably be anticipated that metabolic performance in equivalent sites should be similar to (latitude) One Tree Is., or intermediate (temperature) between One Tree Is. and Lizard Is.

In choosing a site for general comparison with the Australian reefs, it is apparent that there is no ideal candidate. The barrier structure is probably nearest to being oceanic and is almost certainly free from sewage impact. However, it does not appear to be a true recent reef structure (as mentioned earlier). Also there are far too few data available from this site in the present study. Accordingly I will use data from the Central fringing reef site used in the EPA study. This is certainly as close to pristine as any lagoonal structure remaining in Kaneohe Bay, but is "feeling" some effects from the human modification of the bay.

Table 37 summarizes all carbon flux data from the outer "coral" zone of the Central transect. In general this can be likened to the

Table 37

Summary of the Seasonal Means of Hourly Metabolic Rate Data* for the Reef-Flat Perimeter "Coral" Zone on the Central Transect at Kaneohe Bay

Months	Metabolic Variable	Estim. Mean Hourly Rate ($gC\ m^{-2}h^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
Jan./Feb.	y_{max}	0.38	-	1	-
	r	-0.27	0.11	5	18
	p_{max}	0.65			-
	c_d	0.17	-	1	-
	c_n	+0.06	0.02	3	19
June/July	y_{max}	0.39	0.07	6	7
	r	-	-	-	-
	p_{max}	(0.92)**			-
	c_d	0.18	0.05	6	11
	c_n	-	-	-	-
Aug./Sept.	y_{max}	0.43	0.13	13	8
	r	-0.63	0.09	3	8
	p_{max}	1.06			
	c_d	0.19	0.07	13	10
	c_n	+0.09	0.02	3	13
Nov.	y_{max}	0.39	-	1	-
	r	-	-	-	-
	p_{max}	(0.84)**			
	c_d	0.15	-	1	-
	c_n	-	-	-	-

y_{max} : peak hourly rate of net photosynthesis
r : hourly respiration rate
p_{max} : $y_{max} + |r|$ = peak hourly rate of gross photosynthesis
c_d : daytime rate of net calcification
c_n : nighttime rate of net calcification

* Rates are corrected for atmospheric diffusion and the metabolic quotients where applicable.

** These values p_{max} were determined using a value of r prorated on the assumption of a linear rate of change between adjacent time periods.

coral zones of the seaward reef-flat at One Tree Is. and the perimeter D1 zone of the lagoon reef at Lizard Is. However, it should be stressed that here we are considering a zone only 52 m wide, not several hundred meters as are the other two sites. This distinction in scale will prove to be of great consequence in interpreting findings (Chapter 2B). There is no full pavement structure in the zone but general algal cementation of the open coral structure is extensive. The occurrence of living corals is considerable, and comparable in quantity to that found on the seaward reef-flat at One Tree Is. In keeping with all Hawaiian reefs, however, very few species occur.

Seasonality of Metabolism and Calcification

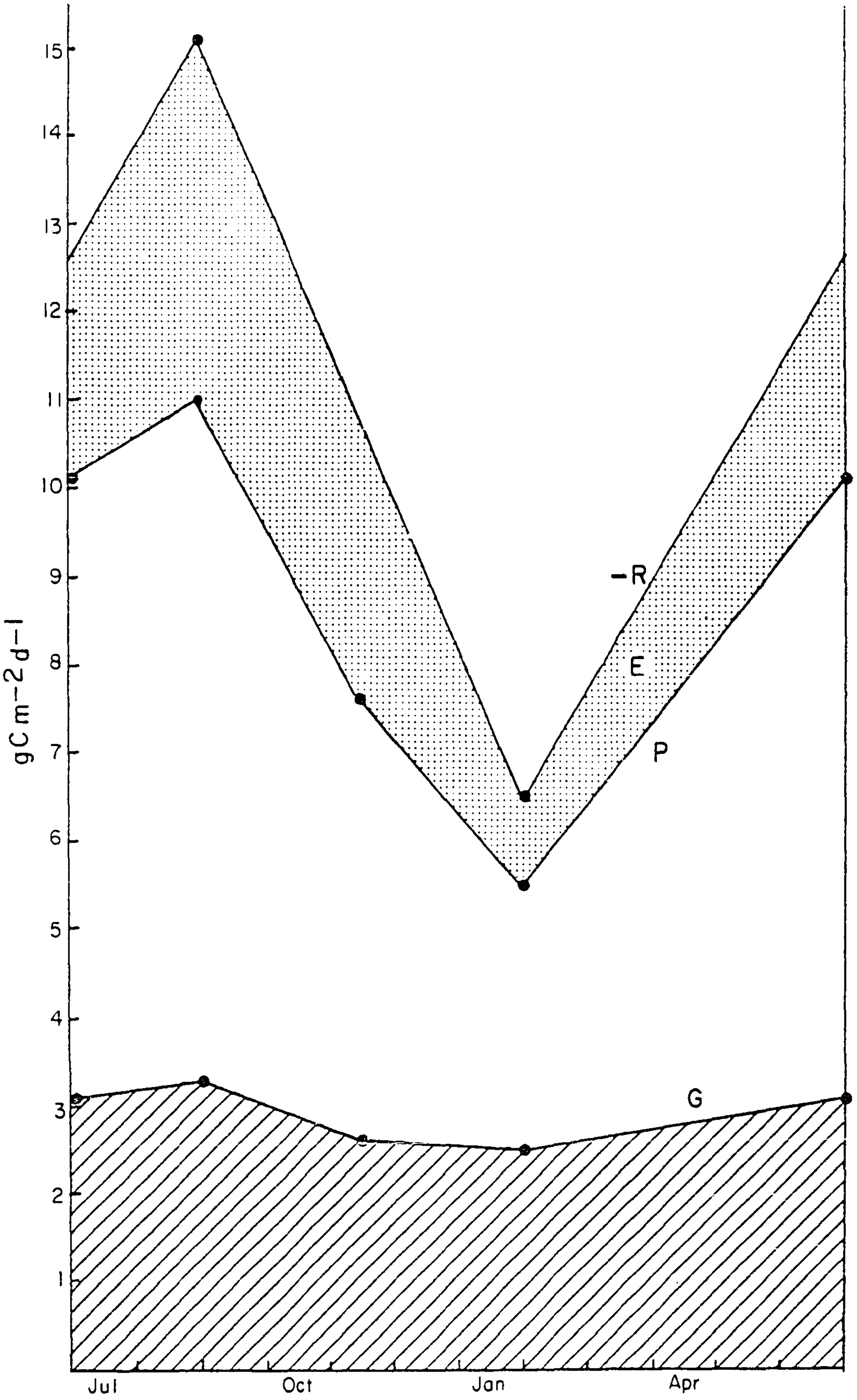
It is apparent from Table 37 that seasonality is similar in Kaneohe Bay to that found at the two Australian sites, with slightly more than a twofold increase in respiration and gross photosynthesis from winter to summer. There is limited reliability in the precision of this finding because of the paucity of respiration data. However, the close support for the findings at the Australian sites gives weight to the indication. In common with Lizard Is. and in contrast to One Tree Is. there is a pronounced drop in activity in the fall. This aspect of seasonality will be discussed later. Photosynthesis is somewhat higher than at either Australian site. Respiration rates are considerably higher. Most of these conclusions are dependent on the reliability of the two mean values presented for respiration. The standard errors for these means are quite moderate and the probability of real difference between the means is high (p = better than 0.01). The difference between the means is 4 x the sum of their standard errors.

Daytime calcification rates are extremely similar to those at One Tree Is. and 50% higher than those at Lizard Is. However, the startling difference in this Hawaiian system is that the nighttime calcification is positive and appreciable, and the few data points leading to this conclusion seem reasonably consistent (standard error of the mean ~ 15%). At Enewetak, Smith (1973) found positive calcification at night over a major seaward coral/algal transect. The amount of carbon fixed in daytime calcification varies from 40% of the amount fixed by photosynthesis during an hour of daylight in winter, to 20% during an hour of daylight in summer. These are identical to the ratios at One Tree Is. and higher than the ratios at Lizard Is. (20% and 13%). Of course the positive nighttime rates are in complete contradiction of this apparent consistency. There is suggestion of a minor amount of seasonality in calcification even in the hourly rates.

The amount of carbon released by respiration (and decomposition) during an hour of darkness varies (Table 37) from 40% of the amount fixed by photosynthesis during the noon hour in winter, to 60% during summer. This exhibits a similar trend to that at Lizard Is. (40% and 50%) and is in contrast to the reverse trend (50% and 40%) at One Tree Is.

The diel integration of the hourly rates discussed above is presented in Fig. 11. These data have not been tabulated as their reliability does not seem to justify it. Comparing these plots with

Figure 11. Daily metabolic rates as a function of the time of year for the fringing reef-flat "coral" zone on the Central Transect in Kaneohe Bay. Cross hatched areas represent net gain and the stippled areas net loss.


gC m−2 d−1
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
Jul
Oct
Jan
Apr
−R
E
P
G

those in Fig. 4 for One Tree Is., and Fig. 8 for Lizard Is., it can be seen that overall seasonality is comparable in all three. The dominance of a negative value for the excess (E) is also apparent in all three, though the value of E is much greater in Kaneohe Bay than at either of the other two sites. The overall annual deficiency is presumably a function of plankton input from the sewage effect but an alternative possibility will be discussed later in this chapter. The seasonality in E is also obvious and generally in line with Lizard Is. (i.e., summer deficiency in photosynthesis the most marked). Thus the same explanation seems at least feasible--i.e., the somewhat higher temperatures in Kaneohe Bay than at One Tree Is. (at least during the period of this investigation) are allowing a winter bloom of benthic algae as occurs at Lizard Is. This bloom enters a phase of decay in the summer even though the summer temperatures are not nearly as high as those at Lizard Is. While winter blooms were not noticed in the Central transect area, they were noted for the Coconut Is. transect (earlier this chapter) and were very marked across the NW transect. The gain in carbonates (G) can be seen to be very marked when the nighttime rates are taken into account. Also a slight seasonality in calcification seems fairly certain for this site.

For the purposes of direct comparison with the conclusions in the previous two chapters:

(1) Calcification is a very high gain process with no positive evidence for dissolution (75% gain at One Tree Is.; 70% gain at Lizard Is.).

(2) Photosynthesis/respiration varies from 15% loss in winter (32% loss at One Tree Is.; 8% gain at Lizard Is.), to 30% loss in summer (14% gain at One Tree Is.; 18% loss at Lizard Is.).

(3) In terms of total carbon flux, photosynthesis (P) and respiration (R) are processing approximately twice as much carbon as calcification in winter ($3\frac{1}{2}$ times at One Tree Is.; 4 times at Lizard Is.), and 4 times as much carbon in summer ($5\frac{1}{2}$ times at One Tree Is.; 10 times at Lizard Is.).

Overall this site is more active than most others for which published data are available (Table 1). One notable exception is the site reported by Gordon and Kelly (1962). Similarly, their site was in Kaneohe Bay and was dominated by very high respiration. These two sites not only had geographical location in common, but were much more narrow and specific (edge zone of a narrow fringing reef) than any others for which metabolic data have been reported. Thus the effect really being emphasized may be one of a level of discrimination (i.e., scale) rather than a genuine metabolic uniqueness. The Central transect "coral" zone also has a reasonable similarity to one other fringing reef site in Tahiti reported by Sournia (1976a) (P = 7.2, R = 8.4, 15% loss).

Zonation of Metabolism and Calcification

Table 38 summarizes the means of all hourly metabolic data for the three zones of the Central fringing reef-flat transect in Kaneohe Bay. The outer "coral" zone has, of course, already been discussed in connection with seasonality and overall performance. A few comments should be made concerning the hourly rates before consideration

Table 38

Summary of the Means* of All Hourly Metabolic Rate Data**
for the Central Fringing Reef-Flat Transect at Kaneohe Bay

Zone	Metabolic Variable	Estim. Mean Hourly Rate ($gC\ m^{-1}d^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
"Coral"	y_{max}	0.42	0.11	21	6
	r	-0.40	0.21	8	19
	p_{max}	0.82			
	c_d	0.18	0.06	21	7
	c_n	+0.07	0.02	6	14
Sand-flat	y_{max}	0.17	0.05	13	8
	r	-0.10	0.03	5	16
	p_{max}	0.27			
	c_d	0.04	0.05	11	41
	c_n	0.00	0.03	5	>100
Algal-flat	y_{max}	0.46	0.23	12	14
	r	-0.11	0.08	3	43
	p_{max}	0.57			
	c_d	0.01	0.03	12	>100
	c_n	-	-	-	-

y_{max} : peak hourly rate of net photosynthesis
r : hourly respiration rate
p_{max} : $y_{max} + |r| =$ peak hourly rate of gross photosynthesis
c_d : daytime rate of net calcification
c_n : nighttime rate of net calcification

* Data from Kaneohe Bay sites are sparse and somewhat erratic. Means are therefore simple means of all data obtained and are not weighted mathematically for each month. All means are likely to be a little high because of a somewhat greater number of data from the month of September which is typically a month of near maximum metabolic activity.

** Rates are corrected for atmospheric diffusion and the metabolic quotients where applicable.

is given to the more useful diel rates. Calcification is so low over the sand-flat and algal-flat zones that the nighttime rates were essentially zero. Certainly no positive rate was detected to support the finding for the perimeter "coral" zone. In Chapter 3B it will be seen that actually both positive and negative nighttime rates are found on various sites around Kaneohe Bay. The explanation of this most peculiar inconsistency is not at all clear (see Chapter 2F). Carbon flux in calcification relative to that in photosynthesis is 22% in the outer "coral" zone averaged over all data. This ratio compares with 22% on the seaward coral covered pinnacle (P1) at Lizard Is., 22% at the seaward reef-flat coral zone at One Tree Is. (DK13), 20% in the lagoon reticulum at One Tree Is. (DK22), 17% in the perimeter zone (D1) of the Lizard Is. lagoon reef-flat, and 16% in the inner coral/algal zone (A2) of the seaward reef-flat at Lizard Is. There is a striking relationship apparent between the level of dominance by corals and value of this ratio. The sand-flat in the Central transect has a calcification-to-photosynthesis ratio of 15% which is only just below the values for the patchy coral-on-rubble zones (Lizard Is. D1 and A2) in the above group, and much the same as the 14% obtained in the small heads/sand/rubble zone (D2) in the lagoon reef-flat at Lizard Is. It is somewhat higher than the lower limit of 11% for coral type environments found for the sand-flat (DK17) at One Tree Is. The ratio obtained for the algal-flat in the Central transect is 2% which is even lower than the nominal 5% obtained for the lagoon algal/seagrass flat (D3) at Lizard Is. These two sites clearly play a negligible role in reef growth. Thus the 11-22% range proposed in Chapter 1A for environments "generically" conforming to coral reef communities and exhibiting operational roles consistent with those of coral reefs is without exception other than the algal pavement at One Tree Is. Importantly, this ratio holds in zones with a tenfold range in actual turnover rates and with enormously varied biotic makeup.

Table 39 and Fig. 12 summarize the diel rates calculated from the hourly rates in Table 38. The calcification rates have been expressed in the common usage form of $kgCaCO_3\ m^{-2}y^{-1}$. Unlike the equivalent condideration given to zonation at One Tree Is. and Lizard Is., this Kaneohe Bay transect is by no means a complete reef system and there is virtually no reason to assume that it will be in any kind of autotrophic balance. Photosynthesis (P) varies appreciably across the flat with fairly "normal" activity concentrated in the "coral" perimeter area and an elevated activity in the shoreline algal zone. A pronounced difference from other reef metabolism zonation so far considered lies in the distribution of excess production (E). All perimeters at One Tree Is. and Lizard Is. were producing an excess which appeared, at least in general terms, to be consumed in the zones downstream. On this fringing reef-flat in Kaneohe Bay, the complete reverse is clearly the case. How can this be explained? There are probably several factors involved. There is almost certainly some significant input of particulate organics (phytoplankton) from the bay water, which would largely be removed by the reef margin filter-feeders and by settling. The subsequent consumption of these particulates would lead to an increased value for R and a lower P/R ratio

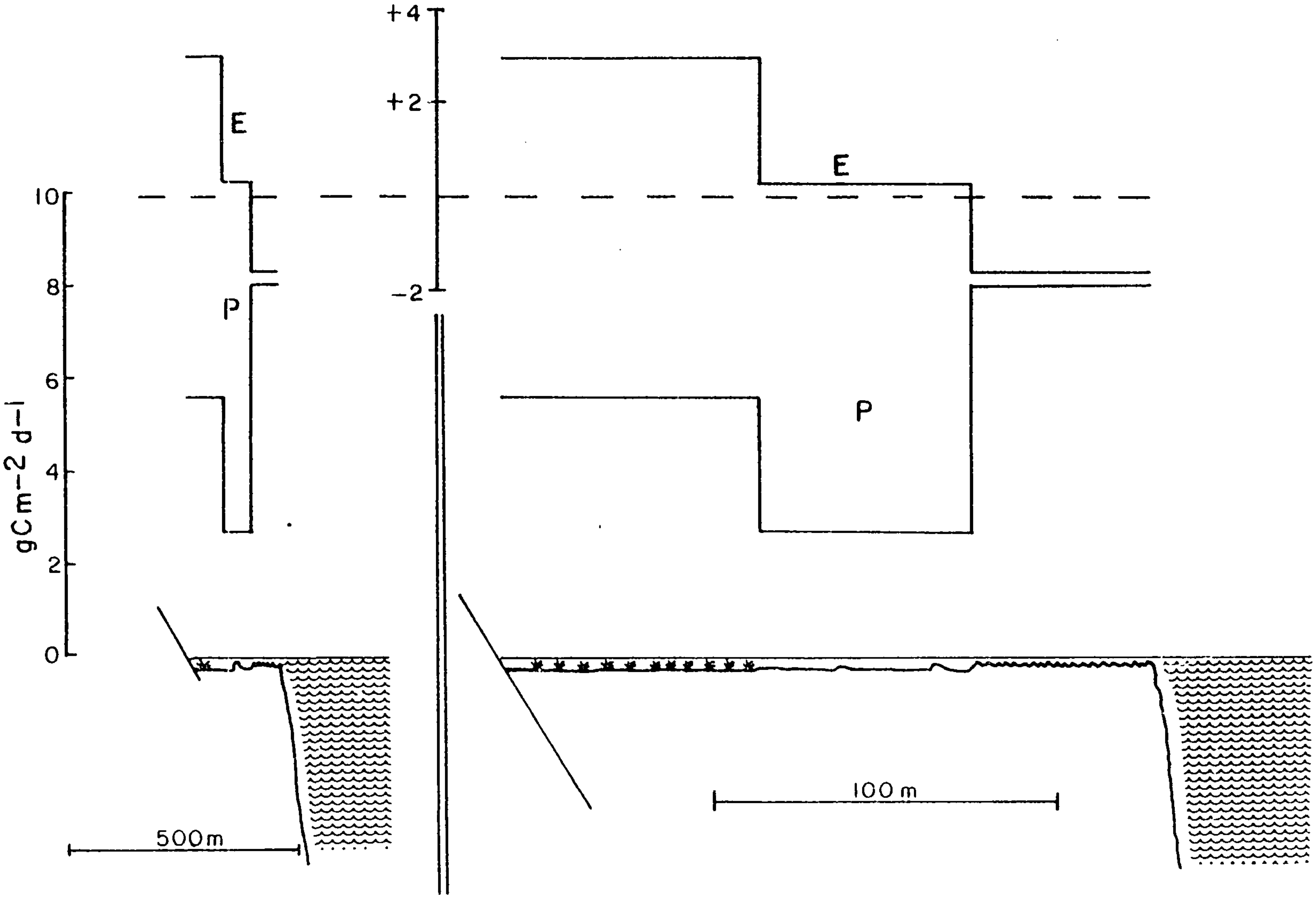
Table 39

Zonation of Community Metabolism Across the Central Fringing Reef-Flat Transect at Kaneohe Bay

Zone	P	-R	E	P/R	G
	(gC $m^{-2}d^{-1}$)				($kgCaCO_3\ m^{-2}y^{-1}$)
"Coral"	8.0	9.6	-1.6	0.8	8.8
Sand-flat	2.7	2.4	0.3	1.1	1.2
Algal-flat	5.6	2.6	3.0	2.2	0.3*
Weighted mean	5.3	4.5	0.8	1.2	2.9

* Based on positive daytime rate only. Virtually no statistical significance.

