RESPONSES OF CORAL REEF SYSTEMS TO ELEVATED NUTRIENT LEVELS

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INTRODUCTION

Coral reefs are dynamic systems. Fringing reefs in particular may be very effective in demonstrating many aspects of system and community behaviour because of the greater variability in environmental parameters to which they are likely to be exposed. In a recent workshop (Baldwin 1987) conducted by the Great Barrier Reef Marine Park Authority to consider the coastal fringing reefs of the Great Barrier Reef Region, a number of relevant and significant conclusions were indicated. They included:

- coral reefs, or at least fringing reefs, exhibit significant instability combined with a significant degree ofresilience
- fringing reefs exhibit a rather discontinuous existence with phases of very active development alternating with phases in which they are virtually "dead"
- nevertheless, fringing reefs exhibit very good long-term survival
- there are very sharp thresholds in stress response beyond which reef biota collapse
- coral reefs can be considered as exhibiting certain specific attributes:
  - -they are normally subject to very low biological and chemical forcing functions
  - -they have principally physical controls, such as turbulence, wave energy, storms, etc
  - -they have an extremely high biological diversity which is an effective mechanism for handling the very low nutrient environment in which they are normally found
  - -they are generally very tolerant of stress
  - -they exhibit rapid collapse when the stress exceeds a critical level

Stress to coral reefs can best be considered in two broad categories: acute stresses are those which kill at least the major groups of reef organisms; chronic stresses are those which the reef is able to withstand through extended time., Typically, a kill by an acute stress such as a major storm, freshwater input, or crown of thorns infestation is likely to be followed by rapid recovery in the absence of chronic stress; A kill by an acute stress in the presence of chronic stress is likely to. lead to

non-recovery of the original reef community with a shift to a low diversity community better able to benefit from the chronic stress situation. I believe nutrients generally constitute a chronic stress, the presence of which may not be evident in community response for a long time.

Much of the Great Barrier Reef has been subject to only low level environmental stresses because of the magnitude of the monsoonal runoff during the wet season. The sediment and fresh water input from this runoff have been so great from time to time that they have caused most of the Great Barrier Reef system to develop seldom closer than 20 km and frequently more than 100 km offshore from the mainland.. Because of the separation of the reefs from the coast, the effects of the input of any threatening materials, including excessive nutrients, have been greatly attenuated by coastal dilution. Further, the Reef has not only been inaccessible for subsistence use, but until recently much of it has been remote even to the present population of Australia. The advent of faster vessels is changing this, but there has not yet been time for major effects to result.

Notwithstanding this apparent degree of protection of most of the reefs of the Great Barrier Reef Region, there are nevertheless many perturbations which can be considered, as possible indications of nutrient stress. The progressive degradation of some inshore reefs such as Low Isles (Rasmussen 1986) and the Green Island reef (summarised by Baxter 1987) is likely to reflect in part the influence of coastal water degradation (Hopley 1982). In the case of Green Island at least, the influence of looalised nutrient enhancement from the island sewer outfall is also generally accepted as being pronounced. Clearly, the increasing use of the Region, its adjacent coastal-areas, and its islands has the potential to lead to more degradation and careful management is essential.

My work has always emphasised the effects of stresses on the total system and has not considered in any detail the specific response of individual organisms. This paper, therefore, will stress system responses. I will discuss some effects of naturally elevated nutrient levels, experimentally enhanced nutrient levels, and the complex effects of treated sewage input on overall community structure and community metabolism (see also Kinsey 1987; in press).

THE NATURALLY OCCURRING SITUATION

The range of nutrient levels within which coral reef's occur is very broad (Smith and Jokiel 1975; Kinsey and Davies 1979; Smith et al 1981; reviewed by Kinsey 1985). They are by no means oases in the marine deserts of the world as they are often presented. In fact, it is probably reasonable to say that coral reefs occur throughout the naturally occurring range of surface nutrient concentrations found in the open tropical oceans of the world.

