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Reevaluation of ENCORE: Support for the Eutrophication Threshold Model for Coral Reefs

The results from the multimillion dollar Enrichment of Nutrients on Coral Reefs Experiment (ENCORE) on One Tree Island Reef (OTIR) suggest that increased nutrient loads to coral reefs will have little or no effect on the algal growth rates and, hence, on the associated effects that increased algal growth might have on the functioning and stability of coral reefs. However, a comparison of the concentrations of nutrients within the OTIR lagoon with the proposed nutrient threshold concentrations (NTC) for coral reefs suggests that all sites, including the control sites, were saturated with nutrients during ENCORE, and, hence, one would not expect to get any differences between treatments in the algal-growth related measurements. Thus, ENCORE results provide strong support for the proposed NTCs and support the ecological principle that algal productivity and, consequently, the functioning of coral reefs are sensitive to small changes in the background concentrations of nutrients. The principal conclusion of ENCORE, namely that the addition of nutrients did not cause the “pristine” OTIR to convert from coral communities to algal dominated reefs, is contrary to the fact that there was prolific macroalgal growth on the walls and crests of the experimental microatolls by the end of ENCORE.

INTRODUCTION

Early work on the evaluation of effects of nutrients on coral reefs and the state of existing water quality and reef degradation in the Great Barrier Reef (GBR) (1–6) prompted much scientific debate and controversy in Australia (7–9). This debate led to public concerns on the state of the health of the GBR. To a large extent, it was such concerns that led to the establishment of the Enrichment of Nutrients on Coral Reefs Experiment (ENCORE) project (10–12). The ENCORE project consisted of the fertilization (from September 1993 to February 1996) of microatolls in the lagoon of the relatively pristine One Tree Island Reef (OTIR) (10, 11) located some 70 km offshore in the southern region of the GBR (Fig. 1). The ENCORE project basically was a repeat, admittedly on a much larger scale, of the Kinsey and Domm (13) fertilization experiment at OTIR (denoted as the first fertilization experiment in the text below) carried out in 1971–1972. The first fertilization experiment incidentally was not designed to investigate the effects of nutrient enrichment and subsequent eutrophication on coral reefs but to investigate the possibility of increasing coral-reef production and, ideally, fish production by the addition of fertilizer (13) to the pristine coral-reef system.

Various descriptions of the reefs in the OTIR lagoon suggest that hermatypic (reef-building) corals dominated the walls and crests of the atolls before ENCORE. Indeed, Kinsey (14) notes that during 1967–1968, there was “very extensive coral growth in the lagoon”; his study area included “deep areas with active coral growth” and that “the prolific and conspicuous coral growths of the lagoon are nearly vertical-sided formations [i.e.,

microatolls] in the form of a spectacular and almost unbroken reticulum of coral walls.” Also, Kinsey and Domm (13) note that the outside walls of the experimental pool had a “vertical face of living coral.” These descriptions of “spectacular” coral growth generally agree with those of McNeill (15), who visited OTIR well before the establishment of the marine research station in 1971. McNeill (15) notes that “many of the lagoons [i.e., microatolls] were 50 yards and more wide with walls covered by abundant masses of living corals.” Kinsey and Domm (13) did note during 1971–1972 that: “algal mat development on the sand bottom is quite typical of the shallower lagoon floor,” but nowhere is there mention of extensive macroalgal overgrowth of the walls and crests of the microatolls that were evident by the end of ENCORE (Fig. 2). At first glance, these observations suggest that ENCORE had caused the once spectacular coral reefs to convert to algal-dominated reefs. However, as is discussed below, there is evidence that the reefs were somewhat degraded before ENCORE.

ENCORE AND THE EUTROPHICATION THRESHOLD MODEL

Much of the scientific controversy that led to ENCORE was related to the proposed (1, 2, 4, 5, 16–18) eutrophication threshold model (ETM) and the associated water-quality threshold concentrations (WQTC), in particular, the nutrient threshold concentrations (NTC). The derivation of the WQTCs was based on correlations between changes in coral-reef health indicators (e.g., coral cover, fleshy algal cover, crustose coralline algal cover, coral recruitment/recovery rates) and water quality over time (i.e., temporal gradients) and/or space (i.e., spatial gradients). Overall, the ETM analysis showed that there was a close similarity in the annual mean (average of at least 30 samples taken over 1 or more years for each site) concentrations of dissolved inorganic nitrogen (DIN [$\text{NH}_4\text{-N} + \text{NO}_x\text{-N}$]), dissolved inorganic phosphorus (DIP [soluble reactive phosphorus, P-PO_4]) and chlorophyll *a*; (Chl *a*) (i.e., $\overline{\text{DIN}}$, $\overline{\text{DIP}}$, $\overline{\text{Chl } a}$) that corresponded to the demise of very different coral-reef communities, namely those in Barbados (19–21) and those in Kaneohe Bay, Hawaii (22–24).