Figure 12. Primary production along the Central Transect fringing reef in Kaneohe Bay, based on the means of all data. Plots of both gross diel photosynthesis (P) and net gain (E) are shown. The horizontal scale in the left-hand diagram is identical to that used for the One Tree Is. (Fig. 5) and Lizard Is. (Fig. 9) sites. The right-hand diagram has been plotted on a more realistic scale. There is no simple dominant current direction because of the adjacent land mass, and transport of suspended detrital material probably occurs in both directions at various times. The lagoon is 15 m deep. Each value is plotted as a line extending across the full zone. The estimation was normally made in a very slowly flowing system right across the width of the zone.


+4
+2
-2
10
8
6
4
2
0
gCm-2 d-1
E
P
E
P
500m
100 m

in the outer zone. Secondly, while the wind driven water-flow tends to be shoreward across the reef, this in turn requires a long-shore component in the case of a fringing reef. Thus there must also be areas of outflow across the reef-flat and back into the lagoon (bay). The high and excess production of the algal-flat can, and probably must, be carried out as algal detritus. This macro particulate organic matter may then be caught up in the outer perimeter zone leading to decomposition and ingestion there with the same result which phytoplankton input would give. This kind of trophic zonation is clearly impossible in a unidirectional flow system such as characterizes the two Australian systems and most other open water reefs. Why, in fact, is there a substantial excess production of algae in the shore line zone in the first place? The implication of this phenomenon is that there is a significant nutrient input which can either come from terrestrial input, or from release, in the reef margin "coral" zone, from the consumption and decomposition of plankton and/or algae. Thus the whole reasoning is cyclic, with the one clear conclusion being that this reef-flat must experience a moderate driving force in the form of nutrient input and/or plankton input. The situation described here may be fairly normal for high island fringing reefs (Marsh 1977).

Calcification across this small reef-flat has already been considered at some length. The most important additional point raised by Table 39 is that the very high activity, localized on the perimeter as has been mentioned to be the case on all other reefs studied, is actually twice as high on a diel basis as that for any reef zone reported for any system (see Introduction; Smith and Kinsey 1976). This either can be interpreted as a real exception to the common "rule" of 4 $kgCaCO_3\ m^{-2}y^{-1}$ for perimeter zones, or as a feature resulting from the use of a finely discriminating scale. A third possibility is that there is actual enhancement of calcification resulting from the nutrient or plankton input. However, this last explanation seems unlikely in view of the findings of Kinsey and Davies (1979) which suggest that nutritional enhancement is likely to cause suppression of calcification. All these possibilities will be covered further in Sections 2 and 3.

Fig. 12 demonstrates more dramatically than any table the importance of considering scale. While the right side of the diagram indicates the zonation of P and E on a scale which allows easy interpretation, it is actually the left side of the diagram which is plotted on a scale identical to that used for One Tree Is. (Fig. 5) and Lizard Is. (Fig. 9) data. Thus, if zonation on comparable scales were to be considered, the activity of this narrow fringing reef would actually be given by the weighted mean of the whole transect. Table 39 indicates that, rather than being of extremely high activity and heterotrophic mode as suggested in the discussion so far for the reef perimeter (P = 8.0; P/R = 0.8), the total reef-flat is really of somewhat low activity and autotrophic mode (P = 5.3; P/R = 1.2). Or, alternatively, and perhaps more logically, the algal-flat should be treated separately as was done for D3 at Lizard Is., and the other two zones should be considered as the true perimeter: then P = 5.1 and P/R = 0.9. None of these options is probably entirely valid but the concept is raised at this time as an issue to be borne in mind when considering zonation and function. This will be discussed much more extensively in Section 2.

Planktonic Contribution

Estimates of plankton activity in Kaneohe Bay waters are of considerable importance to the full understanding of reef benthic metabolism as there is a great deal of plankton growth driven by the nutrient input in the south sector of the bay. The results of a series of plankton metabolism runs are presented in Chapter 3B. However, typical activity in the central bay area is quite low and estimated at less than 0.1 gC $m^{-2}d^{-1}$ over the reef-flat, for both P and R. P/R is high, about 2, because of the phytoplankton activity. Overall, no significant difference exists between the total metabolic activity of the Central reef-flat as so far presented, and the true benthic activity.

Special Calcification Studies

Of the various miscellaneous data collected for other sites in Kaneohe Bay, the only set sufficiently complete and relevant for presentation here is the results of a number of daytime calcification studies. Table 40 gives these data. It can be seen that the very wide barrier structure (2000 m) has an activity near the outer edge which is only moderate compared with other seaward zones reported (c_d = 0.1 gC $m^{-2}h^{-1}$ here, 0.08 to 0.18 at Lizard Is., 0.12 to 0.16 at One Tree Is.). However, it is clearly in general conformity with these, and could represent about 3.3 kg$CaCO_3$ $m^{-2}y^{-1}$ if nighttime

Table 40

Daytime Calcification Rates on Various Sites Presumed Free of Sewage or Terrigenous Sediment Impact--Kaneohe Bay

Description	Desgination	c_d ($gC\ m^{-2}h^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
Seaward barrier slope	K1	0.10	-	1	
Barrier: outer reef-flat	K2(outer)	0.06	0.05	3	
Barrier: outer reef-flat	K2(inner)	0.05	0.01	2	
Barrier reef-flat	K3(outer)	0.05	-	1	
Barrier reef-flat	K3(inner)	0.04	-	1	
Seagrass bed	K4	0.01	0.01	2	
Patch reef with 100% *Porolithon* cover (0.5 m)	#10	0.16	0.06	7	15
Patch reef with 100% *Porites* (1.5 m)	#10	0.30	0.19	10	20
Patch reef with 100% *Porites* (0.5 m)	#11	0.36	0.13	5	16
Patch reef with *Halimeda* (1 m)	#13	0.09	0.07	6	34

rates are not appreciably positive <u>or</u> negative. Coral cover does increase somewhat, seaward of the K1 area but so does depth. It is doubtful that calcification anywhere on this barrier appreciably exceeds the value reported here for K1. Moving lagoonward across the transect, the calcification rate gradually declines to the seagrass bed (K4) at the inner edge where it is no more than 10% of its upper limit. In these wide open areas there was no suggestion of the intense localized activity of the narrow "coral" zone of the Central fringing reef.

Table 40 also gives some values for sites chosen specifically because they represented possible extremes. Unfortunately, nighttime values again are not available. It can be seen that the reef margins with 100% cover of viable <u>Porites compressa</u> have very high calcification activity approaching twice the level (0.36 and 0.30 gC $m^{-2}h^{-1}$) of the already high activity in the mixed coral/<u>Porolithon</u> perimeter of the Central transect (0.18 gC $m^{-2}h^{-1}$). Ignoring the nighttime activity, these very specific sites can be seen to be calcifying at 10-12 kg $CaCO_3$ $m^{-2}y^{-1}$ which exceeds the general value of 4 kg $CaCO_3$ $m^{-2}y^{-1}$ by a very substantial margin. Of course it is reasonable to use the argument that no large-scale zone of this kind occurs anywhere on any coral reef and therefore the exception becomes one of scale alone. However, the next chapter raises some doubts even on that rationale. Another area, of 100% <u>Porolithon</u> cover, can be seen to be calcifying at 0.16 gC $m^{-2}h^{-1}$ which is right in the normal range quoted in the previous paragraph for all the large-scale reef perimeters studied (even including the day rate in the Central

Kaneohe Bay transect). This is highly significant, as it draws further attention (see also DK8 at One Tree Is.) to the fact that corals are not necessary in a reef community for the achievement of normal calcification rates and, presumably, reef growth rates.

The final value in Table 40 indicates that even a fairly sparse cover with the green alga Halimeda can result in quite a high calcification rate (0.09 gC $m^{-2}h^{-1}$). This obviously is made possible by the very rapid growth rate of Halimeda, compared with those of the typical high-standing-crop hard-substratum calcifiers such as corals and coralline algae. No other of the zones or sites used in any of the studies reported in this dissertation is apparently dominated by Halimeda.

The principal value of the data presented in this chapter, for the relatively unperturbed parts of the Kaneohe Bay system, is to point out a large number of areas for caution in the interpretation of metabolic data from coral reef studies. Where a reasonable basis for comparison exists, most findings and conclusions have been compatible with those of the previous two chapters.

D. CENTRAL NORTH PACIFIC

General Information

The only short-term expedition made to a site other than the three principal sites so far reported was to Johnston island, an isolated "tilted atoll" in the central North Pacific Ocean (Tables 41, 42). This shoal area has some of the characteristics of an atoll rim on its lee side only. It has been proposed (Emery 1956) that the lack of a normal reef margin elsewhere is the result of tectonic movement tilting the whole structure faster than upward growth could keep pace (Emery 1956). An alternative hypothesis of asymetrical erosional degeneration of the atoll during the falling sea level at the end of the Sangamon Interglacial, or, more probably, during the rising sea level at the end of the Wisconsin glaciation, has been proposed by Ashmore (1973). However, the peculiar nature of the gross substrate morphology, and the presence of a rim only on the northwest (downwind) side, together with a dominant wave energy input from the northwest (opposed to the wind, Ashmore 1973), has resulted in several areas of extremely unusual coral development. These are characterized by abnormally high percent cover with living corals in shallow lagoon depths. Smith and Harrison (1977) suggest that "Johnston Atoll may represent an environment with nearly optimum reef growth potential". The objective in choosing to work in this obviously atypical environment was to seek exceptions to the Smith and Kinsey (1976) postulate that coral reef growth is characterized by an upper limitation of the reef $CaCO_3$ production to a rate of about 4 kg$CaCO_3$ $m^{-2}y^{-1}$. Davies and Kinsey (1977) extended this postulate to suggest that this rate

Table 41

Field-work Timetable for Johnston Island

Year	Period
1978	June (2 weeks)

Table 42

Johnston Island
Geographic, Meterological and Tidal Information

Location:	16°44'N, 169°31'W, solitary, near geometric center of Pacific, rising from area approximately 5000 m deep. Always in the North Equatorial Current.
Reef Type:	Coral shoal, 22 km x 11 km, sloping to windward (4 m at lee end, 20 m at windward end) suggesting tectonic tilting (Emery 1956). Atoll type rim (200 m wide) exists along 14 km at lee end only. Lagoon inside lee rim with extreme development of reticulated patch reefs and anastomosing pinnacles. All areas fully tidal.
Weather:	Only slight seasonality. Strongly under the influence of the NE trades (ENE-E at 15-20 knot throughout the year). Precipitation greatest in "winter months" (total 75 cm y^{-1}).
Tides:	Semidiurnal--frequently very asymmetrical. Larger spring range 1.0 m Smaller neap range 0.3 m
Currents:	Wave refraction around high lee rim causes complex current patterns with dominant flow having strong southerly component. On the ebb tide there is often a reversal of this flow allowing some water to return over the reef crest.
Flushing:	Probably only one to a few days.

limitation applied over the whole period of Holocene reef growth even though the depth of water cover was mostly in excess of that presently occurring. Checking the effects of moderate depth, on the reef slopes at Enewetak Atoll, Smith and Harrison (1977) found that the rate of carbonates formation was equal to or less than the 4 $kgCaCO_3\ m^{-2}y^{-1}$, decreasing with increasing depth below the first few meters. Johnston Is. not only represented some of the most concentrated coral growth known, on an areally extensive basis, but was possibly a reasonable simulation of the conditions applying on most reefs several thousand years ago during the period of rapid sea level rise. Of course, those Holocene reefs would mostly have lacked any emergent perimeter.

It has already been emphasized in the last chapter that there may be significant exceptions to the "4 kg postulate" in reasonably normal systems but that these may be an effect of scale only, all such observations having been made on very small areas of concentrated coral development. Johnston Is. again represented a useful cross check on these exceptions because of the very extensive nature of the intensive coral development.

Table 42 gives details of location, reef description, weather, tides, etc. Tidal range is small (similar to Kaneohe Bay), weather rather even with trade winds persistent throughout the year, currents complex because of refraction from the leeward perimeter, and flushing rapid. The water in the system is typically more clear than in any of the other sites so far reported.

Figure 13 and Table 43 indicate details of location and characteristics of the sites chosen for monitoring. No attempt was made to

Figure 13. Johnston Island reef with its extensive area of shoal water, and atoll type development only on the northwest of the platform. The lagoon adjacent to the emergent NW perimeter exhibits very extensive reef development both as a reticulum of patch reefs and as coral covered pinnacles. Wave refraction caused by the reef crest modifies the direction of water flow substantially so that the NW perimeter at times is operationally somewhat closer to a true seaward perimeter. The various sites used for monitoring are indicated (see also Table 43).

░	cays (modified by dredge fill)
▓	reef-flat: pavement with some corals
▥	lagoon areas with reticulated patch reefs
▤	back-reef areas with anastomosed coral pinnacles
✚	lagoon area with anastomosed coral pinnacles

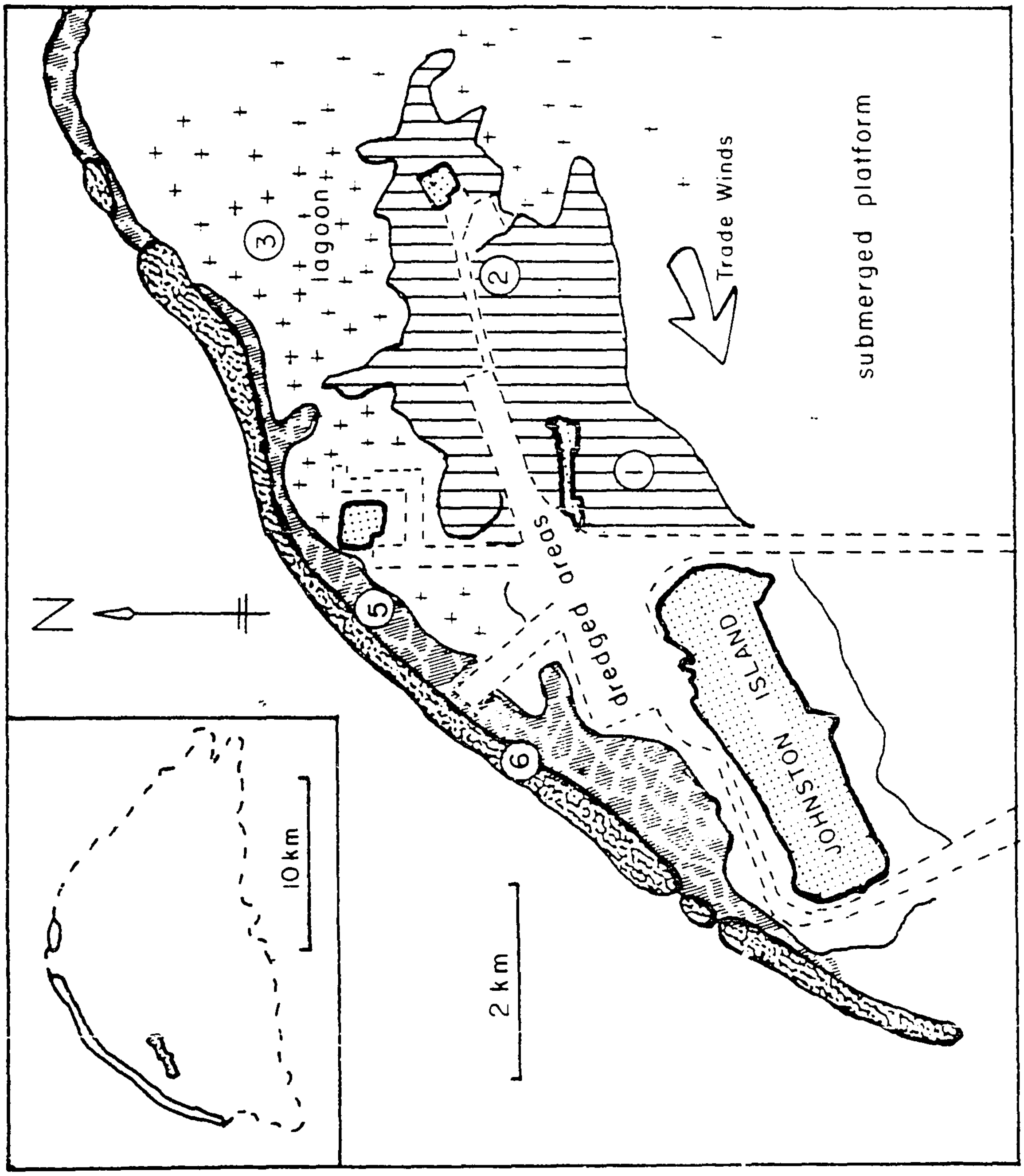

N
lagoon
③
②
①
⑤
⑥
Trade Winds
submerged platform
dredged areas
JOHNSTON ISLAND
2 km
10km

Table 43

Site Summary
Johnston Island*

Zone Description	Zone Extent (m)	Designation	Water Depth at LWS (m)	Hard Bottom (%)
Algal pavement, sparse corals, few foliose algae	150	#6	0.4	90
Back reef area of anastomosing pinnacles with some sand bottom	250	#5	3.7	60
Lagoon area of heavy coral development on anastomosing pinnacles	1500	#3	4.8	90
Lagoon area of reticulated reefs and sand bottom	800	#2	3.3	10
Lagoon area of intense reticulation with sand bottom	800	#1	2.1	20

---

*Contrary to all other tables of "Site Summary" all information in this table is presented in the order of progression away from the exposed leeward crest towards windward. It is nevertheless approximately down current. Zone extent is across the zonal structure--i.e., approx. NW/SE.

consider general metabolism at Johnston Is. Only the calcification rates were monitored. Zones #1 and #2 were chosen because of their marked similarity to the lagoon reticulum (DK22) at One Tree Is. Zone #1 most closely resembles DK22 in both depth and percent cover. Zone #2 is a little more open and deeper. These sites are also similar to the shallow lagoon at Fanning Atoll reported by Smith and Pesret (1974). Zone #6 was chosen as it represented a fairly conventional moderate energy reef-flat. Even though it is a leeward flat, the wave refraction patterns occurring probably made it closer to a normal seaward flat, though with somewhat less impingent wave energy. The area is largely an algal pavement with a low percent coral cover and very limited foliose algae. Zones #3 and #5 were chosen specifically as representing the areas of unique and very high coral cover. Zone #5 is essentially a back-reef area of considerable extent and moderate depth (3.7 m). Zone #3 is more a lagoon environment with extraordinary coral development and moderate depth (4.8 m). Both these zones are characterized by a large number of coral covered pinnacles mostly anastomosed at the base and just reaching the low tide surface. Only very small areas of sandy bottom occur between some pinnacles though this is a little more common at #5.