Reefs occur in waters with nutrient concentrations covering at least the range:

0 -- 4µM available nitrogen   0.05 -- 0.6p available phosphorus

It is interesting, however, to examine the carbon budget data available for complete reef systems throughout the reported nutrient range (summarised by Kinsey 1985). Most carbon budget data indicate that typical

complete systems are in almost perfect trophic balance, fixing almost exactly the same amount of carbon by photosynthesis as they release by respiration and exporting no more carbon than they receive in incoming plankton (there may be considerable spatial variability 'in this balance within the system, ie local source and sink areas); However, the Canton Atoll system reported by Smith and Jokiel (1975), and located in the general vicinity'of the equatorial divergence, is subject to incoming nutrient levels at the top of the naturally occurring range. This reef system was found to exhibit a clear' net production (though <5%), with photosynthesis exceeding respiration, and the system must be assumed to either accumulate organic matter or to export it in significant' quantity to the surrounding ocean.

THE EFFECTS OF EXPERIMENTAL NUTRIENT ENRICHMENT

A study of the impact of deliberate nutrient enrichment was carried out at One Tree Island reef (latitude 23°30'S; 95 km offshore) in the Capricorn Group in 1971-72 (Kinsey and Domm 1974; Kinsey and Davies 1979). In these experiments a small lagoonal patch reef 25 m in diameter was subjected to concentrations of 20µM nitrogen (urea and ammonium) and 2 µM phosphate during the 3 hour ponded slack-water period of each daytime low tide. This experiment was carried out over a period of eight months. While ,the concentrations achieved were considerably above those occurring in reef areas naturally, the time of exposure each day obviously was very limited. The normal lagoon levels of nutrients in One Tree lagoon were less than 0.5µM nitrogen and about 0.05µM phosphorus.

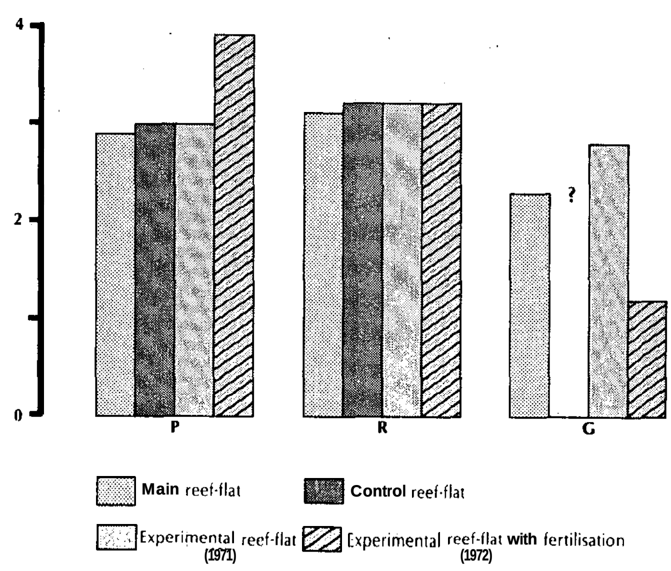

FIGURE 1. The effects of an eight month period of nutrient enhancement on community metabolism in a lagoonal patch reef at One Tree Island, Great Barrier Reef. The effects stabilised to the values indicated after about one month. The 'control reef flat' (on an adjacent patch reef) and the 'main reef flat' areas used for comparison were chosen to approximate the community structure of the experimental patch reef. Each of the sites included appreciable areas of unconsolidated sandy bottom.

P = Gross diel photosynthetic production (g carbon $m^{-2}d^{-1}$)
R = Gross diel respiration (g carbon $m^{-2}d^{-1}$)
G = Net calcification (kg $CaCO_3\,m^{-2}yr^{-1}$)

The effects on community structure were undetectable, however, the effects on community production were appreciable and the effects were residual to the extent that they continued for at least a month after the cessation of nutrient addition.

Figure 1 'indicates the results of these experiments and it can be seen that the primary production of the system increased by approximately 25%, while consumption (respiration) appeared to be virtually unaffected. Thus, the system changed from being approximately in trophic balance to being significantly autotrophic. The fate of this excess production is not particularly clear. As indicated, there were no obvious changes in community structure. It is assumed that the excess production was either lost to the system as algal detritus, or was grazed from the system by itinerant fish and that this did not constitute a major addition to the *in situ* respiratory load.

The most dramatic effect of the nutrient enhancement was a 50-60% reduction in system calcification. This clearly implies the possibility of progressive long-term degradation of structural aspects of the reef, notwithstanding the apparent stability of the community structure.

Overall, a substantial increase in soluble nutrient levels would seem to be a chronic stress able to be withstood for quite extended time periods without visible effects. However, it is clear that enhancement of organic productivity certainly results and that calcification is severely inhibited.

TEE COMPLEX EFFECTS OF TREATED SEWAGE INPUT

Kaneohe Bay, Hawaii, is the best documented example of the effects of combined stresses on a coral reef system (eg Banner 1968, 1974; Kinsey 1979; Smith et al 1978; Smith et al 1981). Kaneohe Bay is quite frequently subjected to the acute effects of fresh water runoff on the reef flat environments. The potential for such events is clearly demonstrated in Table 1. This periodic destruction of reef communities has been tolerated throughout most of the Holocene, with rapid recovery after each event,

During this century, however, the bay has been subject to increasing levels of a series of chronic stresses. Figure 2 indicates the general configuration of the bay and its reef systems. Table 1 gives additional relevant information. The general circulation patterns prevailing and the location of the major streams are also indicated. Since the advent of man, increasing agriculture has occurred, particularly towards the northern end of the bay. This has resulted in substantial sediment runoff exceeding that which had previously occurred naturally. Additionally, urbanisation of the southern end of the bay (now 60,000 people) has resulted in substantially increased sediment runoff in that area also.

Substantial sewage input, representing the domestic output of 100,000 people by 1975, has occurred in the southern end of the bay at the points indicated in Figure 2. As the sewage was largely domestic and received secondary treatment it constituted principally a soluble nutrient input. The inputs are indicated in Tabie 2. However, the principal effect of this sustained nutrient input from a concentrated point source was to create a steady flow of phytoplankton and associated zooplankton in the water column. Thus, the coral reef systems actually were subjected as much to an organic particulate load as to a nutrient input.

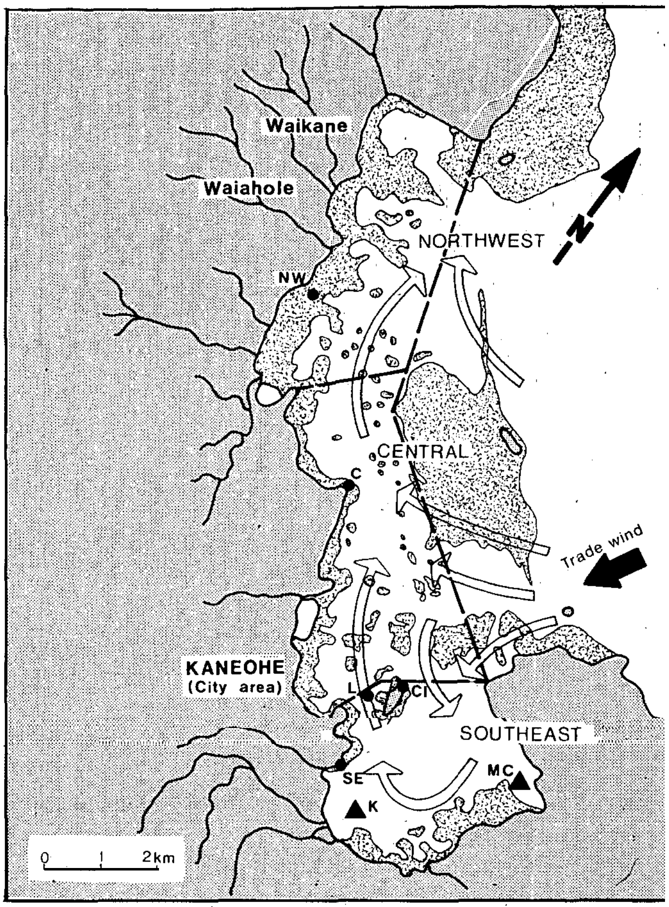

FIGURE 2. Kaneohe Bay on the island of Oahu, Hawaii. 'principal watershed 'streams and all major 'patch-reefs and fringing reefs are shown. The bay is semi-enclosed by a substantial barrier-reef/sand-bar structure and is considered functionally in three, indicated zones: northwest, central, and southeast. The two sewage outfalls, in use to the end of 1977, are indicated A . K is the Kaneohe city outfall and MC is the smaller Marine Corps base outfall. Reef-flat sites referred to in the paper are indicated • . General patterns of tide/wind driven circulation are also indicated.

TABLE 1. General information relating to Kaneohe Bay

Kaneohe Bay	
reef-flat area	9km² at average depth lm
lagoon area	19km² at average depth 15m
total area	28km²
water volume	$270 \times 10^6 m^3$
flushing time	approx. 13 days,
Water-shed	
area	90km²
average rainfall	1.7m y^{-1}
Freshwater input to bay	6m y-f

The concentration of both phytoplankton (as indicated by **Chl.a)** and of soluble nutrients as gradients away from the sewage outfall is given in Table 3.

TABLE 2. Nutrient inputs to Kaneohe Bay in 1977 (mole per day)

	Total dissolved nitrogen	ammonium nitrogen	nitrate nitrogen	total dissolved phosphorus	inorganic phosphorus
Sewage	30000	16000		3300	3000
Streams	7000		5000	320	200

Note: Sewage inputs are continuous and point-source
Stream inputs are episodic and rather diffuse

TABLE 3. Nutrient and **phytoplankton*** (chlorophyll **a)** gradients resulting from treated sewage input to Kaneohe Bay, Hawaii in 1977

Site**	Avail. nitrogen (μM)	Avail. phosphorus (μM)	Chlorophyll a ($mg\ m^{-3}$)
Oahu coastal	0.5-l	0.1	0.1
K (outfall)	4	1.2	10
SE	4	0.7	8
L	3	0.6	5
CI	3	0.6	2
C	2	0.3	0.5
NW	1	0.2	0.5

Data after Kinsey **(1979),** Smith et al **(1978).**
* A gradient of associated zooplankton was also present.
** Site locations are shown in Fig. 3.

Figure 3 indicates the system metabolic response by 1977 to these compounded stresses.

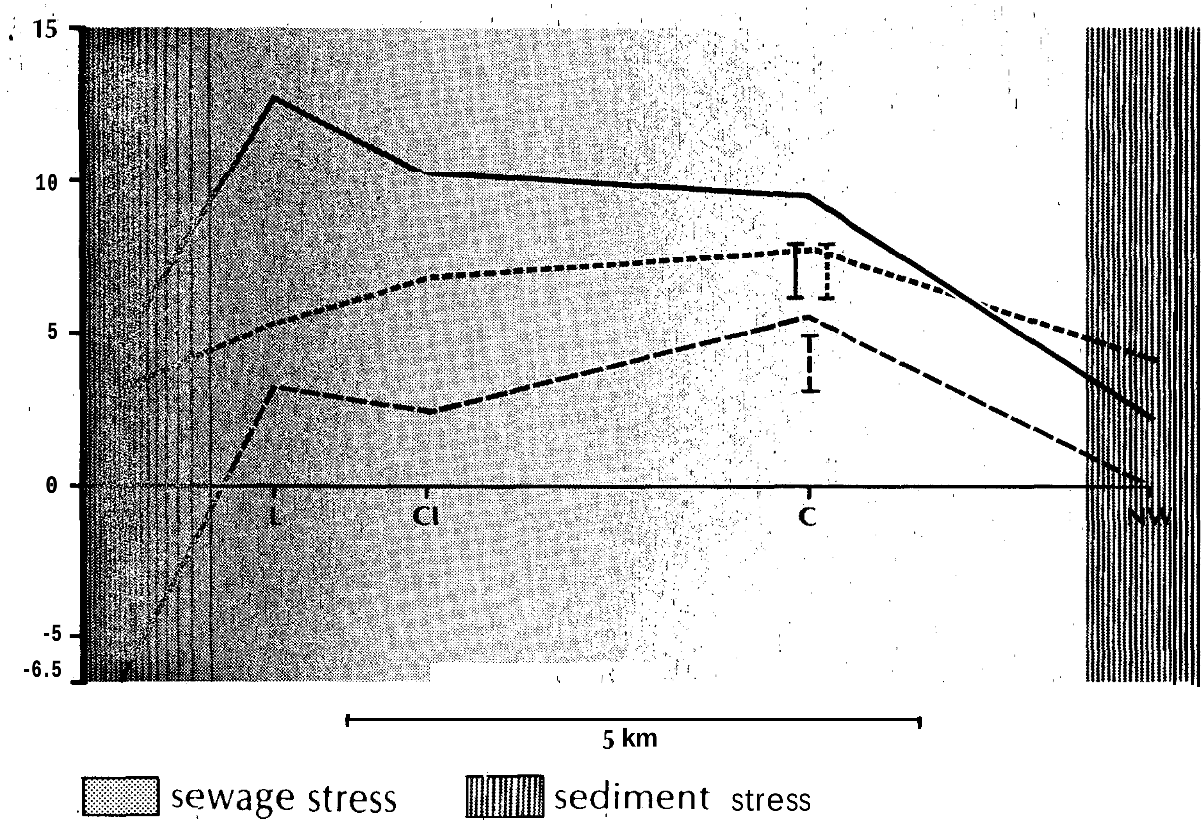

FIGURE 3. The effects on benthic community metabolism of sewage and sediment stress in Kaneohe Bay, Hawaii in 1976-7. Sewage stress in the form of a generated plankton stream and some residual nutrient enhancement applies principally south (left.) of the central site **(C).** The sewer outfall can be considered as the left axis. Sediment stress is most marked at the northwest site (NW) and in the southeast of the bay. The outer reefs in the north were subject to little stress of either kind. Data after Kinsey (1979, 1985, **1987).**

- - - - - -	Gross **diel** photosynthetic production	(g carbon $m^{-2}d^{-1}$)
————	Gross **diel** respiration	(g carbon $m^{-2}d^{-1}$)
- - - -	Net calcification	(kg $CaCO_3 m^{-2} yr^{-1}$)

The vertical bars indicate the normal range for these metabolic parameters in hard substrate areas of natural, unperturbed reef flats (Kinsey 1983).

It is clear that, even in the central bay where the reef systems appeared to be reasonably normal, a slight degree of net heterotrophy existed **(R>P)** and slight enhancement of metabolic activity had occurred with respect to the normal levels found in coral 'reefs. Some algal enhancement occurred in, this area (dominated by **Dichtyosphaeria)** in response to the slight enhancement 'in nutrient levels. The net heterotrophy was reflected visually by slight increases in ,the populations of filter feeders.

The influence of sewage input to the Bay was considerable and resulted in a progressive decline in benthic primary production closer to the source, with a very great increase in community consumption (respiration). Calcification of the system also declined. While this latter outcome may, in part, reflect the direct effect of somewhat elevated nutrient levels (as previously discussed for the One Tree Island experiments), there was also pronounced overgrowth of the normal, calcifying reef communities and framework by particle feeding epifauna and infauna. This, in turn, prevented normal maintenance colonisation by coral and algal communities (the primary producers). A decade or so earlier, the alga Dictyosphaeria was a major component of the overgrowth community (Banner 1974). By 1977, heterotrophic communities were dominant. The principal members of these particle feeding communities were zooanthids, sponges, and barnacles. Very close to the sewage outfall the community consumption also declined. This was the result of the complete destruction of the physical substrate caused by boring, filter-feeding infauna, the activities of which are clearly indicated by the extremely negative calcification at that site. The overall effect near the sewer outfall was that the dense populations of filter feeding epifauna associated with other sites towards the southern end of the bay (eg sites L and CI) were no longer able to be supported by the unstable substrate. A further factor leading to an unsatisfactory substrate composition in the SE end of the bay was the continual input of terrigenous sediment.

Overall, with proximity to the sewage outfall, the benthic primary production declined because of the favouring of particle feeders, the loss of available substrate, and the reduction in light penetration caused by sediment and plankton in the water column. The community consumption increased where available substrate permitted colonisation by particle feeders. The community calcification.. declined because of substrate overgrowth, elevated nutrients, and direct destruction by infaunal boring.

At the far north end of the bay, on the inshore reefs (NW), it is clear that the heavy sediment overload in the relative absence of the effect of sewage input caused -a drop in all community metabolism parameters. However, the system became significantly net autotrophic. This response indicated a progressive loss of the normal coral communities and replacement of these with algal' communities established on the unstable sediment surface.

While the various extreme responses in the southern bay would appear superficially to be the direct result of progressive change under the influence of the compounded chronic stresses of nutrients, sewage and sediments, I believe that there is a clear indication that much of the response evident by 1977 in fact was developed during periods of recovery after acute fresh water kills. A large amount of the community shift occurred since a major surface reef kill in 1965 (Banner 1968, 1974). I believe that it is true to say that the community structure so well established by 1977,' indicates to a large extent a failure to recover from the 1965 kill because of the influence of the well established chronic stresses. This is borne out by the fact that the reef communities in the southern end of the bay, but below' the influence of the fresh water overlay in 1965, survived quite well through to 1977 (personal observations), notwithstanding being subjected to the same chronic stresses as the reef flats: viz poor light penetration, elevated nutrients, and organic particle stress.

Nutrient/sewage loading, with its associated phytoplankton and zooplankton production, has, therefore, been a chronic stress. At low levels in the, central bay it has resulted in: increased benthic primary production; a shift to net heterotrophy; possible slight enhancement in calcification; and general, retention 'of approximately normal community structure. At high 'levels in the'southern end of the bay, the effects are still likely to have' been predominantly chronic and have been:' a reduction in available light; a substantial decrease in benthic primary production; a shift to 'considerable net heterotrophy; . an extreme reduction of calcification to become negative; a conspicuous shift in community structure towards dominance by heterotrophs'and particle feeders; and the virtual certainty of non-recovery of the natural community after acute stress.

Fresh water runoff is most likely to have been an acute stress, the recovery from which has been prevented by the chronic stresses applying in recent decades.

At the end of 1977, sewage was diverted from the southern end of Kaneohe Bay. Sediment input continued at approximately the 'same levels. Assimilable nutrient availability was at a substantially #elevated but decreasing level for several years because of release of combined nutrients from the bay sediments (Smith et al 1981). The community response to this decrease in the overall stress was marked.'

In the northern bay where the only significant stress was sediment, no changes have been evident.'

In the central bay where the community change in response to the earlier chronic stresses was not particularly marked, again the changes have not been particularly evident.

In the southern bay, by 1979, changes in community structure were not marked though some of the filter feeders, particularly the sponges and barnacles had died presumably for the obvious reason that particulate plankton was no longer available in such quantity. Water clarity had improved considerably. By 1982 the previously heterotrophic reef flats had lost most of their filter feeders and the dead substrate of the early reefs had become totally covered with an algal population dominated by reds. BY 1985, algal populations had declined. New: corals were in evidence over all the reef flats with a very high percentage cover in intermediate areas, (eg sites L and CI), and the initiation of small colonies even in the dead crumbled substrate of the reef flats adjacentto the outfall. It was clear at that time that some recovery of all reef flats in south and central Kaneohe Bay was likely to result, from 'the diversion of the sewer from the bay.

However, in 1986 another major fresh water kill occurred causing the destruction of much of the new coral development in the shallow reef flat areas. There has not yet been time to determine recovery from this event, but in view of the clear recovery of the reefs between 1977 and 1985, it is reasonable to believe that complete, recovery of the reef flats to approximately normal reef community types should occur over the next several years.

SUMMARY

Coral reefs occur naturally in a relatively wide range of nutrient concentrations. However, the integral community function in reefs which occur at the more elevated nutrient levels differs from the typical balanced carbon budget so Often described for coral reefs. Such systems are likely to be net exporters of organic matter notwithstanding the fact that they may appear to support "normal" community structure.

It seems that reefs may tolerate elevated nutrient levels well above the natural range for significant periods of time. In this situation the nutrients impose a chronic stress leaving the reef vulnerable to **non-**recovery after an acute event such as a major storm, freshwater inundation, or crown of thorns kill.

Elevated nutrients may cause enhanced benthic primary production (net autotrophy), or, at higher sustained levels, may cause a. heavy **phyto**plankton production resulting in enhanced consumption (particle feeding; net heterotrophy).

Elevated nutrients will always result in suppressed community calcification resulting in decreased real growth and structural maintenance.

Community structure will be resistant to change and may not superficially reflect the chronic nutrient stress for a long time.

Rate of change in community structure may be dramatically accelerated by the occurrence of an acute event, the recovery from which will clearly reflect adaptation to the chronic stress of the elevated nutrient levels.

Recovery from such community structure modification can occur quite quickly if the chronic stress is removed and if good larval input is available.

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