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METABOLISM, CALCIFICATION
AND
CARBON PRODUCTION

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METABOLISM, CALCIFICATION AND CARBON PRODUCTION

Coral reefs not only have one of the highest primary (organic) production rates among natural ecosystems, but they are also the major site of calcium carbonate deposition in the world. On a global scale, coral reefs serve as an important buffer in the earth's CO₂ cycle. On a regional scale, they frequently are located in areas of dense human population. They not only serve an often vital role in local economies, but they are also threatened by a diverse assortment of human activities.

The integrity of the coral reef ecosystem is dependent on the structure and function of its component communities, and they in turn are composed of populations of organisms. The major metabolic processes affecting the carbon cycle are photosynthesis, calcification and respiration. The first two, in turn, are controlled by nutrient supply and light.

In this seminar, we will discuss temporal and spatial patterns of carbon production at two levels: systems or communities (Kinsey) and organism (Gladfelter). Each section is self-contained, with its own separate bibliography. A brief general summary appears at the end. These are not fully comprehensive literature reviews. Instead, we aim to concentrate on a few concepts and approaches to research which we feel will help to increase our understanding of the metabolic processes occurring on coral reefs.

SYSTEMS-LEVEL STUDIES

1. INTRODUCTION

The first and only fully comprehensive review of systems-level processes of organic production on coral reefs is that by Lewis in 1977 though those of Sournia (1977a), Kinsey (1983a) and Smith (1983a) cover major aspects of production rates. Lewis considered many details of community structure, trophic relationships and nutrients fluxes as well as summarising the state of the art with respect to estimates of production rates for coral reef systems. He also considered matters of carbonate production, coral and reef growth, erosion and the hydrographic conditions under which all these processes occur.

Since Lewis' review was written, the proceedings of two further International Coral Reef Symposia have appeared. These contained numerous papers in the area of systems production, nutrient flux and growth studies. There has also been a considerably accelerated rate of appearance of relevant papers in the general scientific literature.

Two further publications of real significance in the summarising of knowledge of systems processes on coral reefs are "Perspectives on Coral Reefs" (ed Barnes 1983a) and the "Proceedings of the Great Barrier Reef Conference" (eds Baker *et al.* 1983). While the latter summarizes the state of the art in some relevant areas up to 1983, the former contains papers mostly summarising the state of the art to the end of 1979.

Recent research has continued to produce more estimates of organic and inorganic production by coral reefs with the somewhat inevitable emphasis on the easily worked reef-flat areas. However, there are a number of important emergent themes from research reported in the nine years since Lewis' review. The availability of higher technology and associated higher precision has led to new concepts of reef performance in time and space. Much finer levels of discrimination are possible and the derivation of data for areas of reefs "inaccessible" to earlier technology can now be attempted. The role of nutrients as important controls on reef production has received considerable attention.

The work of Smith and Atkinson (e.g. Smith and Jokiel 1975; Smith and Atkinson 1983; Smith 1983b; Smith *et al.* 1985) has led to an understanding of the importance of precise estimates of net gains and losses by reef systems. They have stressed the value of determining this variable directly by budgeting "conservative" parameters such as phosphorus or alkalinity rather than by inference from the difference between community production and consumption. The work of Kinsey (e.g. 1977; 1979; 1982; 1983a) has led to theories of modality in reef performance and the concept of predictable "standard" rates for organic productivity and growth. The work of Barnes (1983b,c; Barnes and Devereux, 1984) has resulted in the development of important relationships between reef production and light regime as well as permitting very fine scales of spatial and temporal discrimination.

One of the most important themes just beginning to emerge is that much of the variability previously attributed to "noise" is now seen to be real and to be associated with meaningful trends, some of which may prove to have practical management value. Much attention is being given to variation with latitude and as a function of land proximity. Three major programs have addressed these questions. They are those of: The Australian Institute of Marine Science; The Hawaii Institute of Marine Biology and Hawaii Sea Grant Office (Grigg and co-workers) and the Australian CSIRO Division of Fisheries (Marmion Lab; Wiebe and co-workers).

These systems-level open community biogeochemical studies continue primarily to emphasize the Indo-Pacific region. Even with the advent of several major ongoing programs, the relevant literature continues to be dominated by output from scientists from a wide range of institutions many of which are not primarily concerned with coral reef work.

2. COMMUNITY METABOLISM STUDIES RE-VISITED

The expression "community metabolism" has been in use in coral reef research at least since the major study of the Enewetak reef-flat by Odum and Odum (1955). Fairly obviously, a total community does not have a metabolic entity. However, it is both possible and useful to determine the rates at which materials are imported, incorporated, converted, turned over, excreted and exported by a complete community and even an integrated ecosystem. It is also very useful to determine the net gains (or losses) and, hence, growth rate for the total system. The use of the term "biogeochemistry" is probably preferable to "community metabolism" or to the even more restrictive concepts covered by "productivity".

The biogeochemistry of a reef system is dominated by aerobic, benthic processes of photosynthesis, calcification and integrated community respiration. These, in turn, are controlled by, and reflected in, the dynamics of nutrient fluxes. However, the direct "currency" of all community biogeochemistry studies is carbon. Consequently, it is in terms of carbon flux that most findings are expressed, whether or not they were based on the direct measurement of changes in the CO_2 and organic carbon content of the system.

While reef systems may be benthic dominated, it is becoming more and more evident that we have underestimated the significance of the direct organic flux associated with plankton and detritus throughputs. This error has been encouraged by the fact that changes in such materials in the water column may be quite small over short time and the concentrations of such materials are usually quite low. However, the total flux of planktonic material can easily be demonstrated to be extremely high in open systems. Thus, its potential to have a major but undetected effect on the benthic community is very great. Similarly, the importance of anaerobic processes in the remineralisation of reef detritus has generally been underestimated. While it is obvious that most reefal biological processes are highly aerobic, the business of regenerating and recycling materials, so often stressed as mandatory for reefs to survive in relatively "barren" waters, involves much anaerobic processing.

The organic gain (E) by a reef system is typically very small in terms of total flux of carbon through the system - ie. gross photosynthetic fixation (P) is typically approximately equal to gross respiratory consumption (R) and the net flux of fixed organic matter is typically small. Thus $E(\text{ie } P-R)$ approximates zero over extended time. Because this is so, there is a great deal of relevance to the development of methodology which allows the direct determination of net gain or loss rather than deriving it inaccurately by difference. On the other hand, the potential for a system to yield a harvest on a sustained basis is probably more a function of gross turnover than it is of net gain in the "normal" state. Thus, the gross fluxes P and R may prove very important in management terms.

The "inorganic" gain (G) by a coral reef is a measure of the net gain of biogenically derived carbonates. It is very high relative to organic gain. It is this parameter which determines the long term growth of the reefal structure.

It is extremely important to recognise that, not only the gross rates, but the gain or loss considerations in reef biogeochemistry are extremely time and space dependent - ie., there are pronounced seasonal cycles and possibly variability in other time frames. There are also important redistributions of materials between local "sources" and "sinks" which, individually, may exhibit marked gains or losses. This characteristic in itself may be markedly seasonal.

Finally, it is very important to recognise that what is a "reef" to one worker may not be another's conception of a "reef". Thus, it is critical that comparisons be made of operationally equivalent parts of reefs or, at least, attention be drawn to the relevant differences.

The present state of knowledge in all these areas of research is reviewed in the sections following. The following units will be used because of established convention: P, R and E expressed in $\text{gCm}^{-2}\text{d}^{-1}$; G expressed in $\text{kg CaCO}_3 \text{m}^{-2}\text{y}^{-1}$. Particulate organic matter will be designated POM, particulate organic nitrogen as PON, dissolved organic matter as DOM. GBR will be used to refer to the Great Barrier Reef.

3. METHODOLOGY

As Lewis (1977) pointed out, the basic technique for estimating rates of primary production and respiration on coral reefs has been flow respirometry. Most commonly, this has involved the measurement of changes in oxygen content in the water as it flows across a reef. Oxygen can be measured accurately and simply by either the Winkler or oxygen electrode procedures. The processing of oxygen data to give diel curves of production and respiration is normally based on the logic of Odum (1956) and Odum and Hoskin (1958). These procedures have been updated and are presented as working methods in various chapters of the UNESCO "Coral reefs: research methods" (eds Stoddart and Johannes, 1978) (eg. Marsn and Smith, 1978; Kinsey, 1978a). More recently, Kinsey (1985a) has updated these methods once again and has reviewed the status of methods for short term material flux estimations in coral reef studies (Kinsey, 1983b).

There are three principal disadvantages to using oxygen as the prime monitored variable. Firstly, oxygen exchanges readily with the atmosphere. Secondly, conversion of oxygen anomalies to their equivalent in metabolic carbon requires knowledge of the metabolic quotients (RQ and PQ). Thirdly, oxygen based studies do not give information about the system calcification rates. All three of these subjects will be considered separately.

#4) measurement of water velocity over the reef.

Odum (1956) proposed a field method for handling the estimation of the atmospheric exchange coefficient based on the dangerous assumption that system respiration should be the same before dawn as it was post dusk. This procedure was used in most early community metabolism studies on coral reefs. Kinsey and Domm (1974) and Kinsey (1978a) proposed another field technique based on an alternative (but probably still risky) assumption that respiration and photosynthesis rates were uniform for any one time of the day regardless of the state of the tide or of the actual oxygen concentration in the water. Marsn and Smith (1978) and Kinsey (1985a) have recommended that the safest procedure probably is to use values taken from the most generalised consideration of all available published data rather than to attempt specific estimation of the coefficient in the field situation. This procedure probably has had the most general application in recent studies though values from say Marsn and Smith (1978) have been significantly weighted by values obtained by Kinsey's field technique. A third field approach has been developed by Nixon and Roques (unpublished ms. Grad. School of Oceanogr., U. of Rhode Is.). This method involves the floating of a hemispherical gas filled dome across the water surface at the time of the actual respirometry studies and determining the exchange rates applying at that time. Apart from the obvious inconvenience of having to apply the technique under many strong wind conditions, the potential for error in this approach results from the fact that the surface ripples and waves are modified under the dome. The counter argument suggests that turbulence is the main determinant of diffusive exchange and that it will be unmodified. The only application of the technique to a reef-type study appears to be that of Murpny and Kremer (1983) at Clipperton Lagoon. Murpny and Kremer give some details of the actual approach used and discuss their findings in detail.

The subject of metabolic quotients has been reviewed by Kinsey (1985a). The majority of coral reef studies have made the assumption that $PQ = RQ = 1$ without attempting any experimental verification of this value. Unfortunately most coral reefs studied have been found to have a value for P no more than 20% different to the value for R. That is, gain or loss is small. When these values are based on conversion from oxygen data it can be seen that a value for RQ or PQ of 1.1 or 0.9 rather than the simple stoichiometric 1.0 could effect a dramatic difference in the interpretation of the data in terms of autotrophic balance (ie P:R). Table 1 gives the calculated values for the metabolic quotients available from the literature. These are only available from studies where parallel estimations of community metabolic rate by the oxygen and CO_2 approaches have been made. It should be stressed that $PQ = \Delta O_2 / \Delta CO_2$ whereas $RQ = \Delta CO_2 / \Delta O_2$. Thus, it can be seen that $P_{CO_2} = P_{O_2} / PQ$ and $R_{CO_2} = R_{O_2} \cdot RQ$. Typical coral reef environments would seem to have a PQ of slightly more than unity except where there is a major component of foliose algae. The anomalous low values associated with these algal communities are likely to result from a substantial loss of oxygen to the atmosphere as bubbles rather than from a genuine metabolic difference. RQ follows a fairly straightforward trend from approximately 0.9 in coral dominated communities to appreciably more than unity in mixed communities. Values of 1.5 or more are assumed to indicate environments in which some major level of anaerobic decomposition is occurring. Such processes tend to be associated most with sediment areas stabilised by algal mats.

Table 1. Values obtained for metabolic quotients in coral reef environments.

Community Type	Location	RQ	PQ	Reference
Coral heads and associated community	Pacific Reefs	0.85-0.90	1.1-1.15	Kinsey (1979,85a)
Seaward reef slopes	Pacific Reefs	0.8	1.1	Kinsey (1979,85a)
Reef-flats dominated by corals and coralline algae	Pacific Reefs	0.9-1.05	1.05-1.1	Kinsey (1979,85a)
Reef-flat; coral/algal	Central GBR	0.9-1.0	1.0-1.1	Barnes & Devereux (1984)
Shallow reefal environments; coral/algal	French Frigate Shoals	0.96-0.99	1.01-1.04	Atkinson & Grigg (1984)
Reef-flats with high foliose and filamentous algal cores	Pacific Reefs	1.1-1.2	0.95-1.05	Kinsey (1979,85a)
Algal flats	Pacific Reefs	1.1-3.0	0.6-1.1	Kinsey (1979,85a)
Areas dominated by heterotrophs, filterfeeders	Pacific Reefs	1.1-1.6	0.5-0.9	Kinsey (1979,85a)

The disadvantages of oxygen as an indicator of carbon flux may be avoided by the direct or indirect monitoring of the CO_2 flux. CO_2 is subject only to very limited atmospheric exchange and is, of course, a direct measure of carbon flux. As a major bonus, the estimation may be done in such a way as to partition the flux into the organic carbon cycle (photosynthesis and respiration) and the "inorganic" carbon cycle (calcification). This partitioning requires the monitoring of pH, salinity, temperature and total alkalinity. These methods are now thoroughly developed for use in coral reef environments (Smith and Key 1975; Smith and Kinsey 1978; Smith 1978a) using rationale from earlier coral reef studies (Kinsey 1972; Smith 1973; Smith and Pesret 1974; Smith and Jokiel 1975). The disadvantage of this

indirect CO₂ approach is that it is somewhat less precise than oxygen monitoring and that it is subject to certain interferences in areas with restricted water availability and long residence times. The most usual type of interference is that caused by the build up of organic matter, and the production of inorganic ions which interfere with the simple relationship between alkalinity and the seawater CO₂ system - e.g. ammonia and sulphide. To this time, there is no practical field method for directly monitoring the [CO₂] content of seawater flowing across a coral reef, and, in any case, such a procedure would not allow the partitioning into "organic" and "inorganic" components, in the absence of information on any one of the usual indirect CO₂ parameters (e.g. pH or alkalinity).

The existence of a simple stoichiometric relationship between alkalinity and calcification rate ($\Delta Ca^{++} = \Delta CO_2(\text{calcif.}) = \Delta \text{Total Alkalinity}/2$) appears to be beyond reasonable doubt in open flowing coral reef systems (Kinsey 1978b) and can even be applied effectively in quite restricted experimental situations (Borowitzka and Larkum 1976). However, the need to estimate total alkalinity is a liability as the estimation requires a sample to be taken for a later laboratory procedure. Additionally, this means that direct data logging cannot be used, as it can with the oxygen technique, unless a field autoanalyser is feasible. Barnes (1983b,c; Barnes and Devereux, 1984) recently proposed a combined O₂/CO₂ approach to carbon flux estimation which still allows partitioning into the organic and calcification components but avoids the routine requirement for total alkalinity determination. It therefore allows continuous data logging. The method takes advantage of the fact that (a) ΔCO_2 (organic) can be determined from ΔO_2 provided that credible metabolic quotient data are available, and (b) $\Delta \text{total } CO_2$ can be determined from pH data provided imprecise values for total alkalinity (determined only on occasional samples) are available. Actually, the world-wide range for total alkalinity in open waters would cause errors only up to $\pm 5\%$ in the CO₂ fluxes calculated by this procedure. Thus ΔCO_2 (calcification) = $\Delta [CO_2] - \Delta CO_2$ (organic) = $\Delta [CO_2] - \Delta O_2 \cdot RQ$ (or PQ^{-1}).

In the area of methodology for studying short term (hourly rates, diel cycles) material flux in reefs, the most significant recent advances have been those in the development of higher level technology and higher precision technology. Barnes (1983b, 1983c, 1984) has introduced the use of floating, high precision Lagrangian monitors to reef-flat studies. This greatly improved technology incorporates automatic logging of all data including light. The approach has also taken advantage of the previously mentioned O₂/CO₂ technique to infer alkalinities (and hence calcification rates) directly from the continuously monitored O₂ and pH data. Barnes' equipment has facilitated an improvement of two orders of magnitude in time and one order of magnitude in space over any previous open-system studies. Barnes' equipment is presently only suited to very shallow water. Another major advance introduced by Barnes has been the determination of the full diurnal photosynthesis from observations in only several time periods of the day together with the consideration of detailed light response curves. This is a sophisticated development of the standardised diel curve approach used by Kinsey (1978a). D. Smith (1983; Smith and Horner, 1982) has developed sophisticated computer logic and equipment for automated logging of primary production data based on the usual pH and O₂ parameters. The equipment is intended principally for long term deployment in a fixed position. Kinsey (1983b, 1985b) has developed very high precision techniques for deeper water profiling of the usual oxygen/pH type variables and this technique also incorporates continuous logging capability. Thus, it is now proving possible to monitor metabolic rates for reef systems in up to 20 m of water over effective intervals of 0.5-1 hour. The deep water techniques use both Lagrangian drogue studies involving two or more instrument packages mounted in a vertical string, or fixed Eulerian arrays mounted together with current meters.

The other area of methodology in which there has been a major development is in the use of anomalies in "conservative" variables such as phosphorus and alkalinity, or even in the non-conservative variable total CO₂, over extended time to infer precise estimates of net gains or losses (Smith and Jokiel 1973; Smith and Atkinson 1983; Smith 1983b; Smith *et al.* 1985). These techniques are not concerned with short term fluctuations caused by system community metabolism but with the long term net changes in total concentrations of the monitored variables. Fairly obviously, they are most effective where residence time is measured in weeks or months. However, recent work involving the high precision determination of short term changes in phosphorus in water crossing reef-flats has been used to infer net community metabolism even over time intervals of only one day (Atkinson 1982). The importance of having available procedures for measuring net gains and losses directly has been stressed in the previous section.

The recent work of Dunlap (1985) is a potential break-through in the study of phosphate "metabolism" as an indicator of system carbon flux. Dunlap has reported that extracellular phosphatase activity in reef waters is strongly correlated with system phosphorus flux. The enzyme production, by reef microflora, is activated by reduced inorganic phosphate levels such that the levels are effectively maintained by the resulting hydrolysis of organic phosphates. Appropriate mathematical treatment of results obtained seems likely to provide considerable insight into system function. Clearly, the implication of these findings concerning the role of phosphatases is that the study of concentrations or apparent flux of inorganic phosphate is possibly less useful than previously thought.

Flow respirometry in the open, unmodified reefal environment has the distinct advantages of being able to be continued over long periods (Lewis 1977) and of causing no interference whatsoever in the communities under study. However, it suffers the concomitant disadvantage of lack of specificity, though Barnes' techniques certainly allow a very fine spatial scale to be considered. Reef environments of particular interest may sometimes be further isolated by partial or total enclosure to facilitate the discrete monitoring of the community metabolism of the specific finite area. Such procedures are most justified in areas normally subject to extended periods of standing water where the enclosure basically will not modify the conditions experienced during low tides. A technique using vertical "fences" during standing water periods has been used extensively by Kinsey (1972; 1973; 1978a). This approach

allows relatively normal exchange with the atmosphere but prevents horizontal mixing with water outside the enclosure. Atkinson and Grigg (1984) have used "tents" of flexible plastic sheeting to enclose moderate sized coral heads in a relatively low energy shallow lagoonal situation. This technique can be applied in deeper water than the fences and, while not permitting any water exchange, does allow reasonably normal turbulence because of the mobility of the enclosure. Rogers (1979a,b) has developed effectively, for the first time, an open-ended tunnel enclosure for use on turbulent and deeper reef slope environments. This technique allows fairly natural water exchange and the use of a miniaturised "up-stream down-stream" approach. Turbulence is no doubt somewhat reduced but certainly is not prevented. The principal limitation of Rogers' technique is that it is, by virtue of constructional limitations, restricted to reef slope formations of only modest dimensions. In a rather different option for gaining spatial limits for component communities of a reefal system, Adey (1983) has utilised large scale microcosms assembled in a laboratory environment. He claims very close simulation of the natural reef, and certainly is able to effect very precise control over experimental parameters. The obvious criticism of the approach is to question whether it is ever possible to re-assemble an ecosystem.

4. PLANKTON STUDIES

It has generally been assumed that phytoplankton production in coral reef systems is relatively trivial. However, a number of authors (e.g., Gordon et al., 1971; Polovina, 1984) have drawn attention to probable production rates equivalent to 10% or possibly more of the total system production. If such levels occur frequently, then phytoplankton production may well be of considerable trophic importance to coral reef systems.

Lewis (1977), Sournia (1977a) and Kinsey (1983a) have reviewed the few data available for plankton productivity in reef waters. There have been only a few additional data in the literature since the period covered by those reviews. Table 2 covers most of the data to the present time. Values for P are, in most cases, obtained by ^{14}C techniques. The few values of R are for the total planktonic community (including bacteria on suspended particles etc.) and are all based on O_2 uptake. All values for P and R are expressed on the areal basis. Thus, rates tend to be higher for deeper systems because of the integration of data to cover the whole water column which, in turn, is justified by the considerable light penetration occurring in clear reef waters.

Table 2. Published values for plankton community metabolism in the water overlying reef systems.

Reference	Location	P ($\text{gCm}^{-2}\text{d}^{-1}$)	R	P/R
Sargent & Austin (1949)*	Rongelap	0.2		
Jones (1963)*	Florida bloom condition	0.04-0.06 0.8		
Motoda (1969)*	Palau	0.08		
Gordon et al. (1971)	Fanning Is.	0.5		
Johannes et al. (1972)*	Enewetak		0.003-0.03	
Qasim et al. (1972)	Laccadives	0.02-0.09		
Sorokin (1974)	Various	0.03		
Sournia & Ricard (1975a)	Moorea	0.004-0.03		
" (1975b)	Tuamotos	0.1-0.3		
" (1976a)	Takapoto	0.02-0.4		
" (1976b)	Vairao (Tahiti)	0.1-0.4		
Sournia (1977b)	Gulf of Eilat	0.01-0.03		
Ricard (1977)	Tahiti	>1		
"	Fiji	0.2		
LIMER Team (1976)	Lizard Is.	0.1		
Kinsey (1978a)*	One Tree Is.	0-0.06	0.1-0.3	0-0.3
Hargraves (1982)	Carrie Bow Key	0.14-0.3		0.9-1.4
Ricard (1982a)	Moorea	0.04-0.4		
Ricard & Delesalle (1982)	Scilly	0.4		
Kinsey (1983b)*	Davies lagoon summer bloom	~2		
Furnas & Hopkinson in Kinsey (1985b)	Davies lagoon winter	0.2	1.5	0.1

* Data obtained by gas exchange techniques. Other data obtained using ^{14}C techniques.

While many of the lower rates reported are similar to those of the surrounding oligotrophic oceans, it is clear that there are a number of values which greatly exceed those likely to be found in oceanic waters. Of the 22 data or ranges of data for P in Table 2, three equal or exceed 10% of the typical rates reported for very active reef-flat communities (i.e. > $10 \times 7 \text{ gCm}^{-2}\text{d}^{-1}$; Kinsey, 1983a) and thirteen equal or exceed 10% of the typical rates reported for complete lagoonal systems (i.e. > $10 \times 2 \text{ gCm}^{-2}\text{d}^{-1}$; Kinsey, 1979). Based on the findings of Jones (1963) and Kinsey (1983b, 1985b), it seems that very high values are more likely to be associated with specific bloom periods than sustained. This may be clearly associated with land runoff as reported by Ricard (1977) and Marsh (1977) or with virtual enclosure and retention of nutrients (Sournia and Ricard, 1976a). However, blooms may simply be associated with hot, calm weather and a temporary increase in lagoon residence time (Kinsey, 1985b). Sustained increases in phytoplankton production of two to threefold have been found associated with lagoon areas used for the dredging of sand and coral material (Ricard, 1982b).

The highest phytoplankton production reported for a reef-related lagoon is $4 \text{ gC m}^{-2} \text{ d}^{-1}$ at Clipperton Lagoon (Murphy and Kremer, 1983). However, this lagoon has a salinity of only 4‰ and is totally isolated from the present day sea level.

Overall, it seems important that phytoplankton not be disregarded as an important contributor to primary production in many lagoonal reef systems. Even levels of 10% of the total production may well represent more than 10% of the readily available primary carbon.

5. BENTHIC AND TOTAL SYSTEM STUDIES

Previous Reviews

As mentioned before, carbon flux in coral reef systems is dominated by benthic processes. 10-30% of the total carbon fixed goes into the production of carbonates (Kinsey, 1979), the remainder is fixed via conventional photosynthetic pathways. While not itself a photosynthetic process, the formation of inorganic carbonates by reef organisms exhibits a pronounced diel cycle (Kinsey, 1972, 1979; Smith, 1981) and is clearly locked to the photosynthesis in the reef.

Lewis (1977), in summarizing organic production by coral reefs, concluded that most reefs fell in the range $P = 1-14 \text{ gCm}^{-2} \text{ d}^{-1}$, with a P/R ratio which fell to either side of 1. Thus some reefs seemed to be autotrophic while others required an organic input to satisfy the requirement for community respiration (R).

Sournia (1977a) concluded that "few data depart from the range $2-10 \text{ gCm}^{-2} \text{ d}^{-1}$ " (P) while "net production is much lower, sometimes nil or negative" (here, net production = $P-R$).

Smith (1983a) has summarized available rates for calcification in reef systems. Developing further the hypothesis of predictability in system calcification rates (Smith and Kinsey, 1976; Smith 1978b; Kinsey, 1979), Smith suggests that 1-2% of reef area calcifies at an elevated rate of $10 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ ($G = 10$), 4-8% calcifies at $G = 4$ and 90-95% calcifies at a much slower rate averaging about $G = 0.8$. It is important to stress that these generalisations, particularly with respect to area, are meant to apply as averages over most of the world's coral reefs, not necessarily to any one reef.

Kinsey and Davies (1979a) and Kinsey (1983a) drew attention to the fact that the "reefs" reported in the numerous community metabolism studies are certainly not directly comparable on any simple basis. Some studies encompass a whole reef system, others just the high activity reef-flat. Others give data averaged over the annual cycle, while some cover only the brief period of an expeditionary study. Some utilise methodology or experimental design inconsistent and incompatible with others. Kinsey (1983a) suggests that complete reef systems give values for P in the range $2-6 \text{ gCm}^{-2} \text{ d}^{-1}$ with a P/R apparently always extremely close to 1. The net deposition of carbonates lies in the range $G = 0.5-2 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$. By comparison, reef-flat systems reported in the literature averaged $P = 7.9$ (range 4-16) and $G = 4.2$ (range 3.7-4.6) while P/R fell in the range 0.6-2.5. However, Kinsey (1983a) examined the published data more closely and concluded that those clearly quantifying production in the high activity reef-flat area over periods of time likely to result in a reasonable approximation to an annual average and using comparable experimental approaches, fell within very narrow limits: $P = 7.0 \pm 0.6$, $P/R = 1.0 \pm 0.1$, $G = 4.0 \pm 0.7$. This was described as the "standard performance" for a coral/algal flat over extended time and was claimed to hold at least within the latitudinal range 23°S to 21°N . This "standard" concept builds further on the very uniform rates of calcification ($G = 4$) noted for all reported reef-flat studies by Smith and Kinsey (1976).

Kinsey's review (1983a) proposes a series of absolute modes for coral reef metabolic performance. It is suggested that the following modes cover all reefal environments other than seagrass/algal beds.

100% Coral/algal hard substrate	$P = 20$	$G = 10$
100% Algal encrusted pavement	$P = 5$	$G = 4$
100% Sand and rubble	$P = 1$	$G = 0.5$

However, it is allowed that total cover with coral/algal substrate may result in reduced activity in very limited areas of restricted water availability such as the edges of low to moderate energy patch reefs and fringing reefs. On the basis of this modal split, it is proposed that the "standard" reef-flat of $P = 7$, $G = 4$ is, itself, a mix of the modes given above.

Kinsey and Davies (1979a) and Kinsey (1977; 1979) also emphasize that, while the overall P/R for a complete system may normally approach 1.0 over the full annual cycle, nevertheless there are zones within the reefal system acting as sources and sinks with respect to each other. Thus, a reef-flat could be a net sink ($P/R < 1$) with respect to a very high energy outer slope from which biomass was continually being broken away. Conversely, other reef flats might well be in balance or be net producers and acting as a source with respect to a downstream lagoon.

Larkum (1983) discusses the theoretical limits to sustainable photosynthetic yield and concludes that "annual mean primary productivity of $8 \text{ gCm}^{-2} \text{ d}^{-1}$ is therefore the upper limit that can possibly be expected from a coral reef plant community. However, higher values can be achieved for shorter periods ...". This concept would seem to be in conflict with the highest mode quoted above from Kinsey (1983a) if it can be established that extensive areas of 100% cover actually occur. The rate is, however, in apparently excellent support of the generalized "standard" rate of $P = 7$ claimed above for reef-flats. At least two recent studies

using well developed technological expertise appear to have established sustained high rates for P in areas of very high coral cover. Smith (1981) determined values of $P = 17$ (12 in September, 21 in March) for a coral shoal in the Houtman Abrolhos reefs. Adey (1983; Adey and Steneck, 1985) estimated $P = 30$ (21 in June, 43 in August) for a high-cover inner reef-flat in St. Croix. As both these studies were over an area exceeding 50 m in extent and were carried out over extended time they do seem to support the probability that $P = 8$ is not a real upper limit.

Smith (1983b; Smith et al., 1985) has supported the general conclusion that net production (P-R) in total reef systems "tends towards zero". However, he stresses that "at this time we do not have a very good quantitative grasp of the actual net metabolism of entire systems, nor are we likely to obtain quantitatively satisfactory data from conventional community metabolism studies summed over entire ecosystems". The advances in methodology allowing net metabolism to be addressed directly have been referred to in section 1. It is clear that an accurate determination of gain or loss in a reef system will prove to be of the utmost importance in terms of trophic balance, nutrient input or export, and possibly the determination of some aspects of harvestable yield. Attempts at studies of this kind in coral reef systems have been few, and restricted to those by S. Smith and coworkers (e.g. Smith and Jokiel, 1975 at Canton; Smith et al., 1985 at Christmas Island).

A Reconsideration of the Data

Table 3 summarizes most data presently available for the community metabolism of coral reefs and zones within coral reefs. It is obvious that all "complete" reefal systems reported exhibit a P/R ratio within the range 0.95-1.05. However, Smith (1983b and many others) has continually stressed that the minor departures from unity (particularly those determined by his direct procedures) are real and of the greatest trophic significance. Smith's data indicate that the Fanning Is. system exhibits a slight deficit whereas Christmas Is. system and particularly the Canton Is. system exhibit definite gains and are therefore potential exporters. This, in turn, may be attributed to a positive input of inorganic nutrients. In the case of Canton, this is almost certainly the result of the reef's location in the general area subject to the influence of the equatorial divergence. It is apparent that there is no clear pattern for P or G in total systems, both being quite variable and, no doubt, a function of the particular reef's size and geomorphology.

There are still few data available for true outer reef slopes. Certainly no generalised conclusions can be drawn from those in Table 3.

The high activity areas listed in Table 3 are very variable with respect to their location within the reef complex. Most are either "100%" hard substratum (other than algal pavement) areas on the active edges of low to moderate energy patch reefs or fringing reefs. Some are in the shallow back-reef environment and some are the tops of coral-covered shoals (Smith, 1981; Kinsey, 1979, Pl). Not surprisingly, these areas exhibit the highest rates of all extensive areas reported. P ranges from 8 to 23 while G ranges from 4 to 11.7. The P/R ratio is very variable (0.6-1.7) and clearly high cover with corals and related biota in no sense determines that the balance will be autotrophic or heterotrophic. The claims for percent cover by living corals in these areas range from 30% to 100%. There is little doubt that it is in this area of rather subjective estimation that much of the variability between sites will be explained. Kinsey (1979, 1983a) has stressed that water availability may considerably influence community metabolic activity in these areas of very high cover. It is therefore to be expected that some variability will be attributable to this factor alone. It is notable that all the values reported for such areas of high cover exceed the activity of the "standard" reef-flat ($P = 7$, $G = 4$). Smith (1981) attributed the very high productivity of these coral dominated, hard substrate areas to the three dimensional structure typical of coral thickets. He suggests the increased light-capturing capabilities of such environments facilitates the high metabolic turnover. Whether this factor alone is sufficient to offset the arguments put forward by Larkum (1983) for a sustainable upper limit of $P = 8 \text{ gCm}^{-2}\text{d}^{-1}$ is not clear.

There are only two data available for high-energy algal pavements. They exhibit little consistency. However, it is worth noting that they fall below the activity of the "standard" reef-flat.

The numerous published values for the community metabolism of the main coral/algal zones of reef flats exhibit marked consistency. This, of course, was the basis for proposing the concept of the "standard". There is only one value for P which departs significantly from the range $P = 7 \pm 1$. This value of $17 \text{ gCm}^{-2}\text{d}^{-1}$ obtained by Sournia et al. (1981) in Moorea is the more anomalous as it was obtained only from winter data. The relatively high value of $P = 8.8$ obtained by Barnes and Devereux (1984) is for late summer. Deficiencies of early methodology make it doubtful whether too much emphasis should be given to the values of $P = 4$ and $P = 10$ in the two earliest studies. Typically P/R is close to unity. No simple explanation can be offered for the few major departures from this value. Net calcification rates are generally very uniform, again with the notable exception being that obtained for a fringing reef in Moorea (Sournia et al., 1981). This value is very low principally because of a high negative night time rate offsetting a moderate positive day time rate. In fact, there is great variability in day/night calcification rate ratios between the various studies reported. It may be more satisfactory in the future to determine, and report separately, the gross calcification rates and dissolution rates. There is little evidence to suggest that the two system processes have anything in common biologically or ecologically.

Deep lagoon data are not included in Table 3. However, a few values are reported for shallow lagoon environments containing some patch reefs and the usual mix of sediment-related biota. Three sets of data (3rc-5tn) are quite consistent and for lagoons not exhibiting marked colonisation by seagrasses or algal mats. These data all conform well to the values which would be predicted by Kinsey's absolute modes for the mixture of patch reefs and

soft-bottom areas existing. However, the two recent studies in back-reefs of the central GBR (Kinsey, 1985b) and the study by Qasim et al. (1972) of a lagoon in the Laccadives give values for production much higher than would be predicted using the proportional area/absolute mode approach. These high values have been attributed to the development of extensive dense algal mats over the sediment bottom, and to the existence of dense seagrass and algal beds respectively. It is clear that the simple modality concept proposed by Kinsey (1985b) requires considerable revision if it is to have general applicability to shallow, complex lagoonal environments.

Table 3. Published values for community metabolism in coral reef systems.

Reference	Location	P (gCm ⁻² d ⁻¹)		P/R	G (kg CaCO ₃ m ⁻² y ⁻¹)
<u>"Complete" reef systems</u>					
Smith & Pesret (1974)	Fanning Is.			1	1
Smith & Jokiel (1975)	Canton Is.	6.0	5.9	1	0.5
Sournia & Ricard (1976a)	Takapoto	4	4	1	
Kinsey (1977)	One Tree Is.	2.3	2.3	1	1.5
Kinsey & Davies (1979a)	Lizard Is.	3.2	3.2	1	1.8
Smith et al. (1985)	Christmas Is.			1	0.1
<u>Outer Reef Slope</u>					
Smith & Harrison (1977)	Enewetak				4
Rogers (1979a)	Puerto Rico	2	~3	~0.7	
Adey (1983)	St. Croix	7.1	6.3	1.1	
<u>High Activity areas of near total cover by hard substratum (excluding pavement)</u>					
Gordon & Kelly (1962)	Oahu (outer reef-flat)	14	24	0.6	
Kinsey (1979)	Lizard Is. patch reef P1	9	6	1.7	4
"	" lagoon reef edge D1	14	12	1.2	5
"	Kaneohe Bay fringe reef edge	8	10	0.8	9
"	Kaneohe Bay patch reefs				10-12
"	Johnstone Is. back-reef				10
Kinsey (1983b)	Rib Reef back-reef				10
Smith (1981)	Abrolhos coral shoal	16.6	17	1.0	11.7
Adey (1983; Adey & Steneck, 1985)	St. Croix back-reefs (averages of three reefs)	23	23	1.0	
<u>Algal pavement zone</u>					
Kinsey (1977)	One Tree Is.	2.0	0.5	4	4.0
Kinsey (1979)	Lizard Is.	7.0	6.7	1.0	2.4
<u>Reef-flat coral/algal zones</u>					
Sargent & Austin (1949)	Rongelap	4	3.5	1.1	
Odum & Odum (1955)	Enewetak	10	10	1.0	
Kohn & Helfrich (1957)	Kauai	7.9	7.6	1.0	
Qasim et al. (1972)	Laccadives	6.2	2.5	2.5	
Kinsey (1972)	One Tree Is.				4.6
Smith (1973)	Enewetak	6	6	1.0	4
Smith & Marsh (1973)	Enewetak	6	6	1.0	
Kinsey & Domm (1974)	One Tree Is.	7.5	6.8	1.1	
Marsh (1974)	Guam	7.2	6.6	1.1	
LIMER Team (1976)	Lizard Is.				4
Sournia (1976)	Moorea	7.2	8.4	0.9	
Kinsey (1977)	One Tree Is. DK13	7.2	7.4	1.0	4.6
Kinsey (1979)	Lizard Is. A2	7.8	8.9	0.9	4.6
"	Lizard Is. D1	7.0	5.8	1.2	3.1
Sournia et al. (1981)	Moorea	17	17	1.0	0.5
Atkinson & Grigg (1984)	French Frigate Shoals	~6.5	~4	~1.6	~6.5
Barnes & Devereux (1984)	Rib Reef	8.8	7.6	1.2	3.5
Kinsey (1983b)	Rib Reef line reef	5.7	8.4	0.7	
<u>Shallow Lagoonal Environments (1-4 m)</u>					
Goreau et al. (1960)	Puerto Rico			0.7	
Qasim et al. (1972)	Laccadives	12.9	9.5	1.4	
Kinsey & Domm (1974)	One Tree Is.	2.9	3.1	0.9	2.0
Kinsey (1979)	One Tree Is. DK22	3.1	3.1	1.0	1.5
Atkinson & Grigg (1984)	French Frigate Shoals	2.5	2.3	1.1	1.4
Kinsey (1985b)	Rib Reef	5.0	4.2	1.2	
"	Myrmidon Reef	8.2	8.2	1.0	
<u>Uncertain designations</u>					
Odum et al. (1959)	Puerto Rico (various)	5-16	5-19	0.8-1.6	
Emery (1962)	Guam	4.5	7	0.7	
Jones (1963)	Florida			>1	
Ramachandran Nair & Gopinadna Pillai (1972)	Indian Ocean (various)	4-9			

It is unfortunate that there are too few community metabolism data from Atlantic reefs to facilitate any reasonable comparison with those from the Indo-Pacific. There is certainly a suggestion of higher rates in the very high activity areas based on the data of Adey and Steneck (1985).

Table 4 presents those data available from open system or general enclosure studies, which report activities for specific reef biotopes. Algal turfs and algal/sand flat areas are very variable (note comments in previous paragraph). Perhaps the most notable feature of these areas is the clear trend towards very high P/R values. This suggests that such algal dominated environments are acting as sources for fixed carbon exported to other areas of the reef (Table 3 indicates that a general balance will be found in the system as a whole with P/R = 1).

The two data sets in Table 4 for coralline encrusting algae suggest quite low activity for these environments with a modest autotrophy existing (P/R = 1.3-1.4). There does not appear to be any simple correlation between these findings and the two sets of data in Table 3 for extensive algal pavement zones. Regrettably, calcification data are not available for these specific studies of coralline algal biotopes. The two algal pavements reported in Table 3 were quite inconsistent in their calcification rates.

Table 4. Published values for specific biotopes in coral reef environments.

Reference	Location	P ($\text{gCm}^{-2}\text{d}^{-1}$)	R	P/R	G ($\text{kg CaCO}_3\text{m}^{-2}\text{y}^{-1}$)
<u>Algal turfs & algal/sand flats</u>					
Smith (1973)	Enewetak	11.6	6.0	1.9	4
Smith & Marsh (1973)	Enewetak	10.4	6.0	1.7	
Kinsey (1979)	Lizard Is.	4.3	4.3	1.0	0.3
	Kaneohe Bay	5.6	2.6	2.2	0.3
Hargraves (1982)	Carrie Bow Key	~20		~0.5	
Sorokin (1982)	Various Indo-Pacific	2-4		1.2-1.8	
Vooren (1981)	Curacao	1.9	0.7	2.7	
Hawkins & Lewis (1982)	Barbados	1.0	0.2	4.6	
Rogers & Salesky (1981)	St Croix (turf)	3.0	2.1	1.4	
	(macro)	14.7	4.0	3.7	
<u>Coralline encrusting algae</u>					
Vooren (1981)	Curacao	1	0.8	1.3	
Hawkins & Lewis (1982)	Barbados	0.8	0.6	1.4	
<u>"Sand" areas</u>					
Sournia (1976)	Takapoto	~2			
Sorokin (1982)	Various Indo-Pacific	0.6-1.3			
Kinsey (1977)	One Tree Is. DK17	0.9	1.4	0.6	0.4
Kinsey (1979)	Kaneohe Bay	2.7	2.4	1.1	1.2
Kinsey (1979)	One Tree Is. DK13	1.5	1.5	0.7	1.0
<u>Coral outcrops</u>					
Kinsey (1979)	Various (6 sites GBR)	17-37	19-43	0.9-1.3	9-10
	<u>Leptoria phrygia</u> patch	8	9	0.9	
	<u>Acropora pulchra</u> patch	18	15	1.2	
	<u>Porites andrewsi</u> patch	14	13	1.1	7
	<u>Pocillopora damicornis</u> patch				10
Atkinson & Grigg (1984)	French Frigate Shoals				
	<u>Porites compressa/lobata</u>	~10	~9	~1.1	~9

Note: Values are expressed per unit plane area of reef over which the indicated biotope occurs.

Areas designated as "sand" have generally been found to be surprisingly active with both P and G quite high for areas usually assumed to play only a minor role in the reef material budget. Much of this activity is likely attributable to foraminifera (Sournia, 1976) and this is certainly supported circumstantially by the appreciable calcification rates indicated for the three GBR sites. Hallock (1981) has estimated calcification rates for foraminifera in sediments in the range $G = 0.2$ on seaward slopes, $G = 2.8$ on reef-flats, and $G = 0.6$ on lagoon slopes. Hallock's data were all obtained in Palau, but are clearly compatible with the generalised data in Table 4 for sand areas in the GBR region.

The coral outcrops listed in Table 4 by dominant species were studied using temporary enclosure of large coral knolls or patches. Those sites averaged from Kinsey (1979) without designation of dominant species were determined by enclosure of the sediment bottom in reef-flat areas then determining the coral outcrop activity from the overall reef-flat activity by difference. There is an impressive consistency in the findings, with the value of P showing a marked correlation with the type of coral (where designated). Calcification rates are consistently high and, with the exception of the Atkinson and Grigg (1983) data, have been used to develop the modality theory previously outlined.

It is clear that the activities of these specific coral outcroppings are those which are approached by the "high activity areas of near total cover" in Table 3. It is particularly notable that the open structure, highly branched Acropora pulchra outcrop reported from One Tree Island (23°S) exhibits virtually identical community metabolism to that exhibited by the high activity area in the Abrolhos (29°S) reported by Smith (1981; see Table 3) and also dominated by branching species of Acropora.

Borowitzka et al. (1983) have suggested that typical patch reefs have hard substratum cover made up as follows: 20-70% turf algae; 20-60% coralline algae; 25-30% corals. He suggests that the photosynthetic contribution of these three groups is about equal. Sorokin (1982) essentially supports these findings in suggesting that periphyton covered dead coral is about equal to living corals in activity though exhibiting a higher P/R ratio (up to 2 for periphyton; 1-1.5 for corals). Sorokin does not speculate on the relative contribution of the encrusting corallines. The implication of both these authors' findings would seem to be that the productivity of hard substratum reefal environments should be relatively similar regardless of the percentage cover with living corals. This does not seem well supported by Table 4 which suggests that corals are significantly more active than most of the other reef environments per square metre of projected reef area. Nor is it supported by the data from the high activity areas in Table 3 where the results are rather widely variable though bearing no close relationship to living coral cover.

Seasonality and latitude

The importance of considering seasonality in community metabolism studies of coral reefs was raised by Kohn and Helfrich (1957) and by Gordon and Kelly (1962). Kinsey and Domm (1974) and Kinsey (1977) stressed the marked nature of seasonality and suggested that the phenomenon did not appear to be strongly correlated with latitude despite a greater seasonality of temperature with increased latitude. Table 5 covers most of the studies in which seasonality has been explicitly examined. All data are for shallow areas substantially dominated by corals and related hard substratum. The early data of Kohn and Helfrich are, by their admission, rather imprecise with respect to the reliability of the seasonality information. Excluding that study, it is most striking how uniform the pattern of seasonality is in terms of P and R, with an approximately two-fold summer/winter difference. However, what variability does occur is surprisingly in approximately inverse relationship to latitude. Thus, the greatest seasonality is at Lizard Is. (14°S) while the least is at the Abrolhos (29°S). Net calcification follows the opposite trend, with only slight seasonality at reasonable latitudes but developing very marked seasonality near the limiting latitudes of French Frigate Shoals and the Abrolhos. These trends seem sufficiently clear to be accepted, but no straightforward explanation is indicated. Another aspect of seasonality having a significant effect on the overall data is that winter algal blooms characterize the two lowest latitude sites (Lizard Is. and Kaneohe Bay). This, in turn, accounts for the higher P/R ratio in winter time. The One Tree Is. sites are characterized by summer algal blooms (Kinsey, 1979) which gives the reverse pattern in the P/R ratio. The published information for the other sites does not appear to make clear whether there is a clear seasonality in the standing stocks of labile algae.

Atkinson and Grigg (1984) also report seasonality in the general shallow lagoon environment at French Frigate Shoals. It is notable that the trends in this more algal environment are much less marked (S/W ratios P 1.1; R 1.2; G not given) than those in the reef-flat environment. However, the seasonality in a *Porites* dominated coral outcrop (S/W ratios P 2.7; R 2.6; G 1.9) was generally similar to that of the overall reef-flat. It seems clear that the corals themselves are likely to prove the most seasonal component of high latitude reefs. By contrast, the low S/W ratio in calcification found at One Tree Is., Lizard Is., and Kaneohe Bay suggest that extreme seasonality in the corals is not at all a feature at these more moderate latitudes. By inference then, the more labile primary producers such as the foliose algae must account for most of the seasonality at lower latitudes.

Table 5. Seasonality in community metabolism of shallow reef-flat areas. The ratio of summer (S) to winter (W) values is given in parentheses.

Reference	Location		P ($\text{gCm}^{-2}\text{d}^{-1}$)	R ($\text{gCm}^{-2}\text{d}^{-1}$)	P/R	G ($\text{kg CaCO}_3\text{m}^{-2}\text{y}^{-1}$)
Kohn & Helfrich (1957)	Kauai fringing reef (22°N)	S	8.3	7.6 (1.0)	1.1	
		W	7.7 (1.1)	7.6 (1.0)	1.0	
Kinsey & Domm (1974)	One Tree Is. patch reef (23°S)	S	4.1	3.8 (1.6)	1.1	
		W	1.7 (2.4)	2.4 (1.6)	0.7	
Kinsey (1977)	One Tree Is. reef-flat (23°S)	S	9.0	7.9 (1.5)	1.1	5.0 (1.3)
		W	3.6 (2.5)	5.3 (1.5)	0.7	4.0 (1.3)
Kinsey (1979)	Lizard Is. reef-flat (15°S)	S	9.7	11.8 (3.1)	0.8	3.3 (1.4)
		W	4.1 (2.4)	3.8 (3.1)	1.1	2.4 (1.4)
Kinsey (1979)	Kaneohe Bay fringing reef (21°N)	S	11.0	15.1 (2.5)	0.7	10.0 (1.3)
		W	5.5 (2.0)	6.4 (2.5)	0.9	7.9 (1.3)
Smith (1981)	Abrolhos coral shoal (29°S)	S	21.0 (1.7)	19.6 (1.4)	1.1	18.3 (3.9)
		W	12.1 (1.7)	14.4 (1.4)	0.8	4.7 (3.9)
Atkinson & Grigg (1984)	French Frigate Shoals reef-flat (25°S)	S	8.5	4.9 (1.9)	1.8	10.2 (3.6)
		W	4.3 (2.0)	2.6 (1.9)	1.7	2.5 (3.6)

Adey and Steneck (1985) indicate that the seasonality in the three St. Croix (lat. 18°N) fore-reefs which they studied gave S/W ratios of ~1.5 for P and ~2.0 for R. The three high cover back-reef areas of their study reefs gave S/W ratios of ~1.8 for P and ~1.3 for R. These values are clearly in good agreement with those for the general Pacific reef-flat environments included in Table 5. However, there is a suggestion of lesser seasonality when considered relative to latitude and compared with Lizard Is. reef at lat. 15°N.

Not only does Table 5 demonstrate the generally uniform nature of seasonality with latitude, but it clearly suggests that neither primary production nor calcification in shallow reef environments exhibits any tendency to decline with increasing latitude - at least up to the 29° limit of the data included. This finding would seem to be in total contradiction of the direct radiographic growth rate studies reported by Grigg (1982). Grigg's findings suggest that at least one coral species, *Porites lobata* exhibits a growth rate which declines at a simple linear rate with increasing latitude along the Hawaiian Archipelago. The decline in growth rate of *P. lobata* is quite clear even by latitude 23° at French Frigate Shoals - the system where Atkinson and Grigg (1984) found a very typical, unattenuated calcification rate for the reef-flat as a whole, and one which was not, apparently, the result of increased standing stocks of calcifiers.

In discussing the apparent lack of decrease in metabolic activity with increasing latitude, Smith (1981) states "all (pieces of evidence) suggest that total community metabolism does not drop dramatically as the community composition shifts from coral reef to kelp and seagrass communities; rather, the coral reef contribution to that metabolism drops". Smith goes on to conclude: "Complex coral reef communities which have penetrated beyond their usual latitudinal limits can be expected to function much like complex coral reef communities elsewhere; eventual loss of complexity will attenuate the standing crop and production of inorganic and organic materials commonly associated with coral reefs". Johannes et al. (1983b) support Smith's contention that reef activity and growth does not become lower with increased latitude *per se*, but suggest that competition with macroalgae may set the ultimate latitudinal limit for reef occurrence.

Land Proximity

In general, Table 3 indicates approximately the same level of community metabolism for reefs closely associated with high land masses as it does for oceanic reefs and reefs of the GBR system. A tentative conclusion, based on the data set for St. Croix (Adey and Steneck, 1985) and that for Moorea (Sournia et al., 1981), might be that very high values are sometimes, but not always, associated with high island reefs.

In the discussion of phytoplankton activity associated with coral reefs, it was noted that occasional blooms are associated with periodic runoff (Ricard, 1977; Marsen, 1977). Such land runoff will almost inevitably contain elevated nutrient levels. Is there then any good evidence to suggest that reef benthos responds to either periodic elevation of nutrients or to a general proximity of land? Birkeland (1984) states that "average primary productivity does not differ significantly between high islands and atolls". However, he believes that the response of island systems to "occasional intense pulses of nutrients" is seen at the level of the benthos as well as the phytoplankton.

It is clear from numerous studies that long-term reef community structure is strongly influenced by proximity to land. The present core ecological program of the Australian Institute of Marine Science is primarily oriented to the elucidation of this influence. Williams and Hatcher (1983 - fish), Done (1982 - corals and general descriptive), Drew (1983 - *Halimeda*), Wilkinson et al. (1984 - nitrogen fixation) and Wilkinson and Trott (1985 - sponges) all have reported marked transitions in reefs across the Australian continental margin in the central GBR region. The A.I.M.S. community metabolism studies have not yet reached a stage of establishing clear equivalent and sustained trends. However, they are strongly implied by the first 2 years data. Kinsey (1985b) indicates an appreciable difference in back-reef algal mat metabolism between a mid-shelf reef (Rib) and an outershell reef (Myrmaidon) (see also Table 3). The outer reef exhibited appreciably higher activity but a lower net gain than the mid-shelf reef.

In the previous section it was noted that Smith (1981) has expressed the view that reef community metabolism tends towards constant values regardless of quite marked shifts in community structure. However, this observation does not include consideration of the possible influence of nutrient gradients existing near land masses. At this stage in the development of community metabolism studies, it seems reasonable to suggest that all reefs do tend to common levels of sustained activity in equivalent zones and seasons. However, much of the second order variation in findings previously attributed to "noise" will prove to be real trends. Some of these trends will certainly relate to such influences as land proximity (Kinsey, 1983b). A.I.M.S. data suggest that reef-flat variability within the "standard" range $P = 7 \pm 1$ and $G = 4 \pm 1$ does relate to real gradients. The effects alluded to in these findings are probably different to the short-term pulse responses discussed by Birkeland (1984).

Light relationships

Many community metabolism studies have included measurements of incident radiation and many have included the calculation of photosynthetic conversion efficiencies. However, until recently none have reported the precise nature of the relationship between light and the biogeochemistry of the system.

Barnes and Devereux (1984) have published two elegant diagrams demonstrating the relationships between net hourly production and light intensity, and net calcification activity and light intensity. These two diagrams are reproduced here as Figures 1 and 2. The data are for most of the width of the reef-flat (excluding the surf zone of the reef crest) in late March (late summer) at Rib Reef on the Australian Great Barrier Reef. The data presented are obtained using the continuous logging, Lagrangian approaches referred to in the methods review section. Figure 1 demonstrates clearly that reef-flat photosynthesis and respiration are greatest towards the reef crest and decline towards the back-reef throughout the night or in periods of full isolation. However, it is equally clear that the light saturation characteristics of the community vary considerably with distance from the crest. The outer reef-flat

never achieves saturation whereas the inner reef-flat is saturated at about $1000 \mu\text{E m}^{-2}\text{s}^{-1}$. At light intensities lower than this level, the central reef-flat net photosynthesis falls off much more rapidly than areas to either side.

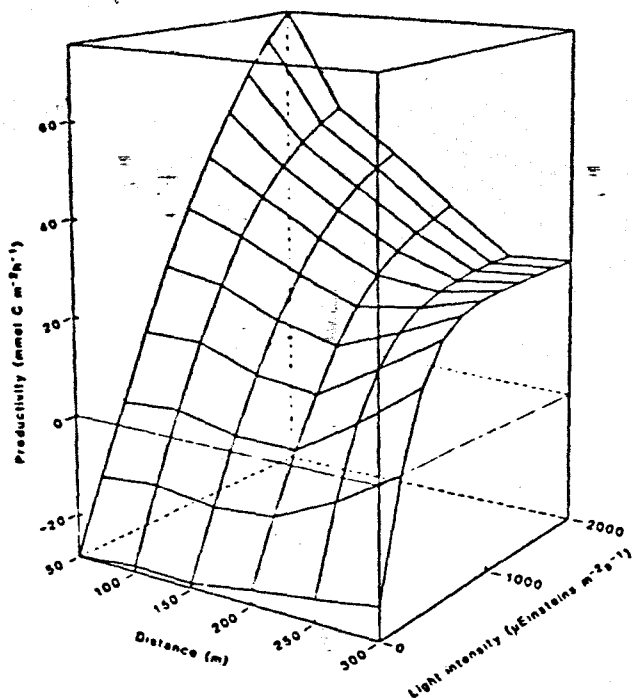


Figure 1. . Perspective diagram of net productivity (positive values) or net respiration (negative values) in terms of light intensity across the reef-flat at Rib Reef, a mid-shelf reef in the Central Great Barrier Reef. The diagram is reproduced from Barnes and Devereux (1984) with permission of the publishers.

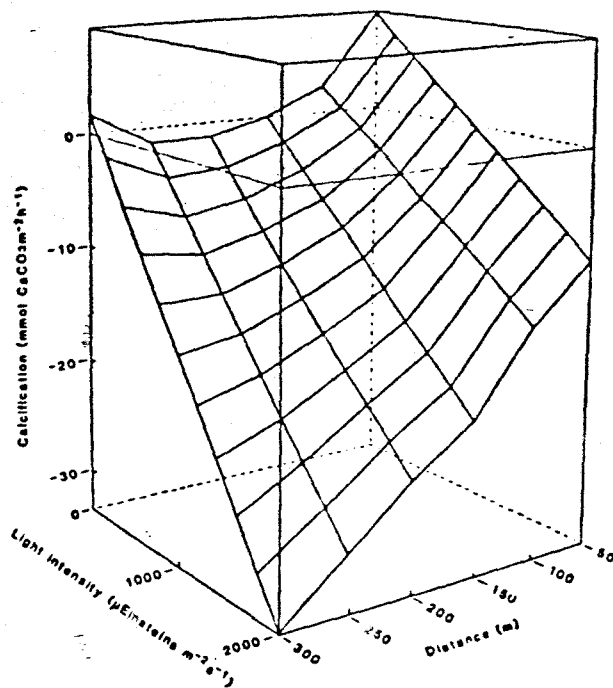


Figure 2. Perspective diagram of net calcification (negative rates) or net dissolution (positive rates) in terms of light intensity across the reef-flat at Rib Reef, a mid-shelf reef in the Central Great Barrier Reef. The diagram is reproduced from Barnes and Devereux (1984) with permission of the publishers.

In Figure 2, Barnes and Devereux (1984) indicate that calcification (here plotted as increasingly negative values with increased activity) never even approaches saturation with increased light intensity and an approximately linear relationship is maintained throughout. However, the slope of this linear relationship varies with position on the reef-flat such that at zero light (nighttime) appreciable rates of dissolution are achieved towards the reef crest and to a lesser degree towards the back-reef, whereas slightly positive rates of calcification are maintained in the central reef-flat throughout the diel cycle. Overall, rates of daytime net calcification increase markedly with distance from the reef crest. Barnes and Devereux (1984) discuss the community structure implications of these findings at length. The value of this kind of study and the interpretive power of detailed data presentation of the kind used by Barnes and Devereux is obvious. This reef-flat, for which this detailed community metabolism analysis is now available, is the same reef-flat for which the generalised information in Table 3 simply indicates a rather normal, virtually "standard" reef-flat.

6. THE FATE OF ORGANIC PRODUCTION

It has already been established that most, if not all, coral reef systems studied exhibit a virtual balance between P and R over extended time. However, it has also been stressed that, while this may be approximately true for the total system, it certainly is not true for all zones within the system. Major imbalance between P and R occurs in various zones. Some of this surplus or deficit may represent build-up or decline in standing stocks over relatively short time periods (e.g. one season). However, the annual imbalance must be considered to represent interzonal transfer of fixed organics (either soluble or particulate).

Smith (1983b and others) has stressed that even the apparent balance between total system P and R may be little better than a generalisation. Import and/or export may be small but very significant. Typically, fluxes in particulates entering and leaving coral reefs have been very inadequately studied, though changes in the concentrations of such materials are appreciable. Studies on fluxes of dissolved organics have proven particularly uninformative because of the high levels of refractory DOM contained in the incoming "oceanic" water, together with the high flux rate for the water mass over shallow reef areas.

Lewis (1977) summarized the status of knowledge concerning detritus in coral reefs. Drawing from the findings of Marshall (1965), Gerber and Marshall (1974), Johannes (1967), Qasim and Sankaranarayanan (1970), Glynn (1973), and others, Lewis concluded that "there are then a number of studies which show that on crossing a reef, oceanic water acquires detritus which is then available to filter feeders and suspension feeders on the reef including corals". He stressed that, while the biomass of zooplankton entering many reefs has been apparently demonstrated to be too low to support the nutritional needs of corals, there were clearly very much higher levels of other material (detritus) to satisfy this need. He also stressed the several studies on mucus aggregates in the literature. Thus, the emphasis is clearly on the production of particulates by the reef and therefore the potential for export to other downstream zones or to outside the total system. No conclusion is drawn concerning the level of ultimate export which may be associated with reefal systems.

Lewis (1977) also summarized the status of zooplankton studies. He reiterates the findings of the early reef studies which concluded that incoming zooplankton clearly cannot support the benthic invertebrates on the reef. He indicates that Tranter and George (1972) and Glynn (1973) measured appreciable reduction of incoming zooplankton biomass indicating that reefs certainly availed themselves of this food supply, to an extent equivalent to perhaps 10% of the total community metabolism (reef-flat only). However, Lewis also stresses that several studies (e.g. Emery, 1968; Sale et al., 1976) have found a substantially elevated level of zooplankton associated with reefs demonstrating that, while reefs doubtlessly remove much oceanic plankton, they may frequently make more of their "own" than they consume from the ocean. Thus, this reef-related zooplankton must be considered as a further component of the organic particulates produced and available for interzonal or extra-system export. Clearly, the original source of this excess production of zooplankton must be reef primary production.

Kinsey and Davies (1979a) summarized essentially the same literature as Lewis. It is noted that most detritus in the water crossing reefs is benthic algal in origin. They stress that interzonal transport of detritus is frequently "up to 10% of the photosynthetic production of the seaward reef zones. Much of the material has been found to be deposited on the inner reef-flats with some net transport into the lagoon (Odum and Odum, 1955; Marshall, 1965, 1968; Qasim and Sankaranarayanan, 1970; Johannes and Gerber, 1974; Marshall et al., 1975)". Kinsey and Davies generalise that "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". In retrospect, it seems that most evidence is insufficiently precise to support this claim. However, it is clear (see previous section) that net gain in the sense of E is very low in total systems. Kinsey and Davies summarize: "the creation and re-utilization of dissolved or suspended particulate organic matter is dominantly an internal function of reef systems with negligible net exchange with the ocean". While this is probably a reasonable first order approximation, the conclusion is based on a totally inadequate data base, particularly for dissolved organics.

Hatcher (1983) has recently reviewed the literature on the subject of the role of detritus. Relatively few new references are cited (e.g. Westrum and Meyers, 1978; Simmons, 1979; Meyers, 1980; Moriarty, 1979; Sorokin, 1978; Crossland et al., 1984; Hatcher, 1982). Hatcher's review is by far the most comprehensive available concerning the sources and fates of particulate and dissolved organic matter on coral reefs. He stresses particularly the importance of quality (in terms of C:N:P) in considering the distribution of organics. In this connection, Glynn (1973) noted that, even though the flux of detrital organics exceeded $\times 10$ that of plankton, no significant depletion of detritus appeared to occur from the water moving across the reef-flat. By contrast, he noted that 90% of the diatoms and 60% of the zooplankton was removed. Atkinson and Smith (1983) have also drawn attention to the relatively low quality of macroalgal detritus (median C:N:P = 550:30:1) compared with phytoplankton. Particularly they stress the low phosphorus levels. On the other hand, Dunlap's (1985) work has stressed the value of exported organic matter in acting as an immediate source for extracellular remineralisation of phosphate. Hatcher's review summarizes the nature of particulate matter: "The particulate fraction in waters bathing the perimeters of CRE's (coral reef ecosystems) is composed mainly of detrital material and living heterotrophic microbes, with plankton comprising only a small portion. On the outer reef slopes and reef crests organic aggregates and mucus flocs derived from the rich coral communities are the major constituents. Over algal ridges and reef-flats fragments of algae, and, to a lesser extent faecal pellets, dominate POM. Total organic loading is highest downstream of these areas In the backreef areas POM concentrations decrease as a result of sedimentation Coral reef lagoon waters are substantially enriched although concentrations are not as high as those over the surrounding reefs (but) a greater proportion ... is living plankton especially zooplankton".

Hatcher stresses the role of bacteria in converting DOM to POM and refers to the evidence for release of substantial quantities of DOM by both algae and corals. He indicates that much of the variability in data for the production and export of organics by reefs reflects the large errors associated with the methods employed. In this connection, he stresses the need for synoptic consideration. Hatcher reconsiders export of organics from reef-flats and concludes that many systems may be exporting more than 20% (as high as 60%) of their gross primary production to downstream areas. He discusses the fate of POM and DOM on its downstream passage through the reef system in considerable detail but does not speculate on the possible rate of ultimate export from the system as a whole.

In overall conclusion, it seems fair to say that the more detail that has appeared in the literature on the subject of the movement of organics through reef systems, the more confused has become any possible hypothesis concerned with the overall trophic balance of the system. However, it is clear that import, creation, redistribution and export of dissolved and particulate (living and detrital) organic matter is proving to be of the greatest possible importance to any complete study of system level carbon flux and trophic balance in coral reefs. Our earlier tendency to assume that a coral reef could be trophically characterised by consideration of its community metabolism was much too simplistic. We have, however, been

encouraged to adopt this simplistic reasoning by the fact that reefs do tend to exhibit overall P/R ratios close to unity. At this stage the only safe assumption to be drawn from a long term P/R = 1 would seem to be that import equals export. Similarly, therefore, P/R = 1.1 should not be interpreted as 10% of P available for export, but rather a situation in which potential export exceeds import by an amount equal to 10% of P.

7. THE FATE OF "INORGANIC" PRODUCTION

The previous section has emphasized the substantial uncertainties concerning the magnitude and fate of the small or possibly negligible excess organic production of a coral reef. It did, however, also emphasize the quite substantial possibilities identified for interzonal transfer. By contrast, the magnitude of excess production of inorganic carbon compounds (essentially, CaCO_3) is now well quantified and substantial. Similarly, a considerable amount is known about the redistribution (interzonal transfer) and export of these materials in the form of sediments. Another review in these proceedings is concerned specifically with the growth of coral reefs, which is the long term expression of the accumulation and redistribution of reefal sediments. This section will therefore be restricted to comments on the status and significance of "metabolically" determined calcification rates.

The earlier section on "Benthic and Total System Studies" has summarized the present state of knowledge concerning calcification rates determined by biogeochemical and methods. Smith and Kinsey (1976) drew attention to an apparent bimodality in reef calcification rates of $G = 4$ for reef-flats and $G = 0.8$ for lagoons or complete systems. Kinsey (1979, 1982, 1983a) drew attention to a much higher mode of $G = 10$ for areas of very high cover. He accepted the mode $G = 4$ for extensive reef-flats and algal pavements but suggested $G = 0.5$ for sediment dominated areas. He also suggested that most reef-flats were themselves a mixture of the $G = 10$ and $G = 0.5$ modes to give an effective weighted mean of $G = 4$. Only algal pavements were conceded to represent an absolute $G = 4$ mode. This present review has presented data from a number of authors which generally closely conform to the above modes. The only appreciable exception is the reef-flat rate of only $G = 0.5$ for a fringing reef in Moorea found by Sournia et al. (1981). There has been little evidence that generalised reef calcification declines with latitude (within those latitudes in which reefs occur) despite the marked decline in growth rates for at least some corals (Grigg, 1982). While there is some evidence for higher calcification rates in the Caribbean than those found in the Indo-Pacific (Adey, 1978), specific comparative studies such as that of Kinsey (1982) suggest that comparable locations in both oceans exhibit very similar calcification rates. The frequency of lower rates reported from the Pacific is likely to prove principally a function of the difference in reef structure forced by the high energy regimes so common in the Pacific (Adey, 1978). Kinsey (1979; 1983b,c) has also drawn attention to the fact that, in addition to the limited areas of high percent cover on reef edges, extensive areas do occur in the Pacific exhibiting elevated calcification rates averaging $G = 10$. These areas are apparently well below present day sea level (to the extent of 1-5 m) and as such are able to grow vertically without restriction. Clearly, the implication of such findings is that elevated growth rates around the $G = 10$ mode were probably normal, or at least common, during much of the Holocene transgression when major vertical framework accretion was occurring. It has been suggested that reduced calcification rates (or departures from the normal mode) may result from upwelling or enrichment of the surface water (Glynn, 1977; Glynn and Stewart, 1973; Kinsey and Davies, 1979b; Kinsey, 1979). Whether this is primarily temperature related or nutrient related is not fully determined. These inhibitory effects are not likely to be "felt" by very many reefs and so the findings are probably of specific interest rather than of wide application. However, Kinsey and Davies (1979b) do raise the possibility that surface enrichment may have been a more widespread phenomenon during the Holocene transgression.

Smith (1983a) has also summarized the available calcification rates up to about 1981 and supported the general modal concept outlined above. As mentioned earlier, Smith has suggested that 90-95% of the world's coral reef area will conform to a $G = 0.8$ mode (Smith's generalised lagoonal mode which includes patch reefs and therefore is not a contradiction of Kinsey's $G = 0.5$ mode), 4-8% to a $G = 4$ mode, and 1-2% to a $G = 10$ mode.

Three important points must be considered in attempting to use these system level calcification rates to predict growth rates for the reef. 1. There is no reason to assume that the biogeochemically precipitated carbonates estimated by the flux studies reported here are retained at the site of their creation; however this is more likely in the deeper and frequently more active areas where in situ framework construction is occurring and the high $G = 10$ calcification mode is probably operative. 2. The values for G are net, and may represent positive rates for both day and night (normally exhibiting a pronounced diel cycle), or may be the resultant of positive precipitation in the daytime and substantial dissolution processes throughout the 24 hour period. In the latter situation, most common in fully developed reef-flat communities, there is no reason to assume any relationship between the processes of precipitation (i.e. growth of corals, algae, forams etc.) and the processes of dissolution (i.e. infaunal boring etc.). Thus, most current precipitation in growth processes may be exported as particulate sediments, while all dissolution occurs from the standing stock of carbonate materials - i.e. a positive value for G does not automatically imply a positive rate of in situ growth. 3. Even the most localised values for G so far determined are averaged over appreciable areas. Thus considerably higher rates of calcification may well be possible in very restricted areas of active coral growth.

If the dominant modes for G are converted to vertical growth potential using a density of 2.9 g cm^{-3} for calcium carbonate and assuming an average porosity for reefal sediments of 50% (Smith and Kinsey, 1976; Davies and Kinsey, 1977) it can be seen that the three modes become: $G = 10$, = 7 mm y^{-1} ; $G = 4$, = 3 mm y^{-1} ; $G = 0.5$, = 0.35 mm y^{-1} . However, as Smith (1983a) points out, very rapid reef framework growth may exhibit porosity up to 90% in some cases. If we allow a more conservative 60% upper limit for framework porosity while

leaving the reef flat and sediment areas at 50% porosity, then the three potential growth rate modes might be better stated: $G = 7-9 \text{ mm y}^{-1}$; $G = 3 \text{ mm y}^{-1}$; $G = 0.3 \text{ mm y}^{-1}$. These modes represent the simple case where all production remains in place. Obviously both higher and lower rates can occur where sediments are imported or exported respectively.

What then is the level of agreement between these growth modes predicted from present day biogeochemical production rates, and the rates of actual reef growth in the Holocene determined from reef stratigraphy. Davies (1983) indicates that framework growth falls within a wide range of $1-16 \text{ mm y}^{-1}$ with modes at $7-8 \text{ mm y}^{-1}$ for patch reef and $4-6 \text{ mm y}^{-1}$ for reef margins. He supports the biogeochemical findings that there is little correlation with latitude. He also reports clear evidence from cores that the most recent surface growth has slowed down (i.e. since approximating the present sea level). Davies et al. (1983) not surprisingly report the same wide range with an upper limit of 14 mm y^{-1} . Hopley (1983) suggests that upper Holocene framework growth tends to the range $5-10 \text{ mm y}^{-1}$ while present sea level growth is at 2 mm y^{-1} or less. This same information is detailed slightly differently by Davies and Hopley (1983). They suggest a mode of 2 mm y^{-1} for coralline algae (note 3 mm y^{-1} claimed above for the biogeochemical rate in such areas), $7-8 \text{ mm y}^{-1}$ for patch reef framework (note $7-9 \text{ mm y}^{-1}$ claimed for biogeochemical rate above), $3-9 \text{ mm y}^{-1}$ for leeward margin framework (note same $7-9 \text{ mm y}^{-1}$ claimed above), and $1-4 \text{ mm y}^{-1}$ for fringing reefs (note 3 mm y^{-1} claimed above for reef-flats). The comparison between actual margin growth or patch reef growth, and the calcification rate for high activity areas appears totally justified as these areas would not have functioned operationally as surface reef-flats during the active Holocene transgression but as areas of framework accretion. Note that these authors indicate the present day growth rates to be lower. The comparison between the actual growth rates for fringing reefs and the calcification rate for present day reef flats also seems reasonable in view of their generally more elevated antecedent platform (maintained by some terrigenous sedimentation) and consequently their more protracted status as a true reef-flat. Glynn and Macintyre (1977) also reported very compatible ranges for real growth in the Pacific Panama area of $1.3-4.2 \text{ mm y}^{-1}$ for reef-flats and 7.5 mm y^{-1} for upper reef slope.

Davies and Hopley (1983) argue that the equivalence of their vertical accretion modes and the present day biogeochemical precipitation rates is not as close as it has been presented above. They suggest that vertical accretion can never involve 100% of the material precipitated as some horizontal growth must be assumed. Over extensive areas of reef perimeter or across a large patch reef this contention seems to be incorrect. They also suggest that their vertical accretion rates based on ^{14}C dating techniques may be underestimates but the evidence to support this seems tenuous. As a first approximation it seems that reef growth rates for *in situ* framework determined from Holocene cores are in good general agreement with present day net biogeochemical precipitation rates. The fact that the chemical rates indicate a somewhat more restricted range than is actually found in cores can be explained, at least in part, by the spatial variability which may be missed by the averaging effects of present biogeochemical technology. The reduction in growth rates associated with many modern surface reefs (Hopley and Davies various as above) does not appear to represent any unexplained change in present day performance. Rather it would seem to be simply a reflection of a transition from the unrestricted framework growth rate of $G = 10$, $= 7-9 \text{ mm y}^{-1}$ to the restricted reef-flat growth rate of $G = 4$, $= 3 \text{ mm y}^{-1}$ associated with reaching sea level; noting particularly that the potential growth of $7-9 \text{ mm y}^{-1}$ in the past is likely to have been realised whereas the potential growth of 3 mm y^{-1} today is likely to be mostly exported by downwind sediment transport.

8. NUTRIENT FLUX STUDIES

The literature concerning nutrient fluxes on coral reefs is now extensive. Regrettably, it is not feasible to cover the subject adequately in one section of this overall review of system metabolism. Our modern understanding of the role of nutrients on coral reefs began with the Symoios Expedition to Enewetak Atoll in 1971 (Jonannes et al., 1972; Pilson and Betzer, 1973; Wiebe et al., 1975; Webb et al., 1975). These studies led to two conclusions of great significance - that coral reefs probably exported nitrogen compounds, thus suggesting that fixation was a major process, and that nitrogen was unlikely to be limiting; that coral reefs had a negligible effect on the phosphorus content of the water flowing across them thus suggesting that phosphorus was tightly recycled. Of course this led to no easy conclusion as to whether any nutrient exerted a controlling influence on reef production. Pomeroy et al. (1974) also stressed the extreme importance of recycling as a phenomenon dominant in coral reef nutrient dynamics.

Lewis (1977) reviewed the early literature up to and including the Symoios papers and concluded "that while various forms of phosphorus might be in low concentrations they are renewed continuously and recycled within the reef system". With respect to nitrogen, Lewis concluded: "Much more work on nitrogen flux ... is needed but the prevailing opinion appears to be that the resources of nitrogen are tightly cycled or conserved at least with the coral plant/animal association. Nitrogen fixation may make an important contribution to the amount in surface waters ..."

Crossland (1983) in reviewing the status of nutrient studies up to about 1980 concluded: "The concentration of dissolved nutrients in seawater provides a tool for use in furthering our understanding of coral reefs". He also stresses: "Nutrient concentrations alone provide minimal information and future study should be aimed towards appraising the dynamics of nutrient fluxes". Citing work in the Lizard Island system, Crossland stresses that there may be major differences between zones of a reef in their strategies for nutrient handling. Thus interzonal transport is as important with respect to dissolved inorganic nutrients as it has been found to be with fixed organic matter (see earlier sections). The overall effect of the Lizard Island system on its surrounding continental shelf water is summarised (Crossland and Barnes, 1983) by suggesting that there is no significant net consumption or export of inorganic

nitrogen, phosphorus, silicate, organic carbon or organic nitrogen. However, nitrate was exported from the windward reef to the lagoon but had returned to background levels in water leaving the leeward reef. Elevated levels of ammonium, POM and PON moved from the lagoon to the leeward reef but were removed by passage over the leeward reef. Thus the lagoon is identified as playing an important role in nutrient balances.

Very wide ranges of concentrations for nutrients in coral reef waters have been published. Crossland (1983) has summarized these to about 1980. There has been no recent complete tabulation of values but it is doubtful that a large table of such virtually random information is useful in this review. Crossland's (1983) values for nitrate range from essentially oceanic at $0.01 \mu\text{M}$ to as high as $2.5 \mu\text{M}$ in some lagoons. Values as high as $5 \mu\text{M}$ are reported for the enclosed areas of the Abrolhos. Ammonia is usually detected and values reported range from 0.07 to $2.5 \mu\text{M}$ with Abrolhos values reaching nearly $3 \mu\text{M}$. Dissolved organic nitrogen tends to be more consistent and in the range 1.7 – $5 \mu\text{M}$ with occasional higher values. Dissolved organic phosphate values are relatively few and typically less than $1 \mu\text{M}$. Values found in specific studies involving nutrient addition and in polluted environments obviously are higher. However, even areas of known chronic pollution of reefs such as Kaneohe Bay (prior to 1978) or Tarawa lagoon are subjected typically to a range of inorganic nitrogen of only 2 – $4 \mu\text{M}$ and of inorganic phosphate of 0.3 – $1.2 \mu\text{M}$ (Smith et al., 1978; Kinsey, 1979; Johannes et al., 1979; Smith et al., 1981).

There have been a number of recent papers addressing specific aspects of coral reef nutrient dynamics. Wilkinson and Sammarco (1983), and Wilkinson et al. (1984) have found nitrogen fixation to be a very general phenomenon in GBR systems with the greatest rates found away from the land influence even though the greatest algal biomass is found inshore. This effect is attributed, at least in part, to increased fish grazing rates offshore which encourage colonisation by blue-green algae. Hanson and Gunderson (1976) suggested that bacterial nitrogen fixation may be more important than fixation by blue-greens in some systems (Kaneohe Bay is cited as a probable case). Dunlap (1985) has drawn attention to the possibility of major and very rapid remineralisation of phosphate from organic matter in the water column caused by the production of microbial extracellular phosphates. This cycle may be sufficiently rapid to result in negligible net changes in inorganic phosphate levels. Entsch et al. (1983a) have reported substantial phosphorus pools in lagoonal sediments with very elevated levels of both phosphorus and nitrogen being detected in interstitial waters. They suggest the possibility of Halimeda flakes as a mechanism for input of nutrients to the sediment pool. Similarly, Andrews and Muller (1983) report the maintenance of elevated nitrate and phosphate levels in the water within the open framework of a patch reef. They suggest that the patch reef indicated a potential for export of nitrogen equal, per unit area, to that reported for the Enewetak reef-flat by Webb et al. (1975). D'Elia et al. (1981) have drawn attention to the possibilities for continuous groundwater input to have a major impact on nutrient supply to fringing reefs and particularly to establish a more usable N:P ratio by virtue of the pronounced elevated nitrate levels normally associated with groundwater. Marsh (1977) had earlier drawn attention to the periodic effects of both terrestrial run-off and groundwater inputs in causing phytoplankton blooms, while Birkeland (1984) has extended the interpretation of the effects to suggest that reef penos also responds to these episodic events. Kinsey and Domm (1974) and Kinsey and Davies (1979b) have suggested that regular daily but intermittent exposure to elevated nutrients (somewhat higher than likely in nature) will cause a substantial increase in reef productivity but a marked reduction in reef calcification. Kinsey (1979) has reported on major shifts in community metabolism of the Kaneohe Bay reefs in response to a marked increase in nutrient loading of the bay (domestic sewage) but stresses that the reef is responding to an elevated organic load (plankton) rather than to elevated nutrients. Rayner and Drew (1984) found marked increases in nitrate in small enclosed Indian Ocean lagoons with clearly associated phytoplankton responses. Crossland et al. (1984) raise the possibilities for substantial nutrient elevation in high latitude reefs by the remineralisation of macro-algal detritus accumulated in the lagoon from areas outside the reef. Andrews and Gentien (1982) have indicated possibilities for nutrient enhancement from shallow upwellings induced by incursions of subsurface water over the continental shelf edge (GBR). No evidence is presented that these upwellings actually cause nutrient elevations "felt" by the surface reefs. Hatcher and Hatcher (1982) have stressed that marked seasonality occurs in lagoonal nitrogen levels at One Tree Island but that levels are always higher than those outside the reef. They suggest that crest levels are the highest of all which is in keeping with the earlier suggestions that reef-flats may be the dominant site for nitrogen fixation (Symbios papers). Entsch et al. (1983b) have raised the frequently ignored issue of whether there is any reason to focus on nitrogen and phosphorus when seeking to explain possible nutrient limitation to reef productivity. They suggest that iron availability may be important in influencing not only production rates but even species distribution. Skyring (1983, Skyring and Chambers, 1976) has raised the potential importance of sulphate reduction in exercising a major influence on the sedimentary environments so important to the remineralisation processes for other nutrients. Contrary to expectation, highest levels of sulphate reduction are found on the apparently well flushed and oxygenated reef-flats (associated with cyanobacterial mats), not in the lagoon floor.