Water Properties

Inadequate information is available concerning water properties at Johnston Is. to allow presentation of overall trends. Based on the present study in June 1978, and the findings of Emery in July 1954, it seems that the early summer period is characterized by a water temperature between 26.8° C and 28° C, a salinity of 34.8‰, and an alkalinity of 2.20 to 2.35. The system is very open with plenty of water flow at all times. Consequently, it is doubtful that any parts of it are stressed by large changes in pH, or oxygen content of the water. However, no data are available for these parameters.

Calcification Studies

Table 44 summarizes all hourly calcification rate findings. It can be seen that data for Zones #6, #2 and #1 conform to equivalent sites on the other reefs reported. The two sites for which there is no reasonable analogy (#3 and #5) both exhibit most peculiar results. The majority of monitoring runs at the deep lagoon site #3 were plagued by rather strong currents which caused very complex mixing patterns in view of the very high frequency of large surface-reaching pinnacles which occurred. Results were very erratic and essentially incredible in view of the fact that the net daytime rate was negative and the net nighttime rate positive. It is therefore assumed that these data are artifacts of mixing phenomena, and that they should be ignored. On the other hand, the first seven data points from this site were all based on runs made on neap tides with very little current. These gave a reasonable mean with the logical value of 0.12 gC $m^{-2}h^{-1}$. This seems to be the only value which can be used for zone #3. Zone #5 was a site similar to #3 but immediately behind the reef-flat pavement. It also had a very high frequency of coral covered pinnacles reaching the surface. Results here were consistent, with the daytime value being similar to the coral zone DK13 at One Tree Is. (0.16), the coral covered pinnacle P1 at Lizard Is. (0.18), and the "coral" zone on the Central reef-flat at Kaneohe Bay (0.18).

Table 44

Hourly Calcification Rates on Various Sites at Johnston Island. Means Represent a Period of Two Weeks in June 1978.

Zone	Designation	Metabolic Variable	Estim. Mean Hourly Rate ($gC\ m^{-2}h^{-1}$)	Standard Deviation	No. of Estim. (n)	Standard Error (%)
Pavement algal/coral	#6	c_d	0.13	0.05	7	15
		c_n	-			
Back-reef heavy coral cover	#5	c_d	0.18	0.09	6	20
		c_n	0.09	0.07	4	39
Lagoon, heavy coral cover	#3					
Slow current data		c_d	0.12	0.16	7	50
		c_n	-			
All data		c_d	-0.36	0.53	17	36
		c_n	+0.80	0.71	8	31
Lagoon, reticulated reefs	#2	c_d	0.04	0.03	6	31
		c_n	-			
Lagoon, reticulated reefs	#1	c_d	0.05	0.05	7	38
		c_n	0.00	0.04	4	>100

c_d : daytime rate of net calcification

c_n : nighttime rate of net calcification

It did not approach the 0.30 and 0.36 gC $m^{-2}h^{-1}$ found for the small Porites patches in Kaneohe Bay. Thus scale may still be the most reasonable rationalization for values as high as 0.3-0.4 from any area of a coral reef. It seems unlikely that such a value will be found for an extensive area. The nighttime value for #5 was very similar to the positive 0.07 gC $m^{-2}h^{-1}$ found only on the Central reef-flat at Kaneohe Bay, and was therefore quite different from the more usual zero or marginally negative values found on other sites including the 100% coral pinnacle P1 at Lizard Is. The extreme variability of the night calcification rates on various sites will be the subject of further discussion in Chapter 2F.

Table 45 uses the available hourly rates to project long-term values for G at the various sites. Regardless of whether one assumes zero (One Tree Is., DK8), or slightly negative (Lizard Is., A1), or slightly positive (Lizard Is., A2) c_n for the low coral, algal pavement zone, #6, it clearly conforms to the "4 kg postulate". The reticulated patch reefs of the shallow lagoon zones #1 and #2 bear a striking resemblance structurally and in percent cover to the lagoon reticulum DK22 at One Tree Is. It is therefore gratifyingly consistent to see that their values for G of 1.6 and 1.3 $kgCaCO_3\ m^{-2}y^{-1}$ are in excellent agreement with the 1.5 $kgCaCO_3\ m^{-2}y^{-1}$ found for DK22. The back-reef pinnacle zone #5 not only exhibits the high positive rate of calcification of night, but overall calcification (G) exceeds 4 kg whether or not the nighttime rate is taken seriously. As there is little reason to doubt the night rate, the overall value of 9.6 $kgCaCO_3\ m^{-2}y^{-1}$ can be accepted as valid, and therefore not only

Table 45

Projected Long-Term* Calcification Rates for Various Sites at Johnston Island

Zone	Designation	Assumed Value for c_n ($gC\ m^{-2}h^{-1}$)	G ($kgCaCO_3\ m^{-2}y^{-1}$)
Pavement coral/algal	#6	0	4.4‡
		-0.02	3.6
		+0.01	4.8
Back-reef heavy coral cover	#5	0	6.0
		+0.09**	9.6‡
Lagoon heavy coral cover (slow current data only)	#3	0	4.0
		+0.06	6.4‡
Lagoon, reticulated reefs	#2	0**	1.3‡
Lagoon, reticulated reefs	#1	0	1.6‡

* The rates are based on the June hourly rates which probably approximate the average rate, based on findings at other sites.

** These rates are the actual estimated night rates. All other night rates used are based on either the rate found for biotically similar areas at Johnston Is. (0 for #1 and +0.06 for #3) or similar areas on other systems (all those for #6).

‡ These are the preferred values.

supports the high value of 8.8 $kgCaCO_3\ m^{-2}y^{-1}$ found in the Kaneohe Bay shallow reef-flat perimeter zone, but, unlike that site, represents a very extensive area. This clear exception to the 4 kg postulate requires that reconsideration be given to the Smith and Kinsey (1976) and Davies and Kinsey (1977) contention that no reef can calcify faster. The other deeper area of lagoon pinnacles (#3) gave rise to such doubtful data that any value for G is highly speculative. However, the general suggestion of the neap tide (low current) data is that the area is likely to equal or exceed (if night rate is prorated from the similar area #5) the 4 kg postulate and certainly greatly to exceed any values ever published for lagoon calcification (Chapters 1A; 1B; Table 2; Kinsey 1977).

Adey (1978) has stressed the relatively common occurrence of vertically rapid, but porous and uncemented, growth in Caribbean reefs, in contrast to the more massive compact growth of Pacific reefs. It is not clear whether this necessarily implies faster mass accretion. Unfortunately, direct reef calcification rates of the kind reported in this dissertation have not been obtained for Caribbean reefs. Nevertheless the possibility exists that the exceptional performance of the Johnston Is. lagoon may be much more common in the Caribbean.

Thus not only does Johnston Is. establish yet another set of performance figures for coral reef calcification activity but strongly supports latitude-independent consistency in some zones (#6, #1 and #2) while totally contradicting this consistency in others. Whether these areally extensive pinnacle zones which appreciably exceed the 4 kg postulate can be considered as typical of the middle Holocene reefs, still submerged by a rapidly rising sea, or whether they are unusual artifacts of atypical geomorphology is very difficult to say. Clearly the presence of an almost emergent reef crest leeward of the areas in question is a condition not likely to have applied during the middle Holocene analogy.

SECTION 2

OPERATIONAL CONCEPTS

This section will be devoted to a discussion of many of the points raised by the data and deductions of the investigations reported in Section 1. Few new data will be included and the objective is to look for operational uniformity or positive differences in the quantitative performance of a series of superficially rather different coral reefs.

A. SOURCES AND SINKS

As has been discussed at some length in Section 1, it is clear that reefs have areas which can be identified as organic source areas. Such zones will be characterized by $P > R$ where it can be established that the implication is not simply an increasing standing crop. That is, the excess production (E) must be exported as detrital fragments or even inside fish and other large fauna which enter the zone to graze but do not respire the major part of their ingested food within the zone. How is the distinction to be made between a positive value for E which implies increasing standing crop, and a positive value which implies exported fixed carbon? Operationally, it seems reasonable to treat any short-term gain (i.e., seasonal only) as probably related to changing standing crop or, at best, suspect. On the other hand, in all but reefs undergoing some sort of dramatic perturbation, it is reasonable to postulate that a net positive value for E over a full annual cycle implies an operational role as an organic source area.

Conversely any area with a negative value for E can be either losing standing crop by respiration and decomposition, or has a requirement for organic carbon input--i.e., is a sink area. Using the same reasoning as for sources, the operational role as an organic sink is held to be valid if the net value for E for a full annual cycle is negative.

With respect to inorganic carbonates, all reef areas reported in Section 1 are source areas, potentially. That is, they all exhibit net positive diel values for G at all times. However, while it is clear that organic material never accumulates to any marked degree on coral reefs over the long term and therefore that a positive value for E must imply export (source role), it is equally obvious that inorganic fixed carbon ($CaCO_3$, etc.) does accumulate. Thus the ubiquitous positive value for G does not resolve whether the gain indicated by the value determined for G is retained at its <u>site</u> of fixation, or is eventually moved physically to other sites before its eventual long-term sedimentary accumulation. This question is usually resolved, at least in a semiquantitative sense, by physiographic observation. Thus a shallow reef-flat cannot continue to accumulate carbonates during a stable sea level stand except by horizontal accretion--i.e., the flat may grow horizontally. This is very commonly the case and is manifested by leeward prograding sand sheets such as is apparent at One Tree Is. (Fig. 1, DK17), and in-filling of lagoons, etc. Some fine sediments no doubt migrate down seaward slopes (MacKenzie et al. 1965; Land 1979), or are washed out of the system altogether as plumes of cloudy water (particularly pronounced in the Bahamas and other Atlantic systems; Bathurst 1976). However, there seems little evidence, at least for Pacific reefs, that the ocean is a sink for a quantitatively significant proportion of the total fixed inorganic carbon (Smith et al. 1971; Smith and Jokiel 1975; Davies and Kinsey 1977). Similarly it is certain that very few reefs receive significant input of fixed inorganic carbon from the ocean unless they are <u>very</u> close downstream from another reef.

The question of whether the ocean is a significant source or sink for organic carbon is much more complex. The flux of dissolved organic carbon (DOC) is clearly very great in view of the throughput of water containing about 1 gDOC m^{-3}. However, there is little evidence for major changes in the concentration of DOC. Marshall et al. (1975) established that there was little net exchange of DOC between the ocean and Enewetak lagoon. Kinsey (1972) presented some evidence, based on BOD estimates, that levels of DOC were a little higher over the One Tree Is. system, and Meyers (1976) found that DOC decreased over one reef at Grand Cayman and increased marginally over another. Overall it seems doubtful that DOC constitutes a major import to, or export from, coral reef systems. On the other hand, increases in particulate organic carbon (POC) may be very marked, and have been noted by a number of workers (Odum and Odum 1955; Quasim and Sankaranarayanan 1970; Tranter and George 1972; Marshall and Talek 1972; Johannes and Gerber 1974; Gerber and Marshall 1974; Marshall 1972; Glynn 1973). This material is predominantly algal detritus (Johannes and Gerber 1972) from the surf zones. However, the major role served by such material is interzonal transfer, not loss to the ocean. This has been directly substantiated by a number of workers (Odum and Odum 1955; Marshall 1965; Quasim and Sankaranarayanan 1970; Johannes and Gerber 1974; Marshall et al. 1975; Smith and Marsh 1973). However, complete reef systems have been found to exhibit a very small net loss of organics to the ocean at a rate equivalent to less than 0.5% of the total *in situ* photosynthetic turnover (Gordon 1970; Smith and Pesret 1974; Smith and Jokiel 1975). Thus the creation and reutilization of dissolved or suspended particulate organics (including reef plankton) are dominantly an internal function of reef systems, with negligible net exchange with the ocean.

Considering the distribution of the fixation of organic carbon (P) and the resulting gains or losses (± E) in the reef systems reported in this study, the overall summary of findings is given by Figures 5, 9, and 12. There is a clear indication from Figs. 5 and 9 that reef margins, even lagoonal margins exposed to only 1 km of fetch (Lizard Is.), are exhibiting substantial excess production. The zones behind these immediate perimeters tend progressively towards decreased net production and eventually net consumption over the 100 to 400 m downstream of the source area (consider the relationships indicated by: DK8, DK13, DK17 = 600 m, One Tree Is. seaward perimeter; P1, A1, A2 = 550 m, Lizard Is. seaward perimeter; D1, D2 = 500 m, Lizard Is. lagoon perimeter). Further leeward of this sink area there is typically a calm water zone of increased production but with neither a source or sink role (DK22 at One Tree Is. and D3 at Lizard Is.). However, this can only apply if there is a continuation of shallow water (absent leeward of A2 at Lizard Is.). Deep lagoon areas such as DK23 at One Tree Is. and the central lagoon at Lizard Is. probably serve as the ultimate sink for any material not settled out on downstream reef-flats.

The next question to be considered is why the operational source area role appears to be on exposed margins. Two explanations seem to be implied. The first suggests that the foliose and filamentous algae, which are presumably responsible for most of the excess, might grow better and be subjected to less intensive grazing in these areas of high turbulence. These effects, together with possibly enhanced activity from the symbiotic algae, also induced by the higher turbulence, seem a reasonable explanation for the elevated activities of the margins, though probably has little to do with their source role. The second explanation is that high turbulence readily breaks off a significant proportion of the production and this abiotic "cropping" results in the conventional response of an increased gain to maintain a constant standing crop. Similarly the sink role is simply one of passive receipt of the material held in turbulent suspension only for a few hundred meters before settling out under quieter conditions.

Tables 17 and 30 establish how amazingly near to perfect balance (i.e., sources = sinks) both the One Tree Is. and Lizard Is. systems are. While it has probably no statistical significance it is interesting to note that the overall excess production for the Lizard Is. system is 1%, which seems in very reasonable agreement with the previously suggested 0.5% for other reef systems, where only total budgets were available. By contrast, One Tree Is. seems to exhibit a slight deficiency with rather more statistical significance. However, this number is based on a transect <u>excluding</u> the seaward slopes. If the Lizard Is. values for metabolism on the P1 area are inserted into the One Tree Is. integration, Table 17 can be recalculated. The result of this exercise is given in Table 46. It can be seen that the whole system now exhibits a 1% excess production, exactly the same as that for Lizard Is. and therefore also in conformity with the marginal excess indicated by the budgetry analysis reported by Gordon (1970), and the virtual balance suggested in the budgeting

Table 46

Integration of Community Metabolism Along the 1 m Wide Main Transect at One Tree Island, Using the Values from the Lizard Island Pinnacle (P1) for the Outer Slope

Zone	Length (m)	P (gC $m^{-1}d^{-1}$)	E (gC $m^{-1}d^{-1}$)	G (kgCaCO$_3$ $m^{-1}y^{-1}$)
Seaward slopes based on P1 from Lizard Island	60	560	230	220
Algal pavement	165	330	250	660
Reef-flat coral zone	200	1080	-30	690
Reef-flat sand and rubble	240	200	-110	100
Lagoon: reticulum	750	2330	0	1130
Lagoon: open	850	1190	-260	430
Total transect	2265	5690	80	3230

analyses reported by Smith and Pesret (1974) and Smith and Jokiel (1975).

How does the inconsistency of the Kaneohe Bay results (Fig. 12) fit in with the very neat and uniform findings reported for One Tree Is. and Lizard Is.? The explanations, or at least rationalization, of this lack of agreement have already been outlined in Chapter 1C. Simply, only two factors need be considered. Firstly, there is the major source area of the Kaneohe Bay lagoon to be taken into account. This is feeding particulate carbon to the reef margin in appreciable quantities (approximately 25 mgC m^{-3}; representing 30-50 gC d^{-1} entering a transect 1 m wide), and it might reasonably be expected that R would be elevated by at least 1 gC $m^{-2}d^{-1}$ if this material was removed by filter feeders, or settled out. Thus the perimeter has a reasonable potential to become a net sink even if it is serving a source role (i.e., turbulent disruption of reef edge algae) with respect to any other zone. However, more importantly, it is necessary to consider the complex and non-unidirectional nature of the water flowing over a fringing reef. As explained earlier in Chapter 1C, the excess production of the shoreline algal flat has to go somewhere, and that can only be out. Thus the reef margin may receive not only POC from the bay, but POC from the algal flat lying behind it. I believe it is therefore unrealistic to expect such a narrow fringing reef to exhibit the postulated predictable source/sink sequences of a "normal" open water reef, regardless of whether the effects of sewage pollution are taken into account or not.

The virtual self-sufficiency apparently established very precisely for the One Tree Is. and Lizard Is. systems does not prove independence from the ocean as a source of POC. However, it does make it seem very probable that dependence of such open water reefs on oceanic plankton as a source of food is quantitatively insignificant. The only alternative is that any appreciable dependence is neatly balanced by losses over and above the net 1% loss.

Considering again the main source areas for inorganic carbonates, it is clear that all systems examined exhibit high carbonate formation in the range of 4-9 $\mathrm{kgCaCO_3\ m^{-2}y^{-1}}$ in the upper seaward slopes and perimeter margins (Tables 16, 29b, 39, 45, and Chapter 1C, Special Calcification Studies). As these are, without exception, very shallow areas, it is apparent that they are all major source areas for sediments to be deposited downstream of the site of their formation. Thus the sink areas will be reef-flat sand sheets and lagoon floors where only low rates of calcification occur in situ. Johnston Is. has unusual extensive back-reef and lagoon areas with very high calcification occurring (Table 45). Unlike the source, but non-accumulation role of the high activity perimeter zones, these very high activity deeper lagoon areas at Johnston I. represent accumulation at the site of formation (i.e., source and sink are the same). This situation obviously cannot be a steady state, but represents a phase of active vertical growth probably made possible by the present-day unusual geomorphology of the substratum (Ashmore 1973; see Chapter 1D). This simulation of a rising sea level obviously creates conditions not occurring on most reefs at present. All other lagoon areas and sand flats on the other study reefs exhibit a maximum calcification rate not exceeding 1.5 kg$CaCO_3$ $m^{-2}y^{-1}$, though this may occur over very extensive areas, greatly exceeding the areas of actual high activity reef perimeter (Smith 1978). In most cases this lagoonal calcification is accumulated where it is formed. Thus the deeper lagoon areas or high relief reticulated patch reef areas are sources and sinks for their own carbonates, as well as sinks for the carbonates formed in the upstream perimeter zones.

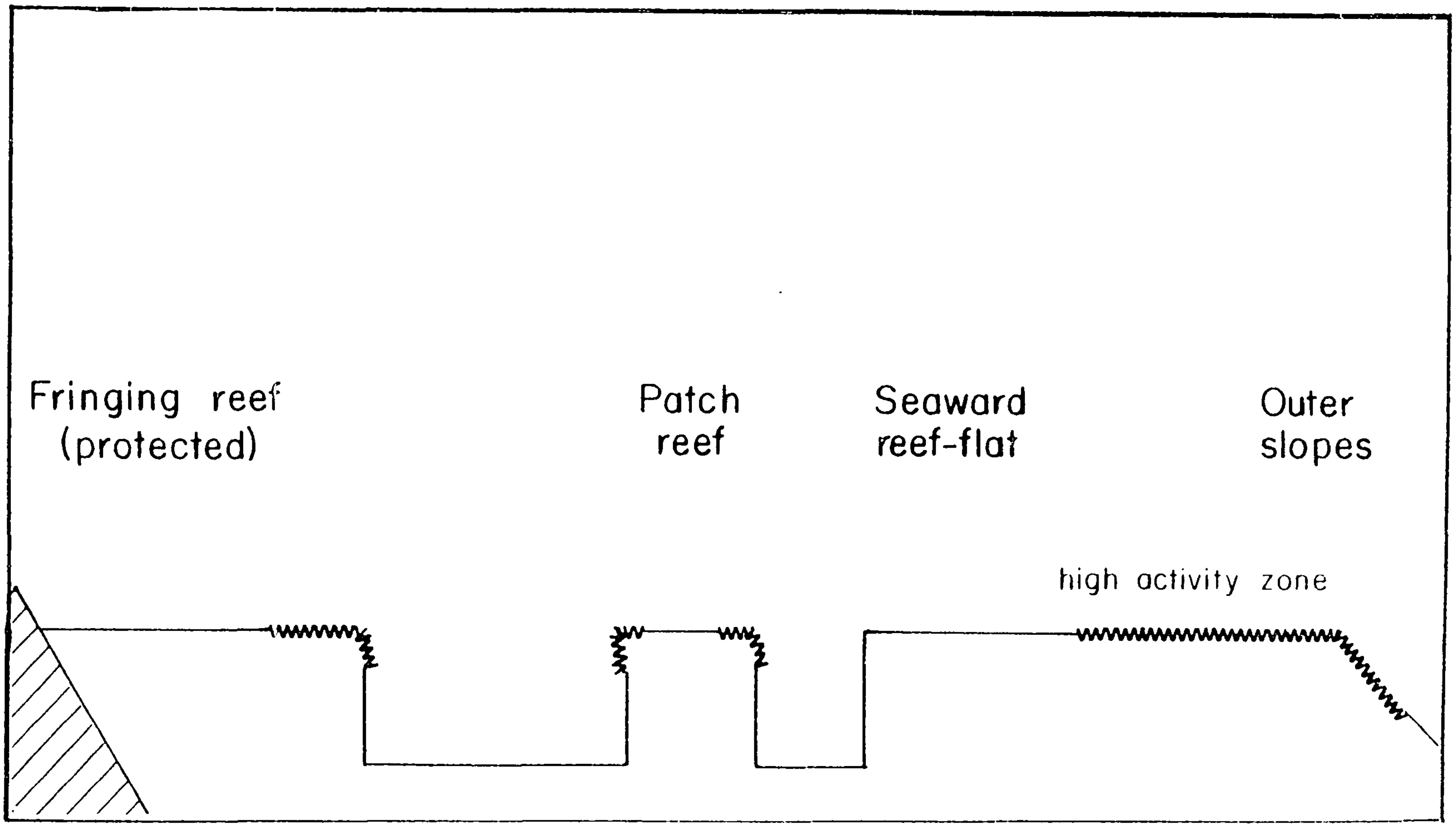
In summary, reef perimeter zones are the major source (interzonal export) areas for both carbonates and POC in typical present-day open water reefs. The sinks for this POC and carbonates are the reef-flats immediately downstream of the outer perimeter zones, and the deeper areas of the lagoons. These sink areas constitute true sinks for carbonates in that they undergo temporally significant stratigraphic accumulation. They are sinks for POC only in the sense that they receive the excess production of the outer perimeters and then respire it (or decompose it) away. It is important to stress that these sink zones also accumulate the carbonates formed, typically at lower rates, within themselves. The source status of the outer perimeters is a function of the higher levels of turbulence--i.e., physical disintegration of the more labile algae and turbulent suspension of sediments. The excess materials produced are then transported downstream (leeward) to lower energy sink areas where they are deposited.

B. BIMODALITY?

This chapter investigates and speculates on the nature of coral reef metabolism as a function of gross physiography and smaller scale morphology. It will be established that coral reef physiography and zonation can both be considered as bimodally distributed. This in turn leads to a bimodal metabolism model. However, in the final consideration, it will be established that there are additional but discrete modes to be taken into account in a steady state system. It is fair to say that more questions are raised here than are answered. However, I believe the conceptual approach to be important in the understanding of ecosystems at an operational level.

If any typical, well developed Indo-Pacific coral reef is examined on a scale of tens to hundreds of meters, it is apparent that the physiography is dominated by two levels. Simplistically these can be described as reef-flats just below the low tide level, and lagoons containing two to many meters of water (Fig. 14). The lagoons, of course, may contain quite complex patch reef or line reef structures but these in turn conform to the same basic very shallow or deep distribution of levels. The slopes within this overall structure occupy a relatively small proportion of the total area (15% in the Central Kaneohe Bay sector, Smith et al. 1978), and an appreciable contributor to this category is frequently the slopes formed by sediments prograding away from active zones on reef-flats into lagoons. Thus active, biologically producing slopes are an even smaller part of the whole system, <u>inside</u> the outer reef crest. However, the outer seaward slopes of the reef can be quite gradual and therefore may

Figure 14. Diagrammatic representation of the vertical and horizontal bimodality of coral reef morphology and zonation. The outer slope is the principal exception to this concept. The zig-zag line represents areas of appreciable metabolic activity. The straight lines represent sediment bottom. The vertical faces do have high activity over a small area but it should be stressed that the diagram has greatly exaggerated vertical scale.


Fringing reef
(protected)
Patch
reef
Seaward
reef-flat
Outer
slopes
high activity zone

represent an important exception to the simple vertical bimodality stressed for the rest of the system.

It has already been established in a number of chapters that the principal operational role for the deeper parts of the lagoon is as a sink for both excess organic production, and most of the inorganic production (sediments) of the shallow reef-flat areas and, in some cases, the slopes. If the other physiographically dominant area, the reef-flat, is considered further and still on a scale of tens to hundreds of meters, it can readily be seen that there is usually a further bimodal distribution to be considered (Fig. 14). This horizontal distribution is between the ubiquitous active perimeter zone, and the sand and rubble flat usually but not always leeward of the active zone. From the air the boundary between these two zones is always very distinct.

If the active perimeter zones are considered on a smaller scale of meters or less, their uniform operational role in the reef system (stressed in all previous chapters) seems to be little supported by the very great variability evident in their biological makeup. The perimeter community can be anything from almost smooth algal pavement (DK8 at One Tree Is.) to uniform cover with living corals (P1 at Lizard Is. and the Porites perimeters #10 and #11 in Kaneohe Bay). In these two extremes, the community is uniform and continuous and there is no apparent scope for any breakdown into further bimodal distributions. However, in the more typical case of mixed coralline algae/coral substratum on the reef-flat, there is, in some situations, a lack of morphological and biological homogeneity which requires another level of bimodality to be considered. For example, the outer zone of the Central Transect at Kaneohe Bay has a continuous cover with mixed active hard substratum. The same occurs on the outermost part of the lagoon reef perimeter (D1 outer) at Lizard Is. However, in other major perimeter reef-flats there is a distinct bimodal distribution of hard substratum active reef populations, and loose sediments. Examples of this are the main reef-flat (DK13) at One Tree Is. (35% hard substratum) and the major part of the lagoon reef-flat perimeter (D1) at Lizard Island (25% hard substratum). Should this kind of reef-flat be considered as operationally the same as the continuous kind, or should it be visualized as a progressive lagoonward attenuation of the true active perimeter?

An examination of published metabolic data, with all the preceding concepts in mind, raises some interesting possibilities. The bimodal distribution of coral reef calcification activity has been recognized by Smith and Kinsey (1976) and Smith (1978a). These papers accepted the typical reef perimeter calcification rate to be 4 $kgCaCO_3\ m^{-2}y^{-1}$ while the more extensive lagoonal systems were considered to exhibit an approximate uniformity in the range 0.5-1.0 $kgCaCO_3\ m^{-2}y^{-1}$. Similarly it was established in the Introduction (Tables 1 and 2) that primary production rates in the literature fall into two general groupings: high rates determined for shallow reef-flats or fringing reefs (P = approximately 7-9 $gC\ m^{-2}d^{-1}$); and low rates determined for total or dominantly lagoonal systems (P = approximately 2-6 $gC\ m^{-2}d^{-1}$). However, at the level of discrimination allowed by the information available in these published papers, the production data could hardly be classified as neatly bimodal.

The One Tree Is. metabolic findings were summarized in Table 16. On superficial examination there is little to support any concept of simple bimodality in this reef system. The major sediment and organic sink areas, DK17 and DK23, do exhibit some uniformity with P approximately 1 gC $m^{-2}d^{-1}$ and G approximately 0.5 kgCaCO$_3$ $m^{-2}y^{-1}$. An upper limit is set by the extensive reef-flat coral zone, DK13, with P = 7.2 and G = 4.6. However, the lagoon area of reticulated reefs falls intermediate between these limits (P = 3.1, G = 1.5), and the algal pavement, DK8, is inconsistent with any of the preceding categories with a high calcification (G = 4.0) but relatively low production rate (P = 2.0). It was previously noted that the reef-flat coral zone exhibited a bimodal distribution of substratum types (35% hard, active substratum; 65% sand and rubble). If the metabolism of this zone is considered in finer detail by isolating its components from one another, it can be seen (Table 47a,b) that the metabolism is also bimodally distributed. This finding is not particularly surprising, but it is interesting to see that the outcrops exhibit more than 10 times the activity of the sand and rubble. If the average data for the sand and rubble (Table 47b) are assumed to apply to 65% of the total area at DK13, it can readily be calculated that the hard substratum must have a metabolism of P = 19 and G = 12 (Table 47c). This is in reasonable agreement with the directly measured P = 14, G = 9 (Table 47a) for specific coral outcrops. Any discrepancy is probably a function of inaccuracy in estimating percent cover.

Table 47

Community Metabolism of Some Discrete Environments at One Tree Island

(a) Coral Outcrops* Isolated by Plastic Fences

Dominant Species	P ($gC\ m^{-2}d^{-1}$)	-R ($gC\ m^{-2}d^{-1}$)	P/R	G ($kgCaCO_3\ m^{-2}y^{-1}$)	No. of Estim. (n)
Leptoria phrygia	8	9	0.9		5
Acropora pulchra	18	15	1.2		6
Porites andrewsi	14	13	1.1	7‡	10
Pocillopora damicornis				10‡	8
Mixed secondary growth	16	11	1.5		4
Mean	14	12	1.2	9	

(b) Sand and Rubble Unconsolidated Sediment Areas**

Site	P ($gC\ m^{-2}d^{-1}$)	-R ($gC\ m^{-2}d^{-1}$)	P/R	G ($kgCaCO_3\ m^{-2}y^{-1}$)	No. of Estim. (n)
Between outcrops at DK13 (plastic fence, 1968)	0.3	1.6	0.2	0.5	3
Between outcrops at DK13 (plastic fence, 1975)	1.0	1.5	0.7	1.0	4
DK17 sand flat (unfenced)	0.9	1.4	0.6	0.3	5
Mean	0.7	1.5	0.5	0.6	

(c) Calculation of Hard Substratum Activity in Coral Zones at One Tree Island (assuming mean values for sand/rubble as given above, and zonal activities as given in Table 16)

Zone	P ($gC\ m^{-2}d^{-1}$)	-R ($gC\ m^{-2}d^{-1}$)	P/R	G ($kgCaCO_3\ m^{-2}y^{-1}$)	% of Zonal Area
Reef-flat coral zone (DK13)	19	18	1.1	12	35
Lagoon reticulum (DK22)	24	18	1.3	10	10

* These formations were all in the coral zone of the seaward reef-flat, near DK13. Formations were 1-5 m across and 0.8 m high, on a sand/rubble bottom.

** 0.4-0.8 m deep at low tide.

‡ Data from Kinsey (1978).

If the other coral dominated zone, DK22 in the lagoon, is considered on the same basis (Table 47c), and assuming the 90% sand bottom to be reasonably equivalent in activity to that estimated in the shallow reef-flat areas, it can be seen that the hard substratum is almost identical at P = 24, G = 10 to that on the reef-flat. Thus the major part of the reef system at One Tree Is. <u>does</u> exhibit a bimodal distribution of metabolism (essentially a function of biomass distribution) regardless of depth and on the basis:

Sand and rubble bottom: $P = 1 \text{ gC m}^{-2}\text{d}^{-1}$, $G = 0.5 \text{ kgCaCO}_3 \text{ m}^{-2}\text{y}^{-1}$

Coral/algal formations: $P = 20 \text{ gC m}^{-2}\text{d}^{-1}$, $G = 10 \text{ kgCaCO}_3 \text{ m}^{-2}\text{y}^{-1}$

The first of the categories includes the shallow sand flats (DK17) and the deep lagoon (DK23) as well as the sediment bottom component of the higher activity areas. The second category covers the activity of all coral/algal hard substratum whether it represents a low percentage of the total area (10% at DK22) or a relatively high percentage of the area (35% at DK13). Thus the remaining exception to the bimodal distribution of metabolism at One Tree Is. is the algal pavement which is not bimodally distributed within itself and has a metabolism of P = 2, G = 4. The outer slopes, of course, remain undefined for this system.

Two overall conclusions seem indicated on the basis of the One Tree is. data. Firstly, it may be better to consider metabolism as trimodally distributed between: sand and rubble bottom; pavement areas; discrete coral/algal outcrops. Secondly, the clear bimodal vertical distribution of reef physiography is not reflected in metabolism distribution, as both shallow and deep sediment bottom serve approximately the same metabolic role.

If we now consider whether other reef systems conform to this kind of simplification, it can be seen from Table 29b that Lizard Is. really lacks any simple unconsolidated shallow sand and rubble areas. The sediments from the seaward reef-flat drop directly into the deep lagoon, and the lagoon reef-flat is already totally filled back to the leeward reefs allowing stabilization by sea grasses and foliose algae (see Chapter 1B). Thus the only extensive loose sediment bottom is in the lagoon, and unfortunately metabolism data are not available for this area. There is no elaborate bimodally distributed lagoon reef structure at Lizard Island. There is simply a lagoon, and two major reef-flats. However, on much of the reef-flats there certainly is a bimodal distribution of hard bottom and sediment bottom. A representative portion of loose sand and rubble bottom has been isolated and its metabolism determined (Table 48a). It is a little more active (P = 1.5, G = 0.8) than the equivalent areas at One Tree Is. If these values are used to allow the determination of the activity of the discrete hard substratum outcrops in the reef-flats, it can be seen (Table 48b) that the results are very similar to those obtained at One Tree Is. The agreement is more marked for calcification (G = 10) than for production (P = 17-37).

If the Lizard Is. sand/rubble metabolism values are used to calculate the possible hard substratum metabolism for the small heads on the sand zone at Kaneohe Bay Central transect (Table 48b), it can be seen that they also may conform to the uniform P = 20, G = 10 pattern.

Table 48

Community Metabolism of Some Discrete Environments
at Lizard Island and on the Central Transect, Kaneohe Bay

(a) Sand and Rubble Unconsolidated Sediment Areas near Transect A, Lizard Island (plastic fence)

	P	-R	P/R	G	No. of Estim. (n)
	(gC $m^{-2}d^{-1}$)			(kgCaCO$_3$ $m^{-2}y^{-1}$)	
	1.5	1.3	1.2	0.8	17

(b) Calculation of Hard Substratum Activity in Coral/Algal Zones (assuming values for sand/rubble as given above, and zonal activities as given in Tables 29b and 39)

Zone	P	-R	P/R	G	% of Zonal Area
Lizard Is. seaward reef-flat coral/algal zone (A2)	17	20	0.9	10	40
Lizard Is. lagoon reef-flat coral/algal zone (D1)	24	19	1.3	10	25
Lizard Is. lagoon reef-flat small heads (D2)	37	43	0.9	10	10
Kaneohe Bay Central sand flat with small heads	25	23	1.1	9	5

What then of the narrow perimeter "edge" zones where there is 100% cover by the same kinds of communities represented in the bimodally distributed reef-flats? Can the very high P = 20, G = 10 type of metabolism be maintained at the level of 100% cover? Results for such areas are given in Table 49a. It seems there is little consistency. As has been stressed in Chapter 1C, the narrow (52 m) "coral" zone of the Central reef-flat with its 100% hard substratum cover does have elevated metabolic rates. In fact, the calcification is as high as the rates calculated in Tables 47 and 48 for 100% outcrops. However, the continuous substratum does not seem to be able to maintain the elevated primary production of the discrete outcrops (P = 8 rather than 20). The other small scale edge zones of 100% coral cover in Kaneohe Bay are also calcifying at the elevated G = 10 rate. All of these elevated rates were previously attributed to scale alone (Chapter 1C). Unfortunately, the consistency of the Kaneohe Bay findings for areas of 100% cover, with the calcification rates in Tables 47 and 48 for discrete outcrops, is not supported by the other two values in Table 49a for areas of 100% cover at Lizard Is. The similarly small scale outer margin (D1 outer, 42 m wide) of the lagoon reef-flat at Lizard Is. exhibits elevated production, but only rather conventional calcification (G = 5). The 100% coral cover on the somewhat more extensive seaward pinnacle (P1, 90 m wide) also fails to achieve the higher rates (P = 9, G = 4). Thus it seems the standard of performance for the continuous hard active substratum edges to lagoonal formations does not conform precisely to either the <u>overall</u> performance of the remainder of the reef-flat <u>or</u> to the performance

Table 49

Community Metabolism of Reef Perimeters and Narrow Edge Zones with 100% Cover (data from chapters in Section 1)

Zone	P	-R	P/R	G
	($gC\ m^{-2}d^{-1}$)			($kgCaCO_3\ m^{-2}y^{-1}$)
(a) Reef edges or pinnacles with 100% coral/algal cover				
Lizard Is. lagoon reef-flat outer edge (D1 outer)*	14	12	1.2	5
Lizard Is. seaward pinnacle (P1)	9	6	1.7	4
Kaneohe Bay Central "coral" zone	8	10	0.8	9
Kaneohe Bay patch reef with *Porites* (#10)				10**
Kaneohe Bay patch reef with *Porites* (#11)				12**
(b) Seaward reef perimeter algal pavements with 100% cover				
One Tree Is. (DK8)	2	0.5		4
Lizard Is. (A1)	7	7		2.5
Johnston Is. (#6)				4
Kaneohe Bay *Porolithon* cover (#10)				5**

* New data based on n = 9 observations.

** These values are all based on daytime data only.

of the discrete formations represented as the hard substratum on the remainder of the reef-flat. Such narrow "edge" areas may need to be nominated as a fourth category in the operational distribution of metabolism. The other three suggested earlier were: sand and rubble bottom; pavement areas; discrete coral/algal outcrops.