It needs to be recognized that the term eutrophication, as encompassed in the ETM, refers to situations where nutrient enrichment increased algal growth/organic production rates (25) to the extent that changes in the benthic community structure had begun (e.g., replacement of hermatypic corals with coralline algae, filamentous algae, macroalgae, and/or a variety of filter feeders [4, 5, 17–24]). The effect of nutrient enrichment on the synergistic pathways related to algal growth and nutrient recycling within the coral-reef system (e.g., the role of zooxanthellae [26]) and other probable effects linked to algal growth (e.g., coral calcification rates [27]) were not explicitly measured in the studies used to derive the ETM, but such effects are implicitly assumed to be taken into account by the ETM.

Initially, a threshold concentration for Chl *a* ($\text{TC}_{\text{Chl } a}$) of $<0.5 \mu\text{g L}^{-1}$ for the onset of eutrophication was proposed (5).

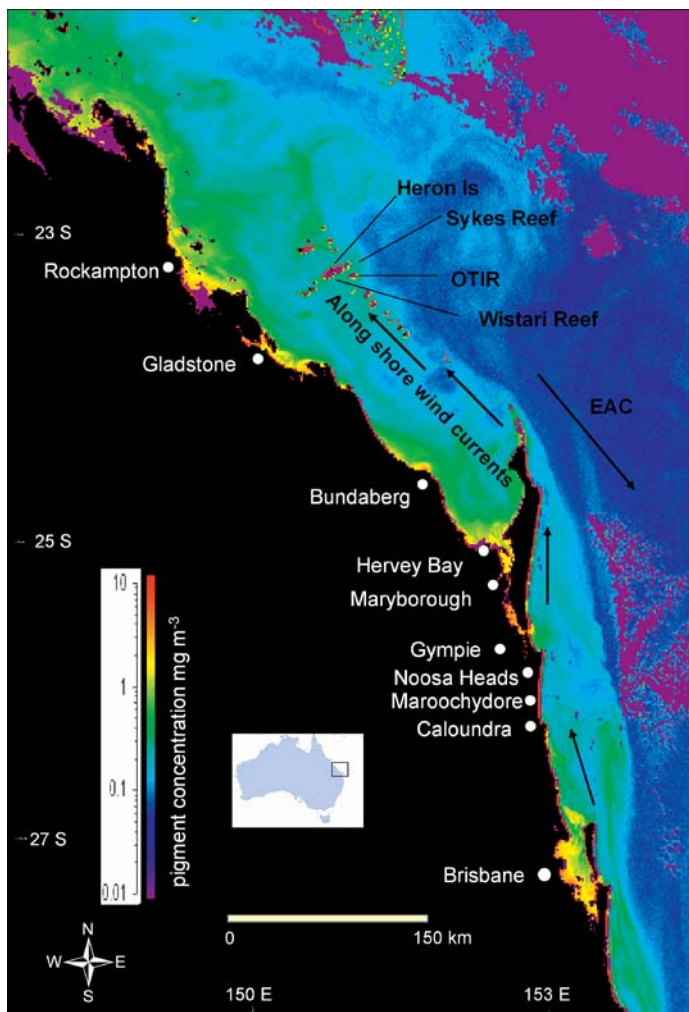


Figure 1. SeaWiFS image 15 October 2000, showing location of OTIR within the enriched coastal waters, which tend to flow in a NW/NE direction (driven by SE/SW winds) for a large portion of the year. The influence of the oceanic East Australian Current (EAC) is evident.

The associated NTCs were $TC_N \sim 1.0 \mu\text{M}$ for DIN and $TC_P \sim 0.1\text{--}0.2 \mu\text{M}$ for DIP. Further analysis of the Barbados data (17) and application of the ETM to the recent demise of the Florida Keys (28–30) suggest that an even lower $TC_{Chl a}$ ($\sim 0.2\text{--}0.3 \mu\text{g L}^{-1}$) is applicable for these regions. It is noted that the lower $TC_{Chl a}$ value is particularly relevant in regions that have a high proportion of sensitive species of corals (e.g., *Acropora palmata*) and, in particular, to regions that are subject to a low flushing regime. Applications of the WQTCs to the Chl *a* and nutrient data within the GBR lagoon (3–6, 8, 17, 18) strongly suggested that much of it was already nutrient enriched/eutrophic. It was concluded (5, 18) that the recorded deterioration of coral reefs in many of the near-shore regions ($\sim 0\text{--}20$ km offshore) over the past century or so was because of the eutrophication, the principