Review article
The Coral Reef: an Owner-Built, High-Density, Fully-Serviced, Self-Sufficient Housing Estate in the Desert — Or is It?

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Abstract

Coral reefs usually are portrayed as the ultimate example of exosystem symbiosis and organisation. It has been suggested that this extreme of integration, and perhaps predictability, is the result of necessity in the "desert" of the oceanic world. Actually, reefs do not need to live in oceanic deserts. In fact, it is doubtful whether the oligotrophic oceans are as desert-like as once supposed. Reefs develop in a wide range of nutrient environments, and the resulting configuration is extremely variable on all scales from gross reef morphology down to detailed community structure. Nevertheless, the majority of reefs have very predictable zonation, zonal width, sources and sink areas, and community metabolic rates. The paper examines the development of the author's "philosophy" of reef biogeochemical performance over 30 years and also draws heavily on ideas developed by S.V. Smith. In reef flats and upper reef slopes there are very high density communities with very predictable activity. The well studied reef flats have gross primary production (P) = 7 g C m^{-2} d^{-1} and net calcification (G) = 4 kg CaCO$_3$ m^{-2}y^{-1}. However, this modal activity is itself only a compromise to suit the physical environment, and ensures that the reef does not bury itself by over production of "housing" materials (carbonate sediments). Absolute modal rates are suggested to be P = 20 and G = 10 for "coral" communities, P = 5 and G = 4 for algal pavements, and P = 1 and G = 0.5 for rubble or sediment communities. Typical controls on activity levels are physical: substrate suitability, depth/space, light/depth, turbulence, and sealevel rise. Reefs typically are not perfectly balanced and internally self-sufficient but exhibit a low

and predictable net ("new") production (2–3% P) almost equal to (but possibly slightly exceeding) the new production of the surrounding ocean. Possible explanations of this consistent net production are: reef slope upwelling, utilisation of residual nutrients not available to the oceanic plankton communities because of additional nitrogen fixed by the reef and/or because of very extreme Redfield Ratios on reefs, utilisation of normally refractory organic phosphorus, and active input of nutrients excreted by planktivorous reef-associated fish feeding off the reef front. Reefs driven or controlled by major external forces such as nutrient/ sewage input or sediment input will depart from this well ordered pattern.

1. Introduction

The concept of talking to an international meeting on symbiosis was, to say the least, intimidating, as I have never in my own perception worked on symbiosis.

After careful consideration I decided it might be more valuable to present aspects of the thirty year development of the broad hypotheses of coral reef ecosystem function and predictability which, I believe, are now my trademark, rather than to concentrate on some of my newer ideas which still draw heavily on those same concepts of ecosystem predictability.

At one level, I believe it is reasonable to consider discrete ecosystems almost to be "organisms" in their own right. Thus, processes and interactions within a largely self-sufficient ecosystem may be considered as a form of symbiosis. I hope the audience is sympathetic to this philosophical concept.

I will draw principally on my own work, and in the later stages of this paper, I will refer particularly to the work of Dr. S.V. Smith, my long time colleague and friend. Steve Smith and I have operated in what generally has been very complementary areas. I, on the one hand, have considered the ecosystem as being made up of internal zones and areas which possibly could be summed to give an understanding of the whole. Steve, on the other hand, has preferred to think on a much more global scale and to consider directly, and therefore with potentially more precision, the processes of the entire ecosystem with less focus on the functions of individual zones and environments within that ecosystem.

Because of the nature of this paper, and with no apology, I propose to be overtly speculative and, in that sense, probably controversial. There will be many generalisations and many simplifications for the sake of being able to see the "wood" with a little less emphasis on the "trees".

Coral reefs mean many things to many people. To a geologist they are a sediment creating and accumulating system. They are frequently considered through extended time and the redistribution of materials by physical forces is often of greater interest than the biological processes which give rise to those materials. Focus may be on the morphological result of processes occurring, or on the processes themselves.

Biologists also consider coral reefs in many different ways. To some, the focus may be the material flux through the system. To others it might be the composition of, and interactions within the community and the community sub-systems of the coral reef. To coral biologists the coral reef may simply be a place where corals exist with the entire emphasis being on that group of organisms. To fish specialists, the coral reef may in fact be primarily a habitat for vertebrates. To the molecular biologist, the coral reef is a source of material in which the processes of physiology, and particularly symbiosis, have proved a very exciting area for study.

I fall into the category of those who study the movement of materials through ecosystems as brought about by both biological and physical processes. I am concerned with mass balances. I am concerned with "who helps whom", whether that be one organism assisting another; whether it be the mutualism within the internal structure of an organism; or whether, in fact, it be the extent to which one zone of the system is balanced by the activities of another zone of the system or, in other words, the source and sink roles between zones.

For a long time, coral reefs seem to have impressed people as somehow illogical or contradictory in that they appear, correctly, to be a very high density accumulation of biological material in which everything functions at a very high level of activity, yet they seem to be doing this in what is, at least popularly, always seen to be a marine desert. Hatcher (1988), in a recent comprehensive review of trophic considerations in coral reefs, described the situation as a "Beggar's Banquet."

Is it reasonable to consider this highly organised, highly integrated community to be virtually a system symbiosis, and has it evolved in this form to cope with the rigors of "desert" existence? The simplistic explanation which is usually offered for the apparent contradiction of coral reefs' existence tends to revolve around such concepts as:

- substrate opportunism, or reef initiation where there is naturally occurring hard substrate;
- total self containment requiring no help from outside;
- total self maintenance or, in other words, the building and maintenance of their own habitat structure by construction in limestone;

and that, to do these things, they require

- a large number of different skills, or, in other words, very high diversity;
- very close proximity, or high density, of the organisms to facilitate efficient exchanges because of the depauperate nature of the environment.

At least some of these concepts need to be questioned and certainly the factors effecting control need to be brought into the explanation.

2. Are Coral Reefs in Deserts?

Let us consider initially whether the concept of the desert setting is reasonable. Perhaps the most usual basis for this assumption has been that the water in coral reef areas exhibits a level of clarity so great that it is "obvious" that it carries completely inadequate plankton, soluble nutrients, or other materials which can serve as a food source for any embedded ecosystems such as coral reefs. In fact, it can be seen from Table 1 that the range of nutrients within which coral reefs exist covers essentially the whole range of nutrient concentrations found in the surface waters of the world's oceans. Thus, it seems apparently incorrect that coral reefs *need* to exist in a marine desert. It can also be seen from Table 1 that the level of productivity in the oceans which surround many of the world's coral reefs, generally accepted as oligotrophic, has been recently redetermined as occurring at much higher levels than previously supposed. In fact, if we accept the Platt et al. (1984) estimate of about $0.5 \text{ g C m}^{-2}\text{d}^{-1}$ as reasonable, it seems questionable whether the oligotrophic oceans are in fact very oligotrophic at all. This, in turn, leads to the reasonable speculation that plankton supply to coral reefs is likely to exceed that commonly supposed.

Table 1. Some real world information about the "desert" (data derived rom Reid, 1961; Crossland, 1983; Kinsey, 1985b; Kinsey and Davies, 1979a; Platt et al., 1984) (refer to Table 3 for definitions)

Nutrient ranges associated with coral reef occurrence		
Phosphate (μM)	Nitrogen (μM)	Chl.a (mg m^{-3})
0.05–0.6	0–4	0–0.5
Production of the "oligotrophic oceans":		
P	$0.5 \text{ g C m}^{-2}\text{d}^{-1}$	
E	$0.06 \text{ g C m}^{-2}\text{d}^{-1}$	

Notwithstanding the evidence in Table 1, it is nevertheless not an unreasonable observation that the majority of the world's coral reefs exist in parts of the oceans which are certainly more depauperate in respect of their surface productivity than average, and, as such, much of the simplistic explanation indicated earlier is likely to have some validity.

3. Is There Structural Organisation?

Are coral reefs organised internally in such a manner as to reflect what might be seen to reflect a system-level symbiosis? An examination of aerial photographs of many coral reefs indicates that the overall size, gross morphology, and bathymetry is extremely variable. Certainly, at this level, there is not very much to suggest a consistent form of internal organisation.

If we look at the general morphology within individual zones such as back reefs or lagoons, again we really fail to see any particularly consistent patterns emerging. Certainly, if we look at the level of individual communities, there appears to be essentially nothing to indicate reproducible levels of organisation even within quite close parts of the same reef zone, let alone between reefs.

However, if we examine again the aerial views of reefs more carefully, it becomes apparent that, notwithstanding great morphological variation, there is, in fact, clear cross-reef zonation which is remarkably uniform when compared among reefs. Not only is there a juxtaposition of zones which, in photographs, appear to be texturally similar, but the widths of these zones, on the whole, are extremely consistent. This perhaps is the first reliable hint that we are dealing with systems with a high level of internal organisation.

4. Are Coral Reefs Really High-Activity Environments?

An examination of Table 2 which gives the results of many early studies which considered the overall metabolism of coral reefs, indicates that the levels of primary production are as high or perhaps higher than any reported for other natural ecosystems. There is also a general suggestion that they are approximately self-sufficient in that photosynthesis roughly equals respiratory consumption. On the basis of these early data, there seems little doubt that coral reefs do exhibit very high activity. However, it should be stressed that all of these early studies, and most since, concentrated on obtaining their biogeochemical flux data on reef flats. Not surprisingly, biogeochemists have always favoured this environment for their studies. Reef flats are shallow, generally approximating horizontal, and changes in the water flowing across

Table 2. Early reef flat studies: Primary production and trophic balance data over a range
of latitude (refer to Table 3 for definitions)

	Latitude	P	P/R
Sargent & Austin (1949; 54)	11N	4	1.1
Odum & Odum (1955)	11N	10	1.0
Kohn & Helfrich (1957)	22N	7.9	1.2
Odum et al. (1959)	18N	5–16	0.8–1.6
Goreau et al. (1960)	18N		0.7
Gordon & Kelly (1962)	21N	14	0.6
Nair & Pillai (1972)	8N	4–9	
Qasim et al. (1972)	8N	6.2	2.5
Smith (1973)	11N	6	1
Smith (1973)	11N	11.6	1.9
Kinsey & Domm (1974)	23S	7.5	1.1
Marsh (1974)	13N	7.2	1.1
Sournia (1976)	17N	7.2	0.9

them are not only easy to detect, but it is relatively straightforward to quantify material flux to and from the communities in this type of environment.

The fact that biogeochemists have concentrated on these environments leads us to one of the sources of much of our confusion concerning coral reefs. Very few biologists whose interests are oriented to community structure, or to individual organisms, concentrate on reef flats. In fact, on the contrary, they tend to see reef flats as fairly uninteresting places and typically concentrate their efforts on the reef slopes, where at least, on first observation, there are very high levels of community density and very complex community structure. Is it possible that reef slopes actually exhibit even higher system metabolism than that found on reef flats, and in what way do the various zones of the reef environment differ in their levels of activity and their contribution to the integrated ecosystem? What controls exist and what exchanges occur?

5. The Scenario Developed From Biogeochemical Data

My own work on coral reef systems began in 1960 and has always involved the biogeochemistry of the carbon cycle within coral reef systems based on derivations from oxygen and carbon dioxide fluxes. Figure 1 summarizes the basic experimental protocol with which I have always worked.

Table 3 summarises the types of data which are derived from these approaches. It should be stressed that coral reefs, in common with essentially all ecosystems, exhibit substantial temporal variability and very significant seasonality (Kinsey, 1977). Much of the variability in data reported and, in
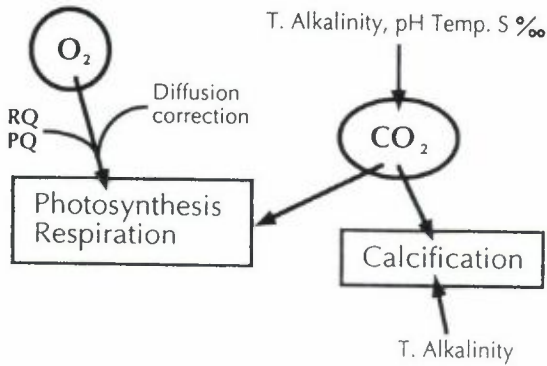
Figure 1. Analytical protocol used in all the author's studies (Kinsey, 1978; 1985a; Smith and Kinsey, 1978). Oxygen data were frequently continuously recorded and converted to their CO_2 equivalent by applying experimentally determined metabolic quotients.

Table 3. Variables used in expressing aspects of total reef community metabolism

P	=	24 hour gross photosynthetic CO_2 fixation (i.e. gross production)
R	=	24 hour gross respiration
E	=	P-R, 24 hour net autotrophy or net heterotrophy (i.e. net or excess production)
		(all expressed in C $m^{-2}d^{-1}$)
P/R	=	proportional autotrophic self-sufficiency
G	=	net production of carbonates (expressed in kg $CaCO_3$ $m^{-2}y^{-1}$

fact, much of the variability indicated in Table 2, comes from the fact that the studies reported were carried out in short time periods not necessarily representing the average condition for the year. Except where otherwise indicated, the data which I will discuss in this paper from my own studies are based entirely on long term data sets acquired over at least one year and, in most cases, several years (Kinsey, 1979). They represent overall average performances for the systems and in fact are therefore very reasonable estimates when it comes to determining such information as the balance within the system.

Early in my studies it became clear to me that coral reefs could probably be considered as essentially bimodal ecosystems (Kinsey, 1979; 1983; Smith and Kinsey, 1976). The bimodality is evident both in their physiography and
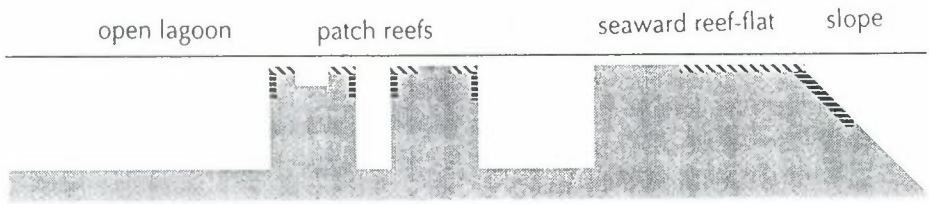
Figure 2. The concept of structural modality in coral reefs. Early studies recognised only
the hard-substrate, high activity perimeter zones and the low activity sediment
dominated zones. Later studies recognised the reef slopes to be a third distinct
mode.

in the juxtaposition of high activity hard substrate zones with soft sediment
zones. This bimodality is demonstrated diagrammatically in Fig. 2. There is,
perhaps, a third component to this modality which was largely disregarded in
my early studies. That mode applies to the area best described as outer reef
slopes. Typically, the slopes do not conform very accurately to either of the
other two modes with respect to physiography or community structure.

Carefully analysing my various data sets from many reefs distributed around
the Pacific region, it became clear that the bimodality which I had recognised
in the distribution of activity zones within the reef was not only, as one might
expect, clearly reflected in the biogeochemical activity, but was reproducible
within a very small range from reef to reef (Kinsey, 1983; 1985b). This led to
the following general hypothesis for modal performance in reefs:

		P	P/R	G
• Mode 1	Active reef perimeters	7 (±1)	1 (±0.1)	4 (±0.5)
• Mode 2	Sand and rubble	1 (±0.3)	0.8 (±0.2)	0.5 (±0.2)

(based on data from 11 reefs)

It seems obvious that there must be very precise and presumably identifiable
control mechanisms which determined these levels of activity. Also, the fact
that there was very little evidence of activity intermediate between these two
levels suggested a very sharp cutoff mechanism. Again, I should stress that
the development of this modality hypothesis essentially disregarded the reef
slopes.

The search for controls on gross community metabolic rates

The search for the nature of these system-level controls can be most readily
discussed by considering the community calcification data. In considering the
makeup of the hard substrate perimeter zones which I have already recognized
to be one very predictable mode in the above bimodal distribution, it became
clear to me from photographs and direct examination of coral reefs that most

of these hard substrate reef flat zones could also be considered as internally made up of a further bimodal distribution of living hard substrate outcroppings and low activity sediment patches. Having determined that this was perhaps a reasonable second order bimodal separation, I examined the reef flat data that had given rise to the above Mode 1 activity more carefully (Kinsey, 1979). I found (Table 4a) that the actual high activity, coral-dominated outcroppings within the reef flat communities exhibited a highly consistent rate of calcification which was not at the rate of $G=4$ as proposed for the original mode 1, but was at a rate of approximately $G=10$. Further, this appeared to be the highest activity which any outcrop was able to achieve.

In the more extensive context of the whole reef flat, the $G=10$ associated

Table 4. The search for order. Very high activity reef environments (based on community calcification rates. Kinsey, 1979; 1983; 1985b).

	G
a.	
A further level of bimodality:	
— "coral" outcroppings within the general reef flat environments where zonal $G = \sim 4$	
One Tree seaward flat	12
Lizard Is, seaward flat	10
Lizard Is, lagoon flat	10
— "coral" outcroppings within extensive, sediment-dominated, inner flats where zonal $G = \sim 2$	
One Tree reticulated lagoon	10
Lizard Is, Lagoon, inner flat	10
Kaneohe Bay, small heads zone	9
b.	
High activity on a very extensive basis:	
— the special case of the shallow, hard substrate reef shoals	
Johnston Atoll reef shoal at 10 m	10
c.	
The more recent realization:	
— most upper reef slopes and small shoals	
Jamaica (Discovery Bay)	8
Kaneohe Bay fringing reef	9
Oahu patch reefs	10
Johnston back reefs	10
Rib Reef (GBR)	10
Abrolhos (W. Aust.; Smith, 1981)	12

with high activity outcroppings was attenuated by its juxtaposition to sediment patches resulting in the very consistent overall Mode 1 (G=4).

This led to two very important questions. Is the community calcification rate of G=10 able to occur on an areally extensive basis? — and — why do the heterogeneous reef flats nevertheless seem always to stabilise at a rate of G=4?

Steve Smith and I decided that it would be best to focus on shallow submerged shoals in the search for the occurrence of extensive areas anywhere in the world where G=10. At that time (1977) we generally viewed the narrower and steeper reef slopes as "not available" for our experimental protocols (i.e. open flow systems). This search led to a detailed study of the calcification rates applying over the Johnston Atoll reef system in the Central Pacific. This is an unusual reef in that it lies somewhat low relative to modern day sea level over much of its area. As such, it is not limited by its ability to achieve vertical growth and is limited only by horizontal space in its ability to maximize community development over its extensive, hard-substrate reef platform. As the depth over much of the platform does not exceed 10 m, light availability also is not a limitation. As we had expected, there were very extensive areas in Johnson Atoll where G=10 (Table 4b) (Kinsey, 1979; 1982).

It seemed that coral communities with no apparent space limitation were able to achieve G=10 but were probably not able ever to exceed this as G=10 appeared to be the absolute limit for the calcification within a coral reef type community.

Since that time (Table 4c), it has become apparent that quite extensive areas of G=10 calcification occur in most coral reefs. These occur almost certainly on outer reef slopes where there are no space or substrate limitations, and provided that the physical energy of the system is not too disruptive. The principal reason that these had not been previously detected was that our technology did not have the precision to be used over reef slopes in the earlier studies. It is also particularly encouraging to note that this apparent absolute upper limit of G=10 which equates to a vertical growth potential of 7–10 mm y^{-1} if the framework remains in place (Kinsey, 1982; Kinsey and Hopley, in press), is very accurately equivalent to the normal and areally extensive rates of vertical accretion reported from geological studies of the Holocene record (Davies and Hopley, 1983). It seems then that G=10 is not only the current upper limit for reef calcification but is inherently the maximum absolute achievable rate.

This being the case, why then is G=4 by far the most normal modal rate over very extensive areas in nearly all the reefs studied? What is it about reef flats that causes them to establish a community structure such that the rate is

not only less than G=10 but consistently G=4? The fact that the rate is less than G=10 is not surprising due to the obvious constraints in vertical space and perhaps to the restrictions on water movement at certain times. But why does this lead to such a consistent compromise of G=4?

The first real hint of the explanation for this is indicated in Table 5. It can be seen that an arbitrary examination of a number of high energy reef flats which by chance were reported for one reason or another in various early papers prior to and including the Proceedings of the Third International Coral Reef Symposium, indicated that nearly all of those flats have a width in the high activity or hard substrate zone remarkably close to 400 m. The only notable exception to this is Elizabeth Reef which perhaps is anomalous because it is a reef existing at quite extreme latitude.

Table 5. Widths of a random sample of high activity zones in seaward reef perimeters (based on data from various papers up to about 1977).

	(m)
Enewetak Atoll (Symbios)	340
Enewetak Atoll (Odum & Odum)	455
Rongelap Atoll (Sargent & Austin)	300
Moorea fringing reef (Souria)	400
Kauai fringing reef (Kohn & Helfrich)	430
Fiji fringing reef (Salvat et al.)	350
Australian GBR generally (Hopley)	350
One Tree reef (Kinsey)	370
Lizard Is. (LIMER)	450
Elizabeth Reef (Slater & Phipps)	200

The fact that coral reef flats exhibit on the one hand a completely consistent rate of calcification of G=4 and on the other hand a remarkably consistent overall width in the high activity zone of 400 m clearly is not simple chance. The explanation of this extraordinary consistency was suggested in work which P.J. Davies and I carried out at Lizard Island during the early 1970s (Davies, 1977; Kinsey and Davies, 1979b).

If we consider a typical 1 m wide transect across the high-activity zone of the reef flat at Lizard Island, with total zone width $\sim$ 400 m; G of $\sim$ 4; average current $\sim$ 0.1 m s^{-1}; average depth $\sim$ 1.5 m; and average suspended sediment load $\sim$ 300 mg m^{-3}; then:

- Overall carbonate production:

$$((4 \times 10^6) \times 400)/(365 \times 24 \times 60 \times 60)$$
$$\sim 50 \text{ mg s}^{-1}$$

- Overall sediment transport off the reef flat towards the lagoon:

$(0.1 \times 1.5 \times 300)$

$\sim 50 \text{ mg s}^{-1}$

Thus, Kinsey and Davies (1979 b) postulated that G=4 was the maximum rate at which a reef flat could calcify in the vertical space available, and that this rate would restrict the horizontal extension of the high-activity zone of the flat to approximately 400 m in a condition of stabilised sea level. As no vertical growth is possible, and all carbonates produced in such a reef flat must be removed downwind by sediment transport processes, any further extension of the reef flat high activity zone would be controlled by self burial. Clearly, this 400 m width is the likely width for high energy reef flats only. The width of the high activity zone will decrease as a function of the average level of wave energy occurring. The rate of G=4, however, should apply on any reef perimeter high energy zone situated at or very close to present sea level. Thus, it seems that the only controls over this aspect of reef biogeochemical performance which we need to invoke are physical.

I suggest that these findings indicate controls similar to those applying to all gross community metabolic rates, and that, in general, population density and the levels of activity in coral reef system parameters are determined largely, if not solely, by:

- existence of a suitable substrate;
- the depth;
- light reaching that substrate;
- any seal level rise occurring (change in space);
- turbulence (wave energy)

They generally are not determined by nutrient input or food input. In fact, the consistency in the various parameters so far discussed would appear to apply over all of of the reefs studied by me (with the exception of reefs known to be stressed) and those reefs occurred in a significant range of nutrient environments.

It must be stressed that the controls discussed to this point relate only to the control of gross metabolic rates and carbonate production. They do not relate to the determination or control of the rates of net community organic production.

A revision of the modality concept

As a result of all of the above considerations, and using reasoning which followed similar logic for other community metabolism or biogeochemical parameters, I revised my earlier concept of modal performance in coral reefs to that given below:

		P	P/R	G
• Mode A	Continuous "coral"	20	> 1	10
• Mode B	Algal pavement	5	>> 1	4
• Mode C	Sand and rubble	1	< 1	0.5

It can be seen that the reef flat mode no longer exists as an absolute mode except in that part of the reef flat usually described as an algal pavement. This latter environment is, of course, uniquely a feature of areas of the reef structure which are at or very near sea level. In fact, all other areas of the reef are made up of mixtures of these modes; most usually Modes A and C but frequently with parts of mode B, at least in the shallower areas.

Self-sufficiency with excess production

Having determined that typical reefs exhibit community performance which is largely physically controlled, the next move towards determining whether reef systems can reasonably be seen as a self-balanced system-level symbiosis is to determine whether an actual trophic balance exists internally within the reef system. Are they, in fact, the perfect mutualistic society? A typical distribution of photosynthetic production across a reef is given in Fig. 3a, and a typical distribution of excess production (net production) is given in Fig. 3b.

It is clear from these diagrams, which draw from trends evident from all my studies to date, that the highest primary production, not surprisingly, is associated with the seaward perimeters of the reef. However, quite high levels of production also may be achieved in areas of lagoon where patch reefs are prevalent. It is also clear that excess production is exclusively associated with the seaward perimeters and that there are several zones within the reef exhibiting significant net consumption. As a first approximation, it is reasonable to assume that these latter zones represent the sink areas for the excess production shown on the outer areas of the reef. Taking a closer look at this apparent balance, it can be seen from Fig. 4 that the reef is certainly very close to balance across its total width. It can also be seen that the lagoons within reef systems play a critical role in the overall material balance and certainly should not be ignored as has tended to be the case in many ecological studies of coral reef systems.
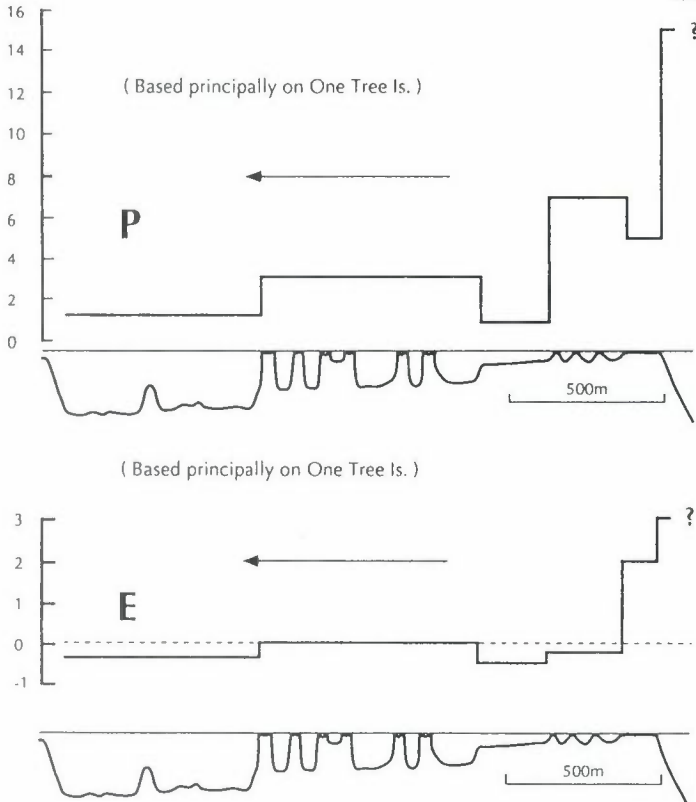
Figure 3. The distribution of rates of gross primary production (P) and of net (excess) production (E) across a typical shelf platform reef. The plots are simplified and stylized, but based principally on data from One Tree Island (Kinsey, 1979).

It has become clear from my own work that the integration of community metabolic rates in the various zones of reefs suggests that the majority of reefs (at least those away from strong external influences) approach an overall balance between photosynthetic production and respiratory consumption and exhibit very low but positive net production within the range of approximately 0 to 3% P (Table 6). It is particularly significant to note that none of the apparently unperturbed reefs which I have studied exhibited a negative excess production. So if we accept that the methodology is sufficiently precise to allow summation of zones in this way (and this is certainly questionable), it seems likely that reefs are driven principally by the internal creation of their own food supplies and are rarely if ever driven by the input of fixed carbon such as plankton or other particulates.

In contrast to my own approach, and as indicated earlier, Steve Smith has always studied reefs on a much more integrated scale. The disadvantage of that
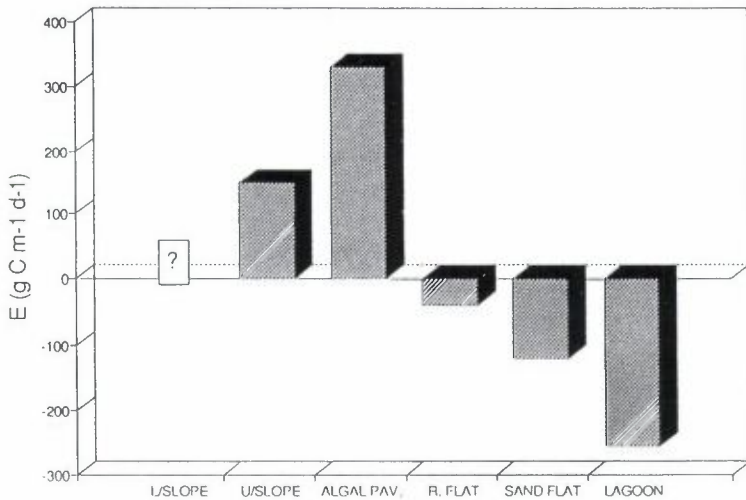
Figure 4. The integrated contribution of various zones to overall net (excess) production in a typical shelf platform reef. The plots are simplified and stylized, but based principally on data from One Tree Island (Kinsey, 1979).

Table 6. Comparison of net production by total reef systems with that of the surrounding ocean.

Net (excess) production by reefs:	
Inferred from integration of zonal data from Kinsey (1979; & various	$\sim 0 - 3\%$ P (say, 0–0.1 g C m^{-2}d^{-1})
Estimated directly by Smith (1988)	~ 0.1 g C m^{-2}d^{-1} (say, 2–3% P)
Net (excess or "new") production by the "oligotrophic" oceans:	
Estimated by Platt et al. (1984)	0.06 g C m^{-2}d^{-1}

type of study is that it gives little information about internal behaviour. On the other hand his approach is normally carried out in extended space and time, and gives a much more accurate determination than mine of the overall system balance. It can be seen also from Table 6 that Smith's data have suggested, in common with mine, that excess production is normal in reefs, and that the most reasonable estimate of this is probably of the order of 2–3% of the total gross primary production. It was recently stressed by Smith and Kinsey (1988) that it is very easy indeed to draw erroneous conclusions concerning

the meaning and significance of material balance, or of a failure to achieve material balance, in coral reef systems. However, the close agreement between Smith's and my estimates of overall net production is very encouraging.

I believe the weight of evidence clearly supports low-level net production in reefs. The most exciting challenge is to identify the source of "new" nutrients to drive this net production.

The search for "new" nutrients

The most important feature of the data in Table 6, is the comparison of reef net production with the new or net production of the oligotrophic oceans. The net (excess) production as inferred both by Smith and Kinsey for typical reefs of approximately 3% of gross primary production, and which can be calculated to represent approximately $0.1 \text{ g C m}^{-2}\text{d}^{-1}$ happens to be extraordinarily similar to the typical net (excess) production of the oligotrophic oceans suggested by Platt et al. $(0.06 \text{ g C m}^{-2}\text{d}^{-1}$.

Superficially, these coincidences suggest the possibility that reefs support net production which might be driven by the same input of new nutrients as that which drives the net production of the surrounding oligotrophic oceans. However, it is not clear how this supply of new nutrients could be delivered over a relatively extensive coral reef environment. Smith (1988) has considered this matter at length. He suggests that it is essentially impossible for the net production of reefs to be driven by the same input. New nutrients are delivered into the oligotrophic ocean by advective input from below. It is clear that direct vertical advection cannot apply in a coral reef because of the physiographic limitation existing. It is possible that active upwelling against the reef slope (Andrews and Gentien, 1982) could offer an alternative explanation. However, both Smith and I feel that this is not by any means a general explanation. It also seems fairly unlikely that these new nutrients could be delivered to a coral reef by horizontal advection as the nutrients input to the surrounding water are likely already to have been utilised in the normal net (new) production by oceanic plankton in those waters. At best, this source might be expected to result in reef net production lower than that in the ocean. At worst, we might anticipate net heterotrophy (negative excess production) in the reef because of reef biota feeding on plankton swept in from the surrounding ocean.

How then can reefs exhibit net production which seems approximately to equal or possibly exceed that of the surrounding ocean? Smith (1988) provides two alternatives, or possibly complementary mechanisms which could explain the level of net production. Firstly, he suggests that any residual new nutrients that do reach the reef will cause considerably higher levels of net carbon dioxide

fixation (production) than the same level of input could have caused in the ocean. This is because of the extreme Redfield ratios associated with reef algae (Atkinson and Smith, 1983; C:N:P = 106:16:1 for plankton; 550:30:1 for reef benthic plants). Secondly, he points out that the ocean typically will be nitrogen limited, even allowing for the new nutrients. Therefore, the water entering a reef will contain excess phosphate. reefs are recognised as being competent in nitrogen fixation (e.g. Wiebe et al., 1975). Thus, it is clear that water already exhausted by the plankton production of the nearby ocean may still serve to provide new nutrients to the reef.

I believe that there are two further potentially important factors which could be invoked to explain the net production of coral reefs. Dunlap (1985) has suggested that there is a considerable pool of relatively refractory dissolved organic phosphorus, some or all of which can become available when in contact with microbial processes (extra cellular phosphatases) of shallow reef environments. Again allowing for the nitrogen fixation capability of reefs, this organic phosphate may constitute a supply of new nutrients.

The final possibility which I wish to raise has some exciting prospects for new biological research. As long ago as 1973, Glynn suggested that feeding on oceanic zooplankton by the outer perimeters of coral reefs was of considerable significance to their overall nutrition. Since that time the majority of studies of coral reefs have led us away from the heterotrophic concept towards the idea that coral reefs are essentially internally self sufficient. In fact, it would seem that plankton feeding by the reef could only result in decreased and probably negative net production (i.e. net heterotrophy). However, more recent studies by Hamner et al. (1988) seem to make it clear that, at least for the particular reef that they studied, the delivery of zooplankton to the reef from the ocean might be removed off the reef front rather than over the reef and be removed by a "wall of mouths" attached to reef-associated fish. The quantity was of sufficient magnitude to be equivalent to perhaps 25% of the net production of the reef system.

Considering a 1 m transect across the total width of a typical shelf platform reef:

- Zooplankton input

    (Hammer et al., 1988)   30 g C d^{-1}

- Integrated gross primary production

    (Kinsey, various)   6000 g C d^{-1}

- Integrated net (excess) production

    (Kinsey, various)   120 g C d^{-1}

Thus:

- Zooplankton input is equivalent to $\sim 25\%$ of total reef net production.

Is it possible for plankton feeding to have the effect of not only introducing new nutrients to the system (which it clearly does), but to do so in such a way as to result in new or net primary production rather than in net heterotrophy? Meyer et al. (1983) and Hamner et al. (1988) offer a feeding mechanism that might well satisfy this scenario. They suggest that there are significant populations of reef fish that move to the reef front where they ingest zooplankton. I suggest that their heterotrophic metabolism at that location is probably not taken into account in either Smith's or my estimates of integrated reef metabolic balance. However, they are likely to be continually releasing nutrients into the water entering the reef. These fish then move back to the reef at night where they are likely to release further available nutrients to the reef waters. Thus, some of the new nutrients delivered to the nearby oligotrophic ocean may still be delivered to the reef in available inorganic form by a process of horizontal "advection" involving fish as "processsors" and, possibly, carriers.

The plankton studies reported to date are not able to give us a clear indication as to whether the "remineralisation" of zooplankton is able to supply the entire 2–3% of the excess production nor whether this mechanism is important relative to those proposed by Smith and that suggested based on Dunlap's work. However, the verification and resolution of the relative importance of these various options certainly provides some fascinating future possibilities for ecosystem-level biogeochemical studies on reef systems. Also, I should stress that it really needs to be conclusively demonstrated that my data and those of Smith are sufficiently precise for the 2–3% to be considered as an entirely robust estimate.

6. What Can We Now Say About Reefs?

Typical reefs:

- do not need to live in deserts
- do not usually live in deserts
- are very predictable
- consist of many zones and sub-systems, all of which are important
- certainly have very high-density communities

- have very high activity within those communities
- have community metabolic rates largely determined by physical factors
    - substrate suitability
    - depth/space
    - light/depth
    - sealevel rise
    - turbulence
- are not perfectly self sufficient
- have net production roughly equivalent to the ocean, and which possibly involves any or all of the following:
    - reef slope upwelling
    - low levels of input nutrients efficiently utilised because of extreme Redfield ratios
    - excess phosphate available because of nitrogen fixation
    - utilisation of normally refractory organic phosphorus
    - input of available nutrients released by plankton feeding fish off the reef-front

7. Do Some Reefs Not Obey the Rules?

What happens where a coral reef has the potential to be substantially driven or stressed by a pronounced input such as applies where there is a major nutrient input from land, or sewage runoff, or a major input of a negative factor such as a high level of sedimentation?

Certainly my own studies have made it clear that not all reefs are controlled essentially by physical forces. It is perfectly possible for a reef to be driven by external influences. It is not within the scope of this paper to discuss the behaviour of reefs well removed from the usual "almost but not quite desert" conditions. However, I recently summarised my hypotheses of stress response in coral reefs elsewhere (Kinsey, 1988).

8. Summary

In summary, I believe the majority of reefs conform to the general concepts outlined in this paper. I hope the matters I have raised will give this particular audience some new perspectives on considering ecosystems generally, and coral reefs in particular. I hope I have left an impression of the considerable systems-level order which exists in coral reefs notwithstanding the enormous variability which clearly exists in community structure, and that this makes a case for the concept of ecosystem symbiosis.

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