The other 100% cover areas, found only in high energy seaward reef perimeters, are algal pavements (already considered in relation to One Tree Is.). The few data available for such areas are also given in Table 49. A fair level of inconsistency again is apparent. However, there is no very high calcification here, and the two primary production values are low relative to those for the high coral-cover areas in the same table. Pavement environments have already been nominated as an operational category in metabolism distribution.

The only remaining reef environment not mentioned in this consideration of the distribution of metabolic types is the foliose algal or sea grass flats. These represent the ultimate colonization of stabilized sediment sheets in shallow water. All such flats considered in this dissertation exhibit near zero calcification and they have been treated as discretely different to other reef environments because of their failure to meet the criterion $c_d/p_{max} > 11\%$ postulated in Chapter 1C. These algal/sea grass flats should therefore be nominated as a possible fifth category in metabolism distribution. Unfortunately, sea grass beds may be sites for considerable epibiont calcification in some reef systems (Land 1970; Patriquin 1972). It is therefore possible that the status of this category, in considering the modal distribution of reef metabolism, may be complex.

There is little doubt that the concept of a disjunct distribution of metabolism is sound, but there are many complications in applying it. The physical separation of the reef into both vertical (reef-flat or lagoon) and horizontal (perimeter structure or sediment area) bimodal distributions is obvious. It also seems that the vertical physiographic bimodality is not mirrored by any direct equivalent in the distribution of metabolism, except to the extent that elevated metabolism is always at the shallow depth (almost certainly less than 5 m; Smith and Harrison 1977). In considering the metabolism of these various morphological entities it seems necessary to acknowledge at least three and possibly four specific categories (Table 50), together with the nebulous additional category of the algal/sea grass flats. These several specific categories can be generalized to a simple bimodal distribution (Table 50) only in the broadest sense. Thus the Smith-Kinsey (1976) concept of a reef perimeter calcification rate approximating 4 $kgCaCO_3\ m^{-2}y^{-1}$ represents the upper category in that broad generalization. More correctly, it seems that there are two dominant categories for hard substratum performance. The first applies to the coral/algal outcrops themselves with a primary production approaching 10-20 $gC\ m^{-2}d^{-1}$ and a calcification rate of a consistent 10 $kgCaCO_3\ m^{-2}y^{-1}$. (It is interesting that a 10 kg rate was postulated by Chave et al. (1972) for potential carbonate production by areas of reefs covered with calcifying communities.) This category includes the coral/algal substratum portion of present-day reef-flats and, much more significantly, may well have applied over extensive areas during the Holocene sea level rise when a slightly greater

Table 50

Proposed Modes for Coral Reef Metabolism
(each category refers to 100% cover)

	Mode	P ($gC\ m^{-2}d^{-1}$)	G ($kgCaCO_3\ m^{-2}y^{-1}$)
1(a).	Coral/algal cover as discrete heads, or continuous where adequate water available	20	10
1(b).	Coral/algal cover with limited water available	10	6
1(c).	Algal pavement	5	4
2.	Sand/rubble	1	0.5

_or_, generalized:

1.	Reef-flats and all extensive, present-day perimeter zones	5-10	3-5
2.	Sand/rubble	1	0.5

Notes:

The outer reef slopes should perform as per the relevant category down to about 5 m. Below that depth, progressive attenuation occurs.

All lagoonal systems should be compounded, on an areal basis, from the above modes.

An additional non-specific mode for algal/sea grass beds should really be considered. See text for discussion of this type of reef environment.

1(a), 1(b) and 1(c) modes are included in the generalized reef-flat mode 1, but 1(a) and 1(b) are only ever a component of the whole--i.e., an extensive present-day reef-flat will never have overall metabolic rates as high as P = 20 or P = 10, and G = 10 or G = 6.

degree of inundation presumably allowed 100% cover by such communities (NB Johnston Is. site #5 today!). The only common equivalent to this 100% coral/algal cover situation today is the small scale edge communities in protected reefs where the full rates are not achieved (<u>at least during the low tide conditions used for monitoring</u>) presumably because of inadequate water availability to the crowded community. The second category of hard substratum performance applies to the algal pavements with a primary production of very approximately 5 gC $m^{-2}d^{-1}$ and a calcification of 4 kg$CaCO_3$ $m^{-2}y^{-1}$. This type of community only occurs at or near sea level and therefore was not a feature of many reefs during the rapid sea level rise.

Thus the typical 4 kg y^{-1} rate of Pacific reef margins, stressed by Smith and Kinsey (1976) as having probable relevance throughout the Holocene, is probably a feature entirely of surface reefs--i.e., either algal platforms, or the "steady-state" reef-flats at sea level which are a bimodal attenuation of the inherently higher 10 kg y^{-1} rate mediated by a limiting degree of inundation. This conclusion in turn suggests that higher rates may have applied over large areas on many reefs during much of the Holocene (in contradiction of Smith and Kinsey 1976; and Davies and Kinsey 1977). Higher rates are likely to have been most marked in reefs growing off Karst surfaces situated 15 m or more below present-day sea level, as water depth over the growing reef probably exceeded 1 m for much of the Holocene (using modified sea level/platform relationships based on reasoning of Davies and Kinsey 1977). In keeping with the recent ideas of Adey (1978), it seems that we should acknowledge two basic operational modes for coral reef perimeter calcification: 10 kg y^{-1} for low or moderate energy perimeters with adequate water cover, and 4 kg y^{-1} for high energy seaward margins at sea level (i.e., algal pavements).

Notwithstanding the concepts of absolute modality hypothesized above, it is still reasonable to propose a present-day standing-sea-level operational bimodality in coral reef performance of:
1) extensive reef-flats and perimeter zones, $P = 5\text{-}10$, $G = 3\text{-}5$;
and 2) sand/rubble areas, $P = 1$, $G = 0.5$.

C. THE FINER CONCEPTS OF ZONATION

The zonation of coral reef metabolism has been a major feature of every chapter in the Results and Discussion section. It is not, therefore, the intention of this chapter to reiterate that concept in detail. However, it is desirable to summarize the major features of metabolism zonation:

1. The highest levels of activity, by a factor of 5-10, are associated with reef perimeters (Table 50).
2. The outermost sections of the perimeters play a major source role for organics (detritus export to the lagoon) and inorganics (sediment export to crest and lagoon). The narrow band of outer slopes down to 5 m is the principal component of this category.
3. The major perimeter area, the reef-flat, is in approximate autotrophic balance and may exhibit a small net export or import of organics. It always must export sediments under present conditions of standing sea level.
4. Dependent on the physical energy level of the environment, there may be an algal pavement between the slopes and the coral/algal reef-flat. This pavement is also a major source area, where it occurs.
5. There is a very great variation in the biotic composition which can occur in a perimeter zone, regardless of clear trends to operational consistency (as above; see also Chapter 2E).

6. Perimeter areas may exhibit an approximately homogeneous (unimodal) community or a heterogeneous (bimodal) community.
7. Perimeter areas exhibit abrupt leeward termination. However, a bimodal reef-flat community may exhibit some attenuation (i.e., increased percent sediment bottom) before its eventual cut-off (cf One Tree Is. main reef-flat; Transect D at Lizard Is.).
8. The concept of high-activity perimeters applies on essentially all scales from small lagoon patch reefs, to the overall reef perimeter.
9. Behind all perimeter zones is a low activity sediment area with a dominant sink role. If this zone becomes sufficiently wide, and is shallow enough, it may eventually stabilize and develop algal and/or seagrass communities.

It was established (Chapter 2B) that the upper limit for reef activity, on the scales considered by me, is probably $P = 20$ gC $m^{-2}d^{-1}$, and $G = 10$ kgCaCO$_3$ $m^{-2}y^{-1}$. These rates appear to reflect the activity associated with the maximum standing crop of coral reef biota which can be physically fitted onto any area at photosynthetically optimum depths of less than 5 meters. It was suggested that this level of activity was uncommon, on an areally extensive basis, in modern reefs because of the limiting depth of water over most present-day reef-flats. This limitation had resulted in the attenuation of the high activity by a bimodal distribution of such substratum with low activity sediment areas. However, while it may be true that water availability limits reef-flat activity, it is nevertheless also true that the most extensive area of elevated activity is the reef-flat. The factor controlling the lateral extent of such elevated activity is likely to be either the attenuation of some nutrient or food resource within the water, or the loss of a physical property (e.g., turbulence) in the water moving leeward across the shallows. It might be expected that such an effect would result in a progressive attenuation of reef-flat metabolism rather than an abrupt cut-off. However, it has been pointed out already that this is only partially true. If the lateral extent of the high activity zone of the reef-flat is a function of the attenuation of some water property, then it should be true that such zones were more extensive during the main phase of Holocene reef development (9000 BP - 4000 BP, Davies and Kinsey 1977) when there would always have been somewhat greater depth over the reef-flat caused by a rapidly rising sea level. At One Tree Is. there is fairly good evidence that this was true, as there are old reef-flat formations behind the present active zone, but currently buried in the prograding sand sheet. This in-filling does not simply reflect seaward growth of the reef-flat, as accretion in this direction has been virtually negligible over the same period (Davies and Kinsey 1977).

If the depletion of a nutrient or oceanic plankton were the factor determining the ability of the incoming water to support reef-flat activity, then it would be reasonable to expect little or no activity in at least those areas of the lagoon immediately in the path of water which has come across the reef-flat. This deficiency clearly is not found, as very well developed back-reef formations and patch reefs occur behind the majority of reef-flats, provided the water is sufficiently shallow to allow their growth. Such development is clearly the case at One Tree Is., though the interpretation is more complex at both Lizard and Johnston Islands because of the possibility of "unused" water impinging directly on the lagoon reefs. On the other hand, Kaneohe Bay has ample organic and inorganic nutrients in the water at any part of the Central area (Smith et al. 1978). Nevertheless, there is only a very narrow zone of high activity. Trophic depletion therefore seems an unlikely mechanism for the control of reef-flat width.

Just as the physical regime determines the shallow water bimodal metabolic compromise across the reef-flats and the presence or absence of an algal pavement, it seems almost certain that it also determines the lateral extent of the perimeter high activity zone. The probability of water motion as the factor controlling reef zonation was suggested by Sargent and Austin (1954).

What do we know of the actual widths of high activity reef perimeters? Table 51 lists a few widths from the literature for identified high activity zones of Pacific seaward (windward) reef-flats both on fringing reefs of high islands, and on open oceanic reefs. It is striking that all lie between 300-500 m except that for Elizabeth Reef which is at a very limiting latitude (30° S). It is equally striking in the literature and by observation that there appear to be no lagoon reefs, patch reefs, or protected fringing reefs and few leeward reef-flat perimeters as wide as 300-500 m. In fact, the width of the active perimeters in these protected formations seems to bear a strong relationship to the open water fetch in the windward direction. In One

Table 51

The Widths of High Activity Seaward Reef-Flats (m)

Reference	Location	Fringing Reefs	Open Water Reefs
Johannes et al. 1972	Enewetak II		340
	Enewetak III		280*
Odum and Odum 1955	Enewetak		455
Sargent and Austin 1954	Rongelap		300
Jaubert et al. 1976	Moorea	400	
Kohn and Helfrich 1957	Kauai	430	
Salvat et al. 1977	Fiji	350	
Slater and Phipps 1977	Elizabeth Reef		220**
Hopley 1977	Carter Reef		350
Kinsey 1972	One Tree Is.		370
LIMER Team 1976	Lizard Is.		450

* Present-day reef-flat is algal only.

** This reef is located near the absolute limit for reef growth at 30° S.

Tree Is. lagoon, and behind the barrier reef in Kaneohe Bay, there are patch reefs within the first 100 m of open water. These both have perimeter zones of only 2-10 m. This situation also occurs throughout the reticulum at One Tree Is. and also the reticulum at Johnston Is. where, in both cases, the fetch is typically 50-100 m between formations. Where there is a longer fetch of say 1000 m, the perimeter is considerably wider: 42 m (D1 outer) at Lizard Is., and 52 m (Central "coral" zone) at Kaneohe Bay. Of course it is questionable whether D1 outer is really the active zone proper, or whether the whole of D1 (270 m) should be included. At this stage it seems sufficient that it be demonstrated that it is substantially less than a seaward reef-flat in the same geographical location.

There are two seaward reef-flats referred to already in this dissertation which should be explained further in the present context. The Kaneohe Bay barrier reef has already been described as largely a relict dune structure. Hence its vague zonation can be rationalized. However, if the complete pavement areas (K2) are considered to be the most reasonable equivalent to a high activity zone, then it still conforms to the 400 m concept. The other reef-flat requiring explanation is the algal pavement at Johnston Is. This area is 150 m across, giving way directly to the back-reef area of relatively unique anastomosing pinnacles. Either one can use the argument that this is a leeward reef-flat and therefore 150 m is reasonable (it <u>is</u> on the lee side, but has been considered operationally as a windward flat), or alternatively one can claim the peculiar pinnacles area to be a deep reef-flat (250 m wide) in which case the total width is 400 m.

The latter explanation is probably the more satisfactory in view of the basic premise that this reef represents an equivalent to a mid-Holocene reef still catching up with the rising sea level--i.e., the outer pavement has already formed at sea level, probably because of a more elevated ancient karst growth platform, whereas the incipient reef-flat is still growing up towards its eventual level.

If the hypothesis is accepted that fetch (average wave height) determines the width of the high activity zone of any reef perimeter, and that 300-500 m seems to be the maximum width achieved on a fully developed present-day reef, then what is the mechanism of this control? It seems sufficient to invoke "self-burial" as the principal if not only mechanism. That is, if the productive zone were to be any wider, its production of carbonates (sediments) would exceed the ability of the water flow to carry that production in turbulent suspension. Similarly, it seems reasonable that somewhat wider reef-flats may have been possible with the slightly greater water depth over most mid-Holocene reef-flats (consider earlier comments on One Tree Is. reef-flat). The greater width would be encouraged both by more extensive penetration of wave action across the reef-flats and by the increased capacity of the deeper water column to carry suspended sediments.

Davies (1977) and Kinsey and Davies (1979) established that the water flowing over Transect A at Lizard Is. held in suspension between 0.5 and 2.5 g sediment m^{-3}. This was measured over a range of conditions varying from 20 knot wind to zero wind and included all tidal states and water flow rates from 3 cm s^{-1} to 20 cm s^{-1}.

Storm conditions were not studied, though obviously these are the conditions under which larger pieces of reef framework are redistributed. It was estimated that average conditions were capable of removing from the reef-flat 5 kg $CaCO_3$ d^{-1} from a transect 1 m wide. The current on this reef is virtually always normal to the reef-flat alignment. It can easily be determined that this removal rate is equivalent to the total carbonate production of a high activity reef-flat 500 m wide producing at the average rate of Transect A (3.6 kg $m^{-2}y^{-1}$; Table 29b), or 450 m wide producing at the typical general rate of 4 kg $m^{-2}y^{-1}$. Thus it seems reasonable to postulate that sediment removal provides a very rational explanation for the approximately 400 m width of the high activity zone of present-day seaward (windward) reef-flats. Any wider development than this would result in a net accumulation of carbonates within the zone. This situation could not long be tolerated under conditions of a stable sea level and a fully developed (surface) reef. I acknowledge that this hypothesis is based on very inadequate data for sediment transport, but it seems highly relevant as an explanation for the consistent relationship between perimeter width and fetch. In principal, I see no reason why the same general hypothesis should not be put forward for explaining the widths of even the very narrow lagoonal patch reef perimeters.

Overall, the physical energy regime has been invoked, albeit highly speculatively, as determining the presence or absence of an algal pavement, the proportional interaction of the various modes of coral reef metabolism (Table 50) to give the zonation of a reef, and the width of the resulting zones.

D. SEASONALITY

In each of the three main results chapters, seasonality was presented in detail for reef-flat "coral" zones. This chapter will summarize the findings of those data and discuss some of the causative factors.

It is reasonable to expect that the seasonal trends may be different in other zones, particularly those more dominated by algae. However, because the available data are generally less precise, I have decided to omit any discussion of these statistically indefinite findings.

Table 52 lists most of the seasonal ratios and other comparisons made in the individual chapters of Section 1. It is obvious that each site experiences a seasonal range of temperature. One Tree Is. and Lizard Is. have temperature extremes in the longest and shortest months (Dec. and June). Kaneohe Bay on the other hand has a temperature cycle 2-3 months out of phase (later) with the solar seasons. The extremes in <u>hourly</u> metabolic rates coincide with the temperature extremes for the two moderate temperature sites, Lizard Is. and Kaneohe Bay. On the other hand, One Tree Is. does not achieve its maximum hourly rates until well into fall even though the minimum rates do coincide with the minimum winter temperatures. This asymetry is attributed (Chapter 1A) to the probably destructive influence of the low winter temperatures which are hypothesized to be the cause of the visually obvious reduction in the standing crop of the labile component of the primary producers (foliose algae). A full recovery does not occur until late summer/early fall.

Table 52

Summary of Seasonal Trends for Metabolic Parameters at the Three Major Sites--Reef-Flat Coral Zones

	One Tree Is.	Lizard Is.	Kaneohe Bay
Latitude	23°30'S	14°40'S	21°30'N
Temperature (°C)			
lowest (month)	18-22 (Jun)	24-26 (Jun)	22-24 (Feb)
highest (month)	25-33 (Dec)	28-29 (Dec)	27-28 (Sept)
Month of extremes in hourly metabolism			
lowest (L)	June	June	Jan/Feb
highest (H)	March	Dec	Aug/Sept
Ratio L/H			
P_{max}	0.5	0.5	0.6
r	0.6	0.3	0.4
c_d	1.0	0.7	0.8
r/P_{max}			
L	0.5	0.4	0.4
H	0.4	0.5	0.6
c_d/P_{max}			
L	0.4	0.2	0.4
H	0.2	0.1	0.2
E (g C $m^{-2}d^{-1}$)			
winter (month)	-1.7 (Jun)	0.3 (Jun)	-1.0 (Jan) (Feb)
summer (month)	1.1 (Dec)	-2.1 (Dec)	-4.1 (Aug) (Sept)

Each of the three sites experiences a twofold (Table 52, L/H = 0.5) range of p_{max} through the year. The seasonal range of r is least at One Tree Is. (L/H = 0.6) and is greatest at Lizard Is. (L/H = 0.3). This latitudinally inverse trend is somewhat consistent with the concept of the damaging influence of low winter temperatures at One Tree Is., as any labile algae killed by low temperature will decompose leading to an elevation in r, offsetting the normally reduced r in winter. Hourly calcification is only marginally seasonal and strangely the least seasonality is again at One Tree Is. The only suggestion which is offered in explanation is that One Tree Is. has a much higher proportional content of corals in the total calcifiers in the "coral" zone than the other two sites. Perhaps the encrusting red algae which are most dominant at the other two sites are also more seasonal in their metabolism than corals.

Considering seasonal trends in the relationship r/p_{max}, it can be seen that again (and inevitably) One Tree Is. is the inconsistent member of the group in having a decreased proportional respiration in the high activity period whereas the other two sites exhibit an increase. This trend implies a more dominant autotrophic mode in the summer at One Tree Is. and in the winter at Lizard Is. and Kaneohe Bay. Most, if not all, of the seasonal variation in this ratio is assumed to reflect standing crop changes in the filamentous and foliose algae (Chapters 1A,B,C and 2A).

When the hourly rates are integrated to give diel metabolism, the day length factor is taken into account. It can be seen in Table 14 that the effect of day length at One Tree Is. is to shift the period of maximum activity close to the true mid-summer period. Lizard Is. of course is uncomplicated in that its hourly maxima and minima already are coincident with longest and shortest days. Kaneohe Bay, by contrast, is so much out of phase with day length that the months of its diel maxima and minima are not shifted appreciably from the periods of the hourly rate extremes (Fig. 11). The overall seasonality in hourly rates are summarized effectively by considering the seasonality in E. It can be seen that One Tree Is. suffers considerable net losses over each day in the winter (E = -1.7). This "loss" is presumed to indicate decomposition of the standing crop of labile algae. The winter reduction in standing crop is replaced by a summer bloom (E = 1.1). By contrast, Lizard Is. experiences a winter bloom with an apparent decay of the excess standing crop in summer. The summer/winter difference of 2.4 (0.3 + 2.1) is close to that at One Tree Is. (2.8). The fact that both summer and winter values are somewhat more negative at Lizard Is. indicates only a slightly greater import of particulate organics to the Lizard Is. transect (see Chapter 2A). Kaneohe Central "coral" zone has distinctly negative values for E throughout the year, reflecting the substantial import of organics to this reef-flat. However, in common with Lizard Is. there is every suggestion of a winter bloom on the Kaneohe Bay site also, followed by a summer decay of the excess (i.e., -4.1 is much more negative than -1.0). The summer/winter difference is 3.1 which is quite similar to the 2.8 and 2.4 found at the other two sites.

In view of the latitudinal and temperature differences between these three sites, it seems reasonable to postulate that the majority of reefs will exhibit pronounced seasonality of organic metabolic functions though calcification will probably prove to be only marginally seasonal. It has been previously suggested (Kinsey 1977) that the general aspects of seasonality seem more closely related to the seasonal light regime than to temperature regime. However, there is a complex set of potential seasonality controlling factors--viz light intensity; day length; annual temperature cycle; diurnal temperature extremes, etc. The data reported here allow only speculation about relative importance. At the more specific level, there seems to be an annual cycle in some component(s) of the standing crop which involves a buildup and a decay but this cycle can occur with a maximum at probably any time of the year. Extremes of temperature are invoked as the probable determinant of this cycle.

In conclusion, it is clear that all metabolic studies require data collection throughout the year to give rise to reliable overall conclusions. Where a short term expeditionary approach is necessary, it has been found most satisfactory to use the spring period. Winter and summer represent extremes, and fall is usually a period of rather abrupt transition.

E. THE "STANDARD REEF"

Throughout this dissertation considerable attention has been given to the notion of uniformity of community metabolism, zonation and other broad operational parameters of coral reefs, regardless of the acknowledged extreme variability in community structure, latitude, and temperature regime. In the chapter on bimodality (2B), it was concluded that there were probably three basic levels of performance for reef systems, with a fourth which most likely constituted a present-day limiting case of one of the other three (Table 50), and even a fifth if sea grass/algal flats were included in the reef system. However, it was also noted, at a more generalized but operationally satisfactory level, that modern fully developed (surface reefs in tectonically stable environments) Pacific reefs could probably be considered as exhibiting two modes of metabolic performance over any extensive areas. The first of these was the metabolic rate of the active reef-flats (including lagoon patch reef perimeters) and was generalized to $P = 5\text{-}10$ gC $m^{-2}d^{-1}$ and $G = 3\text{-}5$ kg$CaCO_3$ $m^{-2}y^{-1}$. The second was the metabolic rate of all sediment zones, both lagoon bottom and shallow reef-flat types. Here the activity was suggested as being an order of magnitude lower. Outer reef slopes were considered to conform very crudely to the first category, while stabilized sea grass/algae beds were not included in the detailed assessment as they were not a consistent feature of the reefs examined.

How variable are the generalized modes of reef metabolism in typical unperturbed reefs? Is there a standard of reef performance, departure from which can be taken as indicative of perturbation of some kind? Table 53 summarizes all those metabolic studies in the literature including the present study, where one can confidently claim that the reef-flat reported conforms to the concept of a fully developed (at or near present-day low tide level), areally extensive (at least 100 m across), high activity, perimeter zone of the coral/algal kind. It does not include transects of "homogeneous" algal pavement (mode 1(c) in Table 50) or the very narrow (2-50 m) bands of heavy cover which may occur on the edges of many lagoonal patch reefs, unless they are included as part of larger high activity systems (e.g., D1 at Lizard Is. includes the D1 outer band). Studies such as those of Odum and Odum (1955), Sargent and Austin (1949), and Ramachanadran Nair and Gopinadha Pillai (1972) which are based on inadequate or doubtful data also have not been included in Table 53. It is apparent that the biotically heterogeneous, generally bimodally distributed reef-flats do exhibit a remarkably uniform "standard" of performance, seemingly regardless of where they are (at least in the Pacific Ocean). This is strong support for the generalized concept of bimodality (Table 50). It seems reasonable to propose that reef-flats will conform to an even tighter standard than that recommended in Table 50, if outer slopes and algal pavements are excluded.

The proposed "standard" reef-flat is:

$$P = 7 \pm 1 \qquad P/R = 1 \pm 0.1 \qquad G = 4 \pm 1$$

Because such reef-flats are by far the most easily monitored area on any reef, the "standard" provides an excellent basis for checking for the effects of stresses and perturbations. It seems inevitable that

Table 53

The Evidence for a "Standard" Performance for Extensive Coral/Algal Reef-Flats

		P ($gC\ m^{-2}d^{-1}$)	P/R	G ($kgCaCO_3\ m^{-2}y^{-1}$)
Enewetak II (seaward coral/algal)	Smith 1973	6.0	1	4
Kauai (seaward fringing reef)	Kohn & Helfrich* 1957	7.2	1.1	-
Guam (seaward fringing reef)	Marsh 1974*	6.6	1.0	-
Moorea (seaward fringing reef)	Sournia 1976a	7.2	0.9	-
One Tree Is. (seaward reef-flat; coral/algal)	DK13 area Table 16	7.2	1.0	4.6
Lizard Is. (seaward reef-flat; coral/algal)	Transect A2 Table 29b	7.8	0.9	4.6
Lizard Is. (lagoon reef-flat; coral/algal)	Transect D1 Table 29b	7.0	1.2	3.1
Mean		7.0	1.0	4.0
± S.D.		±0.6	±0.1	±0.7

* Values as listed vary slightly from those published because of recalculation using equivalent data handling to that in the present study.

any reasonable intereference will cause a shift in at least one of the parameters listed.

As mentioned at the beginning of this chapter, uniformity of all, or at least most, community metabolic functions seems to be a pronounced feature of comparisons made between coral reefs. The principal obstruction to detecting this uniformity seems to be that of identifying an equivalent basis for comparison in the first place. This complication is frequently aggravated by the differences between authors in defining morphological features and community structure. There is also the further complication of differences in methods, experimental philosophy, and interpretation of results. The intercomparisons made in the present study of general Pacific reefs is hopefully not subject to these problems.

Another aspect of uniformity in reef metabolism which was commented on frequently in Section 1 chapters, is the ratio of the annual average noontime hourly calcification rate to the equivalent photosynthetic rate (c_d/p_{max}). All of the values mentioned in the text of Section 1 are summarized in Table 54. It is very important in considering these values of the ratio to stress that they are all based on long term means. It was demonstrated (Table 52) that there was very great seasonal variation in this parameter (at least twofold). Regardless of more than a tenfold range in the gross photosynthetic productivity (P) of a large variety of <u>reef</u> environments (Table 54), it is evident that they conform very well to the $c_d/p_{max} = 0.1 - 0.2$ concept. There is one notable exception, the algal pavement at One Tree Is., with a value of 0.6. All data from this site have been

Table 54

Hourly Calcification Rate as a Function of Photosynthesis Rate (based on annual means)

Reef Environment	P (gC $m^{-2}d^{-1}$)	c_d/p_{max}
Algal pavements		
One Tree Is. (DK8)	2	0.60
Lizard Is. (A1)	7	0.12
100% cover coral/algal		
Lizard Is. (P1)	9	0.20
Lizard Is. (D1 outer)	14	0.12*
Kaneohe Bay (Central "coral")	8	0.22
Bimodal coral/algal		
One Tree Is. (DK13)	7	0.22
One Tree Is. (DK22)	3	0.19
Lizard Is. (A2)	8	0.16
Lizard Is. (D1)	7	0.16
Lizard Is. (D2)	5	0.14
Kaneohe Bay (Central "sand")	3	0.15
Low activity sediment		
One Tree Is. (DK17)	1	0.11
One Tree Is. (DK23)	1	0.14
"Non"-calcifying areas		
Algal flat Lizard Is. (D3)	4	0.05
Algal flat Kaneohe Bay	6	0.02

* Data based on n = 9 observations; not included in Chapter 1B but used in Table 49.

relatively inconsistent and it seems highly questionable whether at least the photosynthesis and respiration values are valid. As has been pointed out before, it seems that most reef environments, even including typical sediment zones, maintain a calcifying community fixing carbon into carbonates at a rate of at least 0.10 the rate of photosynthetic fixation. In fact, if all sea grass/algal flats are excluded, 0.11 is the lowest value obtained in this study. However, eventually the stabilization of sediment sheets reaches a point where they do become extensively colonized by foliose algae and/or sea grasses. This transition is not a gradual gradation but another example of a relatively abrupt bimodal distribution. The examples of these stabilized zones considered in this dissertation are the "non"-calcifying areas mentioned several times already. They exhibit a substantially increased primary production without any associated increase in calcification. This results in a c_d/p_{max} of 0.05 or less. This stepwise transition from a calcifying mode to a virtually non-calcifying mode is likely to be typical of many Pacific reefs but is much less likely to be a feature of the Atlantic reef-flats where such colonization is more frequently dominated by one of the main carbonate producing groups, the calcareous green algae (reviewed by Milliman 1974). Also, epibiont calcifiers associated with sea grasses may play a very significant role in Atlantic systems (Land 1970; Patriquin 1972).

There does appear to be at least a loose relationship between the value of c_d/p_{max} and the makeup of the reef community. The environments with a high content of corals seem to be consistently close to 0.2 (Lizard P1; Kaneohe Bay Central "coral"; One Tree DK13; One Tree DK22) whereas those with the lower values are associated with either a rather marginal population (One Tree DK17; One Tree DK23; Kaneohe Bay Central "sand") or areas with a high ratio of calcareous algae to corals (Lizard A and D transects generally).

In view of the consistency of the 0.1-0.2 ratio for operationally functional reef areas (those actively calcifying), it seems reasonable to propose that any reef area exhibiting a pronounced drop in this ratio, particularly to values less than 0.1, is no longer in a normal operational calcifying mode. It can be assumed either to have evolved naturally into the "non"-calcifying mode exhibited by algal/sea grass beds, or to have been subjected to a damaging perturbation. I believe the determination of this ratio will prove to be a useful diagnostic tool in examining reef performance. This application will be considered further in Chapter 3B. It is interesting to note that Canton Atoll, an almost landlocked lagoonal system in a high nutrient environment of the equatorial Pacific apparently exhibits a G/P (essentially the same as c_d/p_{max}) ratio of 0.03 (data after Smith and Jokiel 1975), indicating that this system is in non-conformity with the general hypothesis. Is it possible that some degree of stress is indicated in this case? Kinsey and Davies (1979) suggest that nutrient stress is a possible explanation for unusually low calcification at Canton Atoll.

F. DIEL CALCIFICATION CYCLES

The remaining aspect of operational performance to be discussed in this dissertation is also by far the least resolved. This chapter will do little more than summarize the various data and comments from Section 1 concerning the diurnal variability of community calcification.

That growth and therefore long term ability to calcify are functions of light in hermatypic corals has been known for a very long time. Since the detailed work begun by Goreau (1959), it has generally been acknowledged that most if not all corals have a diurnal cycle in their calcification. In their review of coral growth, Buddemeier and Kinzie (1976) stress that different coral species vary considerably in their day/night or light/dark calcification ratios, and that not all corals prefer maximum light intensity. However, it is generally accepted that the diurnal cycle includes reduced but positive rates at night. Borowitska (1977), in his review of algal calcification, indicates that most if not all calcareous algae also exhibit diurnal cycles with positive calcification at all times. On the other hand, complete reef-flat communities have been claimed to exhibit both positive nighttime rates (Smith 1973, Enewetak), and negative nighttime rates (Kinsey 1972, One Tree Is.). Specific fenced reef-flat outcrops were found (Kinsey 1973, 1978) to exhibit variable but usually zero-to-positive (very reduced) rates at night. This suggested that the negative nighttime rates found for the overall reef-flat at One Tree Is. were a feature of the sediment areas between the outcrops. However, the very low values for the isolated outcrops suggest that they also contain a substantial dissolution component, almost sufficient to offset the reduced nighttime calcification. All coral reef environments contain organisms capable of boring and dissolving carbonates. It is really the balance between the activities of the calcifiers and these "dissolvers" that is determined when the calcification activity of a reef community is estimated from alkalinity anomalies. It is probable that only the calcifiers have an appreciable diurnal cycle. What then is the typical performance to be expected from complete reef communities? Is the balance predictable as so many other operational parameters seem to be?

Table 55 summarizes all the data available in this dissertation for nighttime calcification rates, together with the corresponding day rates. This table is arranged according to approximate community structure. It is immediately obvious that there is unlikely to be any definitive answers to the above questions to be derived from the present work. Unfortunately, an appreciable number of the nighttime rates are unreliable, a deficiency which does little to help clarify the trends. However, even where values are quite reliable, there are such total contradictions as the two 100% coral cover areas where two of the largest values for c_n are found, but with opposite signs. One might rationalize this contradiction on the basis that the Johnston Is. back-reef site #5 is (as has been suggested in Chapter 2D) an actively constructional incipient reef-flat still approaching the sea surface, whereas the Lizard Is. site is fully developed. For this rationale to have relevance implies that bio-dissolution is more pronounced in surface reefs. This feature would logically aid the erosional redistribution of the carbonates formed, but I have no evidence that such

Table 55

Diel Trends in Community Calcification

Reef Environment	c_d	c_n	c_n/c_d
	(gC $m^{-2}h^{-1}$)		
Algal pavement			
One Tree Is. (DK8)	0.12	0.00*	0.0*
Lizard Is. (A1)	0.08	-0.01*	-0.1*
Areas of total coral cover			
Lizard Is. seaward pinnacle (P1)	0.18	-0.07	-0.4
Johnston Is. back-reef pinnacles (#5)	0.18	+0.09	+0.5
Coral/algal, with high percent coral			
One Tree Is. reef-flat (DK13)	0.16	-0.02	-0.1
One Tree Is. reticulum (DK22)	0.06	-0.01	-0.2
Kaneohe Bay Central "coral"	0.18	+0.07	+0.4
Johnston Is. reticulum (#1)	0.05	0.00*	0.0*
Coral/algal, with low percent coral			
Lizard Is. lagoon flat (D1 outer)	0.14	0.00*	0.0*
Lizard Is. lagoon flat (D1)	0.11	-0.02	-0.2
Lizard Is. lagoon flat (D2)	0.07	-0.02*	-0.3*
Lizard Is. reef-flat (A2)	0.12	+0.01*	+0.1*
Areas with very low population density			
One Tree Is. sand-flat (DK17)	0.01	0.00	0.0
One Tree Is. open lagoon (DK23)	0.02	0.00*	0.0*
Kaneohe Bay Central sand-flat	0.04	0.00*	0.0*

* Value of doubtful reliability; see relevant Section 1 tables.

increased dissolution is actually found. Unfortunately, the possibilities of this reasoning are defeated by the apparently totally inconsistent trends in the more "typical" coral/algal communities reported. Even looking at alternative groupings such as all reef-flats, or all seaward reef-flats, or all lagoon environments, or all deep areas, there seems no pattern.

At this stage in our knowledge of community metabolism it is necessary to accept that the finer points of the diurnal calcification cycle are features of the particular community and do not conform to the operational consistency which is characteristic of so many of the other parameters considered in Section 2. In view of the enormous variability in the community structure which has been demonstrated to lead to many predictable operational roles, it is probably inevitable that there must be many other community level parameters which will prove to be inconsistent.

SECTION 3

PERTURBATIONS

This section will consider the results of two long-term investigations into the effects of trophic modification on the metabolic performance of reef systems. The findings will be considered relative to the concepts of operational uniformity established in Sections 1 and 2.

The first chapter summarizes the outcome of a previously published experiment but stresses those parameters now considered to be important. The second presents the results of a sewage impact study carried out on the reef systems of Kaneohe Bay prior to the final shut-down of all significant sewage input in early 1978. The second chapter also considers some effects of long-term chronic terrigenous sediment input on reef performance.

A. FERTILIZATION EXPERIMENTS

Over the years 1971-73 an experiment was carried out to determine the effects of enhancement of the nutritional environment on a typical lagoon patch reef at One Tree Is. The patch reef is located immediately adjacent to the narrow leeward reef-flat of the main lagoon level (F in Fig. 1). Insofar as this reef-flat is itself further protected by the lower level, leeward, accretionary lagoon, it is problematical whether the experimental site is best considered as a patch reef or as a leeward reef-flat. The reef is 25 m in diameter with a narrow, hard substrate perimeter of typical coral/algal composition, and a miniature lagoonal center 1 m lower than the perimeter, and consisting of sand and rubble with some coral head development (Kinsey and Domm 1974).

The total experiment is covered by Kinsey and Domm (1974) and Kinsey and Davies (1979) and will not be detailed in this presentation. However, it is important that the results be considered in the context of concepts of reef performance developed in this dissertation. The patch reef was monitored intensively in 1971 and 1973 before, and subsequent to, the period of fertilization to determine the metabolism in the absence of enrichment. Occasional monitoring was also carried out in 1974 and 1975. The nutritional enhancement experiment was performed in 1972 and consisted of adding a mixture of urea and monoammonium phosphate to elevate the composition of the contained water in the "lagoon" to 20 μg atom N liter^{-1} and 2 μg atom P liter^{-1} (10% of the N was as ammonium, the remainder as urea). Typical water entering the One Tree Is. system contains about

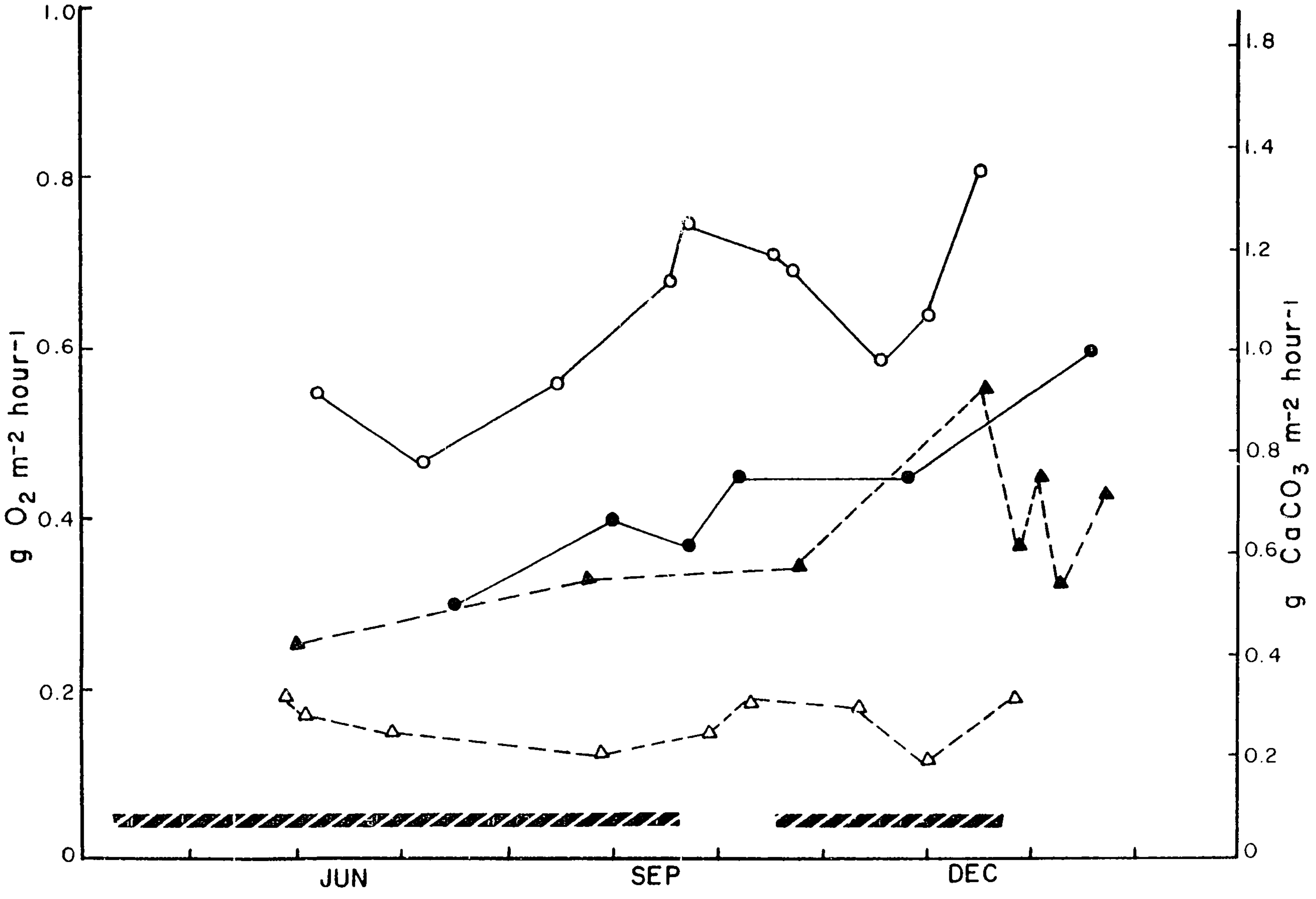
0.2 μg atom N liter^{-1} and 0.05 μg atom P liter^{-1}, with very low (< 0.1 mg m^{-3}) chlorophyll a (phytoplankton). The enrichment was sustained over about three hours on each daytime low tide (see Chapter 1A for details of the standing water cycle at One Tree Is.). The enriched water was then flushed out abruptly by a rising tide. This procedure was carried out over a nine month period with a total cessation for one month in the sixth month. Metabolic functions were monitored at least once in each month during the actual enrichment period. A monitoring sequence consisted of running fixed instrumental monitors for three consecutive 24 hour periods.

Chlorophyll a was not monitored in the water during the periods of enrichment, but the productivity of the water was monitored using the procedures outlined in Chapter 1A (Table 18). There was no suggestion of increased planktonic activity associated with the three hour periods. There was also no visually obvious modification of the reef communities during the nine months--i.e., there was no overgrowth of the dominantly coral/calcareous algal community by foliose or filamentous algae. Of course this does not mean that there was no increased productivity of the smaller algae with an associated increased consumption by itinerant grazers. All motile animals were free to enter or leave the experimental area.

The overall trend of the metabolism results is well demonstrated by Fig. 15 which is taken directly from Kinsey and Davies (1979). It should be stressed that the plots are in somewhat different units from those used elsewhere in this dissertation: y_{max} is plotted in g O_2 m^{-2}h^{-1}; and c_d is plotted in g $CaCO_3$ m^{-2}h^{-1}. It is very clear

Figure 15.* The effect of fertilization (open symbols) on community primary production (circles) and calcification (triangles) of a lagoonal patch reef at One Tree Island. Fertilization was carried out daily during the indicated period (cross hatched) of the year 1972. Control data for the same site (closed symbols) were from the preceding year (1971 - Jan. 1972) in the case of primary production (●). Calcification control data (▲) were from 1971 - Jan. 1972 (points 4,5,7,8), 1974 (points 1,2,3), and 1975 (point 6). Primary production (data after Kinsey and Domm 1974) is expressed as hourly net rate of oxygen production at noon. Calcification is expressed as hourly net rate of $CaCO_3$ production at noon. Final "control" points in January 1972 probably marginally reflect a brief fertilization experiment carried out during that month (Kinsey and Domm 1974).

* Diagram reproduced from Kinsey and Davies 1979.


1.0
0.8
0.6
0.4
0.2
0
g O$_2$ m^{-2} hour^{-1}
1.8
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
g CaCO$_3$ m^{-2} hour^{-1}
JUN
SEP
DEC

that the effect of this three hours per day of enrichment was to cause a large increase in photosynthetic production and a massive reduction in calcification. As has already been indicated, neither of these effects was accompanied by any obvious change in community structure. Kinsey and Domm (1974) also indicate that there was no significant change in respiration rates. This means that the increased production either represents an increasing standing crop, or detrital washout, or removal by itinerant grazers. I favor the final alternative at this time (with no proof). It is also obvious that the effect of nutritional enhancement was cumulative, as the one month without fertilizer additions caused no shift in metabolism. However, monitoring in the years 1974 and 1975 clearly indicated a complete return to the original status. Kinsey and Davies (1979) attribute the reduced calcification found to direct suppression of the calcification process rather than to any indirect effect such as overgrowth by algae.

Table 56 indicates the overall mean diel metabolism for the experimental system, and includes the parameter c_d/p_{max}. The lagoon reticulum (DK22) and the overall seaward reef-flat (coral zone, DK13, and sand zone, DK17) are included for comparison. Both these systems have comparable ratios of perimeter hard substratum community to sand/rubble bottom. It can be seen that all three sites (i.e., excluding the data from the period of fertilization) are very similar indeed. The experimental patch reef (F) may be a little closer to a reef-flat than to the lagoon reticulum in view of the P/R = 0.9. This implies proximity to a high energy zone (reef slopes, etc.) which is providing detrital input (see Chapter 2A). All three have a high c_d/p_{max} ratio

Table 56

Overall Mean Community Metabolism of a Fertilized Patch Reef at One Tree Is., Compared with Areas of "Standard" Performance

Site	P	-R	P/R	G	c_d/p_{max}
	$(gC\ m^{-2}d^{-1})$			$(kgCaCO_3\ m^{-2}y^{-1})$	
Lagoon reticulum (DK22)	3.1	3.1	1.0	1.5	0.19
Total seaward reef-flat (coral and sand zones)*	3.1	3.4	0.9	1.9	0.22
Experimental patch reef (F) <u>without</u> fertilization**	2.9	3.1	0.9	2.0	0.24
Experimental patch reef (F) <u>with</u> fertilization**	3.8	3.1	1.2	0.8	0.08

* This is the total reef-flat environment consisting of the high activity bimodally distributed coral zone, typified by DK13, and the low activity sand flat typified by DK17. Data are derived using information contained in Tables 9, 14 and 16, and Fig. 5.

** Also consisting of a high activity perimeter zone and a central sand/rubble zone. Data based on information covered by Kinsey and Domm (1974) and Kinsey and Davies (1979).

which is indicative of a high coral component (Chapter 2E). The effect of fertilization is very obvious. Firstly, it has shifted the P/R ratio from a logical 0.9, to 1.2 which would only be associated with a high energy zone in a normal reef-system (Chapters 1A and B). However, this patch reef is <u>not</u> in a high energy area. Secondly and perhaps most dramatically, it has depressed the c_d/p_{max} ratio from a very high 0.24 to 0.08 which is below the lower limit of 0.1 proposed for any true reef system (Chapter 2E).

Thus substantial nutrient enhancement, in the absence of plankton enhancement, is capable of perturbing a reef system into an "unnatural" mode which is characterized by enhanced and persistent photosynthesis and strongly suppressed calcification. Most interestingly of all, in the context of this dissertation, the elevated nutrient level has forced the reef outside the "accepted standards" of performance.

B. SEWAGE AND SEDIMENT IMPACT ON KANEOHE BAY

The long-term impact of both sewage and terrigenous sediment inputs to Kaneohe Bay has been visually obvious for many years. The SE to NW transition in community structure among the experimental transects has already been described in detail in Chapter 1C as have all general aspects of physiography, reef zonation, and meteorology relevant to the results to be presented in this chapter. It was also mentioned in Chapter 1C that the daily input of 30,000 moles dissolved nitrogen and 3300 moles of dissolved phosphorus (now discontinued) served principally to drive a phytoplankton chemostat rather than to cause any major increase in the nutrient concentrations of the water over the reefs. Thus it is probable that the trophic perturbation to this system was that of continuous particulate organic loading (beginning as phytoplankton), rather than a nutrient loading as was the case in the previous chapter. It should be stressed that all comments which follow are relevant to the situation prior to November 1977, when full sewage input was still occurring.

Table 57 indicates typical chlorophyll a content for the water over the experimental sites, and Table 58 gives the results of several estimates of plankton metabolism carried out on this water. These estimates were done using 250 l water samples sealed in plexiglass hemispheres which were placed within the water mass such that the flat face was just beneath the surface. Continuous agitation was provided by a small impeller and all monitoring was done within the closed system. The information in Tables 57 and 58 has been used to determine probable plankton metabolism over each of the major sites.

Table 57

Typical Chlorophyll a Content of Water Over Reef-Flats (period 9/77 through 11/77)*

Site	Chlorophyll a ($mg\ m^{-3}$)
SE	10 (range 4-17)
Lilipuna	5 (" 4-10)
Coconut Is.	1.5 (" 0.6-3.5)
Central	0.5 (" 0.3-0.8)
NW	0.8 (" 0.2-1.0)

* The assumption has been made that the values are applicable over the experimental period of Sept. 1976-Sept. 1977.

Table 58

Metabolic Rates for Plankton Based on SE and Lilipuna Site Water Samples*
(rates prorated to water 1 m deep and 10 mg m^{-3} chlorophyll a)

P ($gC\ m^{-2}d^{-1}$)	R ($gC\ m^{-2}d^{-1}$)	P/R
1.6	0.6	2.7

values derived from y_{max} = 0.14 (n=7) S.D. = 0.02
r = -0.024 (n=8) S.D. = 0.007

* Three separate samples used: SE with 14 mg Chl a m^{-3}; Lilipuna with 10.3 mg Chl a m^{-3}; SE with 12.9 mg Chl a m^{-3}. Each sample monitored for 24 h in 250 l plexiglass hemisphere placed flat side up.

These values can then be subtracted from the total community metabolism measured on site to give a reasonable estimate of the metabolism of the benthic community. It is obvious that plankton metabolism will prove to be a major component of the total community metabolism at the SE and Lilipuna sites. This finding is, of course, in total contradiction of the more usual coral reef situation as outlined in Tables 3 and 18. It is also obvious that the SE site will be subjected to the considerable organic loading of at least 0.5 g POC m^{-3} (assuming C = Chl.a x 50) in the overlying water. Of course there will be associated detritus and zooplankton elevating this concentration further. Lilipuna received approximately half of this loading. The presence of large amounts of particulate organic matter allows considerable scope for heterotrophic feeding by the benthic community, in line with the Chapter 1C comments on community structure.

Table 59 gives the nutrient levels found in the Kaneohe Bay system during sewage input. It can be seen that even the highest levels which might have been expected by dilution alone (with no utilization) would be about half those deliberately added in the One Tree Is. experiment. However, utilization was actually rapid and the levels found over the experimental sites are almost within the range of natural reef occurrence (Smith and Jokiel 1975, 0.6 µM phosphate, 4 µM nitrate + ammonium at Canton Is.).

Table 60 summarizes the means of all hourly metabolic data for each zone of each site, obtained during the period prior to sewage diversion. Rather obviously the extent to which one can feel confidence in the results of the study vary rather markedly from site

Table 59

Average Dissolved Nutrient Levels in Kaneohe Bay Water

Site	Ammonium + Nitrate (μM)	Phosphate (μM)
Hypothetical maximum sewage effect in South Sector*	7	1.5
Actual outfall**	4	1.2
SE reef-flat	4	0.7
Lilipuna patch reef	3	0.6
Coconut Is. reef-flat	3	0.6
Central reef-flat	2	0.3
NW reef-flat	1	0.2

* This is based on the average residence time (Smith et al. 1978) and the assumption of no utilization.

** Data from Smith et al. (1978). All other sites have data from the present study.

Table 60

Summary of the Means* of All Hourly Metabolic Rate Data for EPA Transects, Kaneohe Bay

Transect	Zone	Metabolic Variable	Estimated Mean Hourly Rate (gC $m^{-2}h^{-1}$)	Standard Deviation	No. of Estim.(n)	Standard Error (%)
SE	o/all (120 m)	y_{max}	0.28	0.21	22	16
		r	-0.22	0.19	20	19
		c_d	-0.055	0.106	15	50
		c_n	-0.118	0.102	7	33
Lilipuna**	o/all (62 m)	y_{max}	0.09	0.07	12	22
		r	-0.65	0.31	8	17
		c_d	0.077	0.042	12	16
		c_n	0.014	0.038	9	90
Coconut I.	"coral" (30 m)	y_{max}	0.29	0.12	18	10
		r	-0.43	0.24	5	24
		c_d	0.079	0.036	13	13
		c_n	-0.006	0.017	5	100
	sand (84 m)	y_{max}	0.17	0.05	16	7
		r	-0.28	-	1	-
		c_d	0.014	0.023	11	47
		c_n	-0.008	-	1	-
	algal (100 m)	y_{max}	0.15	0.06	14	11
		r	-0.12	-	2	4
		c_d	0.007	0.012	9	57
		c_n	no useable estimate			
Central	"coral" (52 m)	y_{max}	0.42	0.11	21	6
		r	-0.40	0.21	8	19
		c_d	0.181	0.061	21	7
		c_n	0.071	0.024	6	14
	sand (62 m)	y_{max}	0.17	0.05	13	8
		r	-0.10	0.03	5	16
		c_d	0.040	0.054	11	41
		c_n	-0.002	0.028	5	>100
	algal (75 m)	y_{max}	0.46	0.23	12	14
		r	-0.11	0.08	3	43
		c_d	0.007	0.032	12	>100
		c_n	no useable estimate			
NW	o/all (285 m)	y_{max}	0.33	0.22	27	13
		r	-0.10	0.06	10	18
		c_d	0.007	0.048	18	>100
		c_n	-0.006	0.029	8	>100

* Means are of all data, 9/76 through 9/77, and are not weighted mathematically for each month.

** Data cover only the period 7/77 through 9/77.

to site. Generally there is greater variation in calcification data than was obtained for production and respiration rates.

The consideration of the findings with respect to primary production and respiration is better done with subsequent tables. However, there are a few points requiring discussion at this point. All noon production rates are positive indicating that all zones of all sites achieve better than photosynthetic compensation, at the middle of the day. All daytime net calcification rates are positive with the notable exception of the SE site, where any calcifiers remaining in the community are no longer able to match the activity of the boring organisms at any time of the day. However, the nighttime net calcification estimates are quite variable with site. In every case calcification is less at night than in the day. However, while both the Central coral zone and the Lilipuna site continue to exhibit some net calcification into the night, all other sites and zones exhibit net dissolution. As indicated in Chapter 2F, these variations in diurnal calcification cycle are probably functions of the specific community but there seems tobe no clear lead as to the primary determinants. It is not appropriate to consider trends in the ratio c_d/p_{max} on the values in Table 60 as these still contain the planktonic component in p_{max}. These trends will be discussed later.

All rates in Table 60 are means of all data obtained. As suggested earlier, these rates will be somewhat higher than a true annual mean because (a) two Septembers are included in the 13 months, and (b) there are fewer data from the winter/early-spring period when rates are almost certainly lower. While general logical seasonality is evident in most of the less noisy data sets (see Chapter 1C for Central site seasonality), no presentation of seasonal trends is included here. They are generally poorly definable and contribute little or nothing to the conclusions concerning the effects of sewage.

Table 61 presents some integrated total community metabolic data averaged over the total time period. The most difficult aspect of presenting these data is to determine sites or zones where comparison may be assumed to have some relevance. This problem is particularly aggravated by the fact that Lilipuna, SE and NW sites have all lost (at the time of these experiments) the zonation which presumably they once had. They will be considered as operationally homogeneous, whereas the other two sites still exhibit "normal" zonation on a rather miniature scale (see Chapter 1C), and their data can be treated accordingly.

Table 62 is the direct equivalent to Table 61 except that the plankton component has been subtracted. Certain trends are dramatically obvious. The Central site "coral" zone has already been commented on at length in various chapters of this dissertation. It is more active than the "standard" reef-flat (Chapter 2E) but probably fairly typical of a fully developed 100% hard substratum coral/algal zone. Such low energy edge zones, of necessity, are very narrow in present-day standing sea levels (Chapters 2B and 2C). It is indicating some heterotrophy (P/R = 0.8), and as discussed in Chapter 1C this undercompensation could be either an indication of organic input (POC) from the Bay, or input of the excess algal production from the associated shoreline algal flat. The former option seems more in keeping with the trend exhibited by the other sites listed in Table 62.

Table 61

Community Metabolism and Calcification for Perimeter Zones and the Three "Homogeneous" Sites (SE, Lilipuna, NW). Benthic plus planktonic activity included.

Transect	P	R	P/R	G
	($gC\ m^{-2}d^{-1}$)			($kgCaCO_3\ m^{-2}y^{-1}$)
SE	4.9	5.3	0.9	-6.5
Lilipuna*	6.0	13.0	0.5	3.1
Coconut Is.	7.1	10.3	0.7	2.4
Central	8.0	9.6	0.8	8.9
NW	4.2	2.4	1.8	0.0

Table 62

Community Metabolism and Calcification for Perimeter Zones and the Three Homogeneous Sites (SE, Lilipuna, NW). Benthic activity only.

Transect	P	R	P/R	G
	($gC\ m^{-2}d^{-1}$)			($kgCaCO_3\ m^{-2}y^{-1}$)
SE	3.3	4.6	0.7	-6.5
Lilipuna*	5.2	12.7	0.4	3.1
Coconut Is.	6.9	10.2	0.7	2.4
Central	7.9	9.6	0.8	8.9
NW	4.1	2.3	1.8	0.0

* Rates corrected for the bias of the shorter sampling period (7/77-9/77).

The requirement for organic carbon input (R-P) to the Central "coral" zone can be seen to be 2 gC $m^{-2}d^{-1}$. Calcification is extremely high, suggesting that the perimeter of this reef is still very actively maintaining itself and presumably growing. It is, therefore, a sound reef crest with some organic overload.

At the Coconut Is. site, which is closer to the sewage input, it can be seen that there is some reduction of production, though it still falls in the "standard" reef-flat range (P = 6-8). The consumption has increased, clearly suggesting a substantial organic input. The heterotrophy is now such that more than 3 gC $m^{-2}d^{-1}$ of input is required. Calcification is much lower and well below the "standard" reef-flat range (G = 3-5). Thus, while a hard substratum reef perimeter is still recognizable, its long-term survival under these conditions of organic overload (i.e., sewage-input/plankton-production) seems very doubtful. One directly apparent mechanism for the suppression of calcification and consequent lack of reef maintenance is the overgrowth of the Porolithon-bound hard substratum by zoanthids, preventing continuing development of the Porolithon and in turn reducing sites for colonization by corals. It seems rather doubtful that the nutrient levels are sufficient to cause direct suppression of calcification as was claimed for One Tree Is. (Chapter 3A).

The Lilipuna site in the direct plankton stream makes a somewhat awkward comparison with the above two sites because of its small size. It is apparent that production is even lower and consumption is now enormously high with a requirement for more than 7 gC $m^{-2}d^{-1}$ of organic input. The calcification is actually higher than that on the

Coconut Is. reef, apparently contradicting the comments on the reduced calcification on Coconut Is.--particularly if Lilipuna is to be viewed as even more degenerate. Actually, the higher calcification is all associated with a higher nighttime rate, suggesting a substantial community structure difference between the two sites (see Chapter 2F). A reasonable explanation seems apparent. After the zoanthid overgrowth such as occurred at Coconut Is., Porolithon development and reef structural maintenance probably cease for all practical purposes. This lack of maintenance in turn causes gradual breakup of the reef initially to a rubble environment. On Lilipuna, this rubble top is clearly evident though the mechanism of its formation is obviously conjecture. It has served not only as a suitable site for sponge colonization, but also as a reasonable site for secondary (young) coral development. Thus some recovery of calcification activity may have occurred. However, it is doubtful that this recovery represents useful reef maintenance as there is little suggestion of Porolithon growth here; hence any corals which grow are not likely to be cemented into an integral reef structure.

At the SE site, production is even lower, but so is consumption, probably representing the near total degeneration of the reef system. There is no longer adequate firm substratum except near the reef edge, to allow the full development of the surface filter feeders, though infaunal standing crop is high. Consequently the consumption falls regardless of the proximity of the plankton source and the high plankton concentration. Further, the reef-flat is a well agitated environment, and passive settling of the plankton with subsequent microheterotroph mediated consumption does not appear to be an important mechanism here. The major part of the plankton swept onto the reef is swept off again. The most obviously dramatic change in the metabolism of this extreme site is the very large negative calcification. Not only has the substratum now become too fine and unstable to support any appreciable development of opportunistic corals (as suggested for Lilipuna), but the activity of boring organisms as the mechanism causing much of the breakdown of the substratum is now obvious.

Finally, the data for the NW site indicate that an entirely different trend is occurring. The production is relatively low (all foliose algae) but the consumption is even lower. Thus this site is an autotrophic environment (P/R = 1.8) with probably little or no input of outside organics. The calcification is zero but there is no conspicuous dissolution of substratum occurring. The most probable explanation of this obviously "non-reef" is that the original fringing reef was progressively inundated with sediments from river run-off with the eventual total destruction of any reef type organisms and the development of an estuarine algal flat. The effect of the sewer here seems to be totally negligible.

Table 63 handles the information a little differently, presenting totally integrated (all zones) data for _all_ sites. This handling does not seem to do very much to change the interpretations above. It rather obviously decreases the magnitude of the P and R values for the Central and Coconut Is. sites by virtue of the inclusion of the low activity sand and algal back-reef zones. It does, however, make clear

Table 63

Community Metabolism and Calcification for Complete Sites (all zones included). Benthic activity only.

Transect	P	R	P/R	G
	(gC $m^{-2}d^{-1}$)			(kgCaCO$_3$ $m^{-2}y^{-1}$)
SE	3.3	4.6	0.7	-6.5
Lilipuna*	5.2	12.7	0.4	3.1
Coconut Is.	3.8	5.3	0.7	0.4
Central	5.2	4.5	1.2	2.4
NW	4.1	2.3	1.8	0.0

Table 64

Community Metabolism and Calcification for Back-Reef Area (sand and algal flat zones) and for the Three Homogeneous Sites (SE, Lilipuna, NW). Benthic activity only.

Transect	P	R	P/R	G
	(gC $m^{-2}d^{-1}$)			(kgCaCO$_3$ $m^{-2}y^{-1}$)
SE	3.3	4.6	0.7	-6.5
Lilipuna*	5.2	12.7	0.4	3.1
Coconut Is.	3.3	4.5	0.7	0
Central	4.2	2.4	1.8	0
NW	4.1	2.3	1.8	0.0

* Rates corrected for the bias of the shorter sampling period.

that the Central site overall is not heterotrophic as is its outer coral zone. Thus the organic input required by that coral zone (Table 62) may be at least partially satisfied by internal movement of fixed carbon--i.e., algal detritus from inner zone moving out.

If it is more appropriate to compare the undifferentiated sites with only the back-reef zones of the two other sites, this comparison is made in Table 64. Here it is obvious that the back-reef area of the Central site is just as autotrophic as, and virtually identical in activity to, the NW site. Thus it seems reasonable to suggest that, if organic input (principally plankton) is of any consequence to the Central sector reefs, its influence does not extend beyond the coral zone. In contrast, the heterotrophic mode of the back-reef areas of the Coconut Is. reef-flat stress the definite shift of every part of this reef toward the consumption of organic material.

Table 65 lists the values for the ratio c_d/p_{max} for each zone of each site. Using this "standard" of performance, it is obvious that no other zone matches the very high 0.22 exhibited by the Central "coral" zone. It is not too unreasonable to propose that all the narrow reef edge zones in this low energy bay probably once matched this value. The much lower values for the Coconut Is. "coral" zone and the Lilipuna site both still fall close to the lower end of the hypothetical 0.1-0.2 "standard" range. The Central sand flat, at 0.15, conforms entirely to the "standard" (Table 54) as do the algal flats at 0.03 and 0.01, but it is interesting that the Coconut Is. sand-flat has slipped to 0.03 suggesting that it has ceased to play a normal operational role in reef maintenance (see Chapter 2E). The NW site

Table 65

Values of the Ratio c_d/p_{max} for All Zones Used in EPA Study, Kaneohe Bay

Transect	Zone	c_d/p_{max}
SE	o/all	-0.11
Lilipuna	o/all	0.10
Coconut Is.	"coral"	0.11
	sand-flat	0.03
	algal-flat	0.03
Central	"coral"	0.22
	sand-flat	0.15
	algal-flat	0.01
NW	o/all	0.02

value of 0.02 is entirely in keeping with its present non-reef status. The SE site establishes a new category not covered in Chapter 2E. This is the active degeneration role, which really is independent of the value of p_{max}--i.e., it could occur in the absence of light.

It is clear that there has been a marked response of the Kaneohe Bay surface reef systems to sewage input. There has been a shift towards considerable heterotrophy logically involving the utilization of particulate organics (largely diatoms) resulting from the southern sewage outfall "chemostat" effect. The degree of excess heterotrophy bears a strong relationship to the normal planktonic chlorophyll a content of the overlying water and therefore varies considerably in various parts of the bay. Associated with the increased emphasis on the heterotrophic mode has been a major change in the biotic makeup of the communities.

The facility with which these responses have occurred probably has been aided by both episodic and chronic input of terrigenous sediment as a result of suburban development within the bay watershed. It seems inevitable that an initially normal reef-flat community exposed to a substantial particulate organic input would experience a gradual shift, not only in its trophic mode but in the actual community structure. However, Kaneohe Bay reefs exposed to an unnatural degree of terrigenous sedimentation together with episodic freshwater inundation, which has been recognized as causing considerable community kills (Banner 1974), would logically recover from such damage favoring the development of biota which would benefit from the modified trophic environment--e.g., killed corals would be replaced by filter-feeders.

A secondary, but critical effect of the biotic shift has been a gradual loss of adequacy in reef framework maintenance. Coral growth has declined in the areas most affected, and encrusting corallines, so critical to structural maintenance, have been seriously overgrown with zoanthids, sponges, etc. Further aggravating this effect has been the increased population of detritus-feeding infauna (Smith et al. 1978) with their frequently substantial mechanical and chemical boring habits.

Reasonable examples of each permutation of the effects discussed above can be found among the sites used in the present study:

(a) The NW site appears to have been inundated with sediments from the adjacent streams, resulting in the loss of virtually all major reef organisms, even though there is no evidence of a trophic stress in this area. As the situation is chronic, there is no suggestion of biotic recovery to a reef format. The result has been to favor mostly soft bottom algae (<u>Calerpa</u>, <u>Hypnea</u>, <u>Acanthophora</u>, etc.). This type of community has contributed a high degree of autotrophy (P/R = 1.8) at a moderate level of productivity (P = 4.1). This autotrophic excess is doubtless maintained by a reasonable level of direct nutrient input associated with land runoff. Nutrient input of this kind does not tend to lead to phytoplankton production such as that found at the sewer outfall, because it is less locally concentrated and because it is delivered directly onto a shallow flat where the benthic algae are favored sufficiently to benefit. The modified biotic makeup at this NW site is maintained right to the outer reef edge, with the consequence that there are virtually no calcifiers remaining (except molluscs, forams, etc.). However, the autotrophic mode of the environment has not encouraged erosion by infauna. Hence the net calcification here is maintained at zero, implying that this reef-flat turned sand/mud-flat is relatively stable structurally.

(b) The Lilipuna site appears to have been influenced principally by particulate organic loading. Even though this site is adjacent to areas receiving considerable terrigenous sediment on an episodic basis, it is small enough and freestanding (patch reef) so that accumulation of sediment is very low. Here the shift to a heterotrophic mode is dramatic (P/R = 0.4). However, considerable primary production (P = 5.2) is maintained because the low level of sediment inundation has allowed the concurrent survival of much of the hard-bottom organisms, with the filter-feeding and infaunal organisms encouraged by the trophic environment. Consequently, a fairly high level of net calcification (3.1) is also maintained, regardless of the very large amount of infaunal erosion which is visually obvious. It is probable that this net calcification is operationally relatively useless to framework maintenance as it appears to be associated with numerous but discrete surface colonies (mostly corals). The cementing activities of the encrusting corallines are no longer apparent, and the structural integrity is being seriously affected by erosional activities. Thus the positive net calcification is probably doing no more than creating unconsolidated sediments.

(c) The SE fringing reef site adjacent to the main sewage outfall is an obvious extreme case of the ultimate degeneration resulting from <u>both</u> sedimentation and particulate organic loading. Both episodic and chronic terrigenous sediment loading has occurred here over a long period. There is no longer any recognizable reef structure or normal reef community structure, in common with the NW site. However, here the biotic shift has been entirely different from that at the NW site. Because of the very high organic loading, the shift has been to a dominance by filter-feeding organisms and both infaunal and epifaunal detritivores, with lower levels of autotrophs (P = 3.3). However, because of the relatively unconsolidated bottom caused by the sedimentation, it has not been possible to maintain the high population of heterotrophs associated with the Lilipuna site. Consequently, the SE site exhibits a much lower consumption of organic particulates (R = 4.6; P/R = 0.7) than occurs at the Lilipuna site (R = 12.7; P/R = 0.4), regardless of the fact that organic loading is typically considerably higher at the SE site. Also, because of the terrigenous sedimentation, all significant calcifiers have ceased to be productive in this environment, even in the production of unconsolidated carbonate sediments. However, in contrast with the NW site, the invasion by erosional infauna has been very great here, encouraged by the trophic environment--hence the extreme negative net calcification (-6.5). These findings imply that this reef-flat turned sand/mud-flat is totally unstable (cf NW site) and logically would gradually lose its physiographic integrity. The removal of the sewage input should, at the worst, lead to a situation developing here which is approximately analogous to that presently found at the NW site.

(d) The Central fringing reef site is the nearest to being unaffected by either influence. However, here one sees marginal effects of both. The inner reef-flat (sand and algal areas) is maintaining a status virtually identical (Table 64) to that of the whole NW site. This status is presumably encouraged by limited terrestrial nutrient input and even more limited terrigenous sediment input. These influences probably can be identified up to the outer limit of the algal zone. Thus the sand zone is probably more correctly visualized as a normal carbonate sand back-reef zone related to the outer reef-flat. The outer flat retains all the normal characteristics of a true coral reef perimeter zone, with a reasonable biotic makeup, no conspicuous buildup of filter feeders or abnormal level of erosional activity, and a very sound level of cementation maintenance by encrusting corallines. However, the influence of particulate organic loading is already apparent here (P/R = 0.8) even though a very healthy and relatively normal primary production is being maintained (P = 7.9). The fact that there is no elevation of organic consumption (R) on the inner flat compared with that occurring at the NW site suggests that all organic loading at the Central site is effectively removed by the outer reef-flat (see discussion in Chapter 1C). The calcification level (8.9) of the Central outer flat is very adequate for good maintenance of the reef framework, and its significance has been discussed extensively in Chapter 2B.

(e) The remaining site, on the Coconut Is. reef-flat, displays some of the characteristics of all the other sites. Because of the much larger size and associated high island, this reef is probably experiencing a little more terrigenous sedimentation than the Lilipuna site. However, Coconut Is. reef is certainly experiencing much less organic loading. The outer flat still retains some of its original identity, though biotic modification is considerable. Calcification is sub-optimal, though physical destruction by boring infauna has not progressed as far as it has on Lilipuna reef. This observation seems to be compatible with the somewhat lower organic consumption occurring (R = 10.2, compared with R = 12.7 at Lilipuna). Unlike the Central site, the organic load here is not totally removed by the outer reef-flat. Consequently, the inner reef-flat is not performing in the same mode as the NW site or the Central site back-reef, but has both a higher consumption (R = 4.5; Central R = 2.4; NW R = 2.3) and a lower production (P = 3.3; Central P = 4.2; NW P = 4.1). The lower production could be, in part, because of the much lower level of direct terrestrial nutrient input on this reef as it is not directly fringing the main land mass. The fact that the inner reef-flat on Coconut Is. has a nearly identical organic performance (P, R, P/R) to that across the whole SE site is probably largely incidental. Its calcification (zero) is entirely different. It reflects a complex interaction between a performance which should approximate those of the NW site or the Central inner flat, with the effects of receiving that part of the organic loading which the outer reef-flat is not capable of fully removing.

This study has left a large number of questions unanswered, but it has thrown considerable light on the quantitative trophic response of land-associated reef systems to both sedimentation and sewage input. The data base established should be very adequate to facilitate sound comparisons with post-sewage-diversion data to be obtained during 1979.

SUMMARY AND CONCLUSIONS

It seems reasonable to propose that the "sample" of coral reefs used is representative of Pacific reefs in general. The lack of detailed work on an oceanic atoll could be criticized. However, the good general agreement between the present findings and the less detailed published studies on Pacific atolls seems to vindicate the omission.

It is clear that there is a great deal of uniformity in coral reef metabolic performance. This uniformity seems to be operational, and almost "in spite of" very great lack of uniformity in small-scale morphology and community structure.

The reefs studied, and probably many other Pacific systems (Atlantic reefs remain largely unknown in relation to studies of this kind), have been found to exhibit the following characteristics:

1. Closely comparable community metabolism where there is a reasonable basis for comparison (same season, same zone, etc.).
2. Sufficient consistency in community metabolism that a set of "standard" performances is proposed.
3. Strongly seasonal pattern in the organic photosynthesis/respiration cycle (> twofold range) but relatively little seasonality in the inorganic calcification/dissolution cycle.
4. Considerable seasonal variation in the P/R ratio, but with a pattern varying reef to reef--probably a function of standing crop cycles.
5. Over and above the effects of seasonality, predictable upstream source zones (outer slopes, outer reef-flats, patch

reef perimeters), and downstream sink zones (inner reef-flats, lagoon floor, patch reef centers). In the case of organics, the sink is a zone of heterotrophic consumption. In the case of inorganics, the sink is the site of "permanent" accumulation.

6. A very pronounced relationship between calcification rate, and gross primary production rate (20% in high coral areas, 11% at lower limit), with departures being good indicators of perturbation or ultimate transition into algal/sea grass flats.
7. A strongly disjunct or modal distribution of community metabolism, bearing a pronounced relationship to zonation of biomass and to overall physiography, but very little relationship to detailed community structure. All modes appear to conform to the concept of "standards". There seem to be both absolute modes and equally distinctive mixtures of these absolute modes to give more normal operational modes (see discussion below).
8. A response to elevated nutrient regime which is characterized by increased P, increased P/R, and markedly decreased G (apparently direct suppression).
9. A response to elevated loading by particulate organics, characterized by decreased P, increased R, decreased P/R, and eventually decreased G (a response largely reflecting community composition changes).

The most consistently invoked mechanisms for the control of all operational parameters discussed have involved various components of the physical regime--i.e., wave fetch, turbulence, etc.

These explanations have been invoked, just as they were by Sargent and Austin in 1954, by default. There seems no other mechanism to suggest. It is important that these relationships be properly resolved in the future by seeking actual correlation between parameters of the physical regime and the operational performance of the reef.

The "standards" of performance implied by previous publications (Smith and Kinsey 1976; Kinsey 1977) are upheld by the present detailed findings. However, it is apparent that even those standards are themselves only compromises brought about by shallow water and therefore accentuated by the present standing sea level. Thus the ultimate standards are probably a 100% hard-substratum-cover mode of P = 20, G = 10, or a sediment bottom mode of P = 1, G = 0.5. The "standard" reef-flat of P = 7, G = 4 is a small-scale bimodal distribution of these two. The only system which is probably not compounded from these two modes is the seaward high energy algal ridge. This system is a feature of standing sea sevels and has "adopted" an operational mode (P = 5, G = 4) which is essentially similar to the bimodal compromise of the normal reef-flat. It is, of course, entirely encouraging to the present philosophy that such a homogeneous feature as the algal ridge, evolved during a standing sea level, should stabilize with a metabolic performance approximately equal to the heterogeneous compromise forced on normal coral areas by a present-day lack of water depth. The most far-reaching implication of the ultimate G = 10 mode, is that coral reefs in the Pacific may have had the potential during the Holocene to grow vertically at about 8 mm y^{-1} rather than the 3 mm y^{-1} maximum proposed by Smith and Kinsey (1976).

Such higher rates would have applied only during periods when the sea level rise sufficiently exceeded the reef's potential for vertical growth, that water depth exceeded the growth limiting range (without exceeding the 5 m upper limit also proposed). Unfortunately, the present investigation has not indicated what the lower limit to the optimum depth range might be. It seems necessary to query the absolute validity of Holocene growth models such as that of Davies and Kinsey (1977) which is based on the concept of a 3 mm y^{-1} maximum. This whole question now requires reexamination.

Given sufficiently detailed information and insight to allow the application of standards, it seems reasonable that departures forced by perturbations will be reasonably easy to identify. It may be feasible to use such metabolic criteria as early warning systems for stress, even where the "control" rates were not measured. Where monitoring is being carried out on a regular basis, the most sensitive indicator of stress may be a decline in the c_d/p_{max} parameter (or perhaps the alternative c_d/r).

The theme of uniformity, and predictability of metabolic responses which has emerged from this study, raises interesting possibilities in relation to all ecosystems. I feel confident that the concepts will prove to have general applicability. The principal difficulty in making such applications will always be to identify a logical basis for comparison.

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