In reviewing the status of phosphorus studies, Atkinson (1982, 1983) has indicated that recent work demonstrates that small changes in phosphate do occur in the water crossing reef-flats and that these bear a definite relationship to net community metabolism (E). He indicates that high input of phosphorus (by virtue of large water exchange rates) provides a continual source to maintain high biomass and the small net production (export). However, he stresses that the low concentration of phosphorus probably limits the specific growth rate of the community. He summarizes: "Coral reefs have high areal production and high elemental turnover times because they maintain high biomass. The specific growth rate of a coral reef community is low, reflecting the low concentration of nutrients ...". Atkinson indicates that nitrogen is also likely to prove limiting to specific growth rate by virtue of its low concentrations whether or not it is actually being produced by fixation or even exported.

Smith and Jokiel (1975) were probably the first to raise the importance of a definite relationship between overall or net productivity of a coral reef system and its nutrient supply (input and residence time considerations). Smith and Atkinson (1983), in their study of the Shark Bay system (a hypersaline, seagrass dominated, long residence time, negative estuary) stressed that the rate of delivery of nutrients (phosphorus specifically) controls net productivity whereas "local transfer of materials from one component of the system to another allows the metabolism of those individual components to be amplified until they are metabolically controlled by other factors. The ability to accumulate biomass appears to be at least the major immediate control". In systems free from land input, rate of delivery can be equated with input of water. However, Smith (1984) and Smith et al. (1985) stress that this form of net production control is only relevant to systems such as Canton Atoll or Shark Bay where very low levels of water exchange occur. Smith (1984) summarizes the roles of nitrogen and phosphorus in marine systems: "If hydrographic fluxes are small, then biochemical fluxes of nitrogen are likely to obviate nitrogen limitation while phosphorus is exhausted. If hydrographic fluxes are large, then neither biochemical fluxes nor hydrographic supply of either nitrogen or phosphorus is likely to limit net ecosystem production of organic matter. Other limiting factors must be sought". Thus, open flow systems have gross production rates limited by concentration while net production rates are limited by factors probably not yet identified. Lagoons etc. have gross production rates limited by both concentration and supply with supply limiting the net production as well. Phosphate is always the more likely limiting nutrient, particularly in lagoons because of the accumulation of nitrogen from fixation.

Jonannes et al. (1983a) have developed a further hypothesis concerning nutrient control on coral reef productivity. They propose three patterns of community metabolism: Type 1: Nutrient fluxes display no diel rhythm but are correlated with ambient dissolved nutrient concentrations (found with the lowest nutrient concentrations relative to demand). Type 2: Nutrient fluxes are not concentration dependent and exhibit clear diel rhythm, i.e. are dependent on metabolic activity at the time (found with intermediate nutrient concentrations). Type 3: Nutrient fluxes display neither concentration dependence nor a diel cycle (found with elevated nutrient concentrations). They believe all three protocols are found with the high latitude reefs of the Abrolhos. They also claim all three patterns can occur simultaneously for different nutrients, also that patterns can shift with time (or season) in the one community.

Overall, it seems clear that a rather effective picture is being built-up concerning the role of nutrients in controlling both gross production rates and net productivity in coral reef systems. A major distinction is made between the concepts of nutrient supply and nutrient concentration. Concentrations are likely to prove the only significant factors in such places as reef-flats and seaward slopes whereas supply is probably the dominant influence in most large lagoonal systems. Nitrogen fixation is clearly established as a general reefal phenomenon but is more pronounced in shallow areas. New emphasis is indicated for studies concerning the recycling of nutrients, particularly phosphorus. Where a major nutrient limitation is indicated, it is virtually always likely to be phosphorus but the possibility of limitation by other nutrients is raised.

9. THE MANAGEMENT APPLICATION

It has been concluded earlier in this review that recent studies (e.g. Barnes and Devereux, 1984) are reaching a level of sophistication where second order variations in community metabolism previously attributed to "noise" will be found to identify real trends (Kinsey, 1983b). It has certainly been identified that relatively major shifts from the "natural" nutrient availability patterns may cause community metabolism to alter to a degree easily detectable as a perturbation (Kinsey and Domm, 1974; Kinsey and Davies, 1979b). In a patch reef at One Tree Island, P was increased by about 10-20% (seasonally variable), R remained unaltered while G was decreased by about 50% following a nutrient enhancement, for about 3 hours each day, to 20 μM nitrogen and 2 μM phosphate (experiment lasted 8 months). Similarly, Rogers (1979b) has considered the metabolic response of reef slope communities to shading using manipulative experimentation and obtained very marked response in P and R. In a rather different form of manipulative experimentation, Kinsey (1973) studied the effects of floating oil films on air/sea diffusion of oxygen by studying the metabolic patterns of the reef community underlying the oil film.

In an extended study of the response of the Kaneone Bay reef-flats to both sewage input and increased terrigenous sedimentation, Kinsey (1979; Smith et al., 1981) found clear patterns of variation in the system's metabolic parameters. Table 6 indicates the findings of that study based on data obtained over all seasons of an approximately one year period. All reef-flats listed in Table 6 would have been similar prior to man's impact on Kaneone Bay as far as can be deduced at this time. At the time of the study, a gradient of sewage effect existed from a maximum at the "SE" reef to a minimum at the "Central" and "NW" reefs. This effect, as noted in the previous section, was identified primarily as being one of POM (plankton) loading. The NW site and the SE site were both subject to extensive sedimentation. It is clear that reef primary production is reduced by either of these adverse influences. It is equally clear that heterotrophy (i.e. R and P/R) is markedly increased by the effects of the organic loading but markedly decreased by the effects of sedimentation. The reason for more extreme heterotrophy at the Lilipuna site than at the SE site is because of the sedimentation at the SE site and additionally because of a total collapse of the original SE outer zone hard substratum caused by heterotrophic infauna (hence reduced substratum for filter feeding epifauna). The latter effect is clearly demonstrated by the values for G which decrease with increased organic loading and have become severely negative at the SE site (infaunal boring). G simply approaches zero with sediment overload alone (NW site). The overall conclusions are not much affected whether the total flat is considered (Table 6b) or only the outer, or originally hard substratum areas (Table 6a). In this context it should be noted that the Lilipuna site is small and all hard substratum; the SE and NW sites originally had an

outer hard substratum zone which is now totally unidentifiable; the Central and Coconut Island sites still have outer hard substratum zones.

The Kaneohe Bay study has established that marked shifts in community metabolism are associated with equally marked and visually obvious shifts in community structure and sedimentary make-up. The critical question to be asked concerning the management value of metabolism studies is whether the changes in biogeochemical parameters will be statistically significant as early warnings before the adverse effects of outside influences become obvious. The answer to this question simply is not certain at this time. However, the level of sophistication which we are reaching with our methodology (Kinsey, 1983b; Barnes and Devereux, 1984; Smith et al., 1985) suggest that we are close to achieving sufficient precision to make use of system metabolism tools in management.

TABLE 6. Community metabolism for various perturbed* reefs in Kaneohe Bay, Hawaii during the period September 1976 - September 1977.

(a) Benthic metabolism for the outer reef-flat, originally hard substratum zones (SE and NW reefs currently lack any true hard substratum, Lilipuna is all hard substratum).

Transect	P ($\text{gC m}^{-2}\text{d}^{-1}$)	R ($\text{gC m}^{-2}\text{d}^{-1}$)	P/R	G ($\text{kg CaCO}_3 \text{ m}^{-2}\text{y}^{-1}$)
SE	3.3	4.6	0.7	-6.5
Lilipuna	5.2	12.7	0.4	3.1
Coconut Island	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

(b) Benthic metabolism for the complete reef-flats (all zones integrated)

Transect	P ($\text{gC m}^{-2}\text{d}^{-1}$)	R ($\text{gC m}^{-2}\text{d}^{-1}$)	P/R	G ($\text{kg CaCO}_3 \text{ m}^{-2}\text{y}^{-1}$)
SE	3.3	4.6	0.7	-6.5
Lilipuna	5.2	12.7	0.4	3.1
Coconut Island	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

* Sewage impact primarily in the form of increased plankton loading (Chlorophyll a gradient: 10 mg m^{-3} at SE to 0.5 mg m^{-3} at Central and NW) and, to a lesser extent, some nutrient enhancement (inorganic nitrogen gradient $4 \text{ } \mu\text{M}$ to $1 \text{ } \mu\text{M}$; inorganic phosphorus gradient $0.7 \text{ } \mu\text{M}$ to $0.2 \text{ } \mu\text{M}$). Terrigenous sedimentation marked at both SE and NW sites, but low on all other sites. Data after Kinsey (1979).

10. SUMMARY AND CONCLUSIONS - SYSTEMS STUDIES

Studies of coral reef metabolism or biogeochemistry have extended over approximately 35 years. However, relatively few studies have considered any particular systems for longer than the period of an expeditionary visit. We are, therefore, very lacking with respect to studies involving detail and replication. Logistic constraints are likely to allow no real improvement in this situation in the future except with respect to the output from a very small number of institutions located on or near coral reefs. However, innovative new techniques involving "high tech", high precision, continuous logging equipment will enable very fine discrimination in both time and space, together with the inclusion of a greater number of monitored variables. Simultaneously with this increase in the rate of data acquisition, there is likely to be a reduction in actual personnel field time required. More extensive consideration of such "conservative" variables as phosphorus is also likely to continue to improve the quality of the information which we are obtaining. All these new techniques will allow not only an expanded output in the future for the same expended effort but the consideration of more discriminating questions.

Studies of pelagic metabolism have demonstrated a pattern of great variability with substantial responses to seasonal or episodic influences. However, it is clear that phytoplankton production generally has been under-emphasised as a factor in overall system production. Gross production and calcification in coral reefs are, nevertheless, clearly dominated by benthic processes and have been proven to conform to rather predictable rates. Anomalous rates are generally explained by some recognised abnormality in the system, but there remain some reported rates which are anomalous and unexplained. Net gains or losses in organic production are typically very small but are proving vital diagnostic attributes in characterizing reef trophic status. Seasonality has been demonstrated to be a marked feature of reefs at apparently all latitudes. Little variation occurs in seasonal rate differences with latitude for parameters of organic production and respiration. However, seasonality in calcification rates appears to have a marked latitudinal dependence, increasing with increased latitude. Overall reef metabolic rates do not seem to attenuate with latitude; rather reefs and reefal communities eventually cease to exist beyond certain latitudinal limits. This is most usually attributed to biological competition. Proximity to land has been demonstrated to be a detectable influence on system metabolism but, to date, there are few published studies reporting clear trends in response. There are many opportunities for future research in this area. Instantaneous correlation between production/calcification and light are proving to be of great significance and must be an area of major research effort in the future. The flux of particulate and dissolved organic carbon is still very poorly elucidated but proving to be of the greatest importance in understanding the overall trophic structure and balance of coral reefs. Calcification rates determined for total reefal environments have been shown to correlate well with geological studies of the sedimentary record. Finally, nutrient studies have recently given information from which effective hypotheses of system-metabolism control have been developed. There appears to be great scope for further work in this area, together with the area of studies of nutrient recycling.

Perhaps the most important incentive required to ensure the productive continuation of systems-level studies of the kind reviewed here will be the establishment of a definite value for the data and techniques in environmental management. This is not yet the case. Some studies have demonstrated clear patterns in response to environmental gradients. However, it has yet to be demonstrated that such patterns can be detected with a level of discrimination sufficiently fine to act as an advance warning before visual change is already obvious. It does seem probable that such sensitivity will be achieved with the present improvements in techniques.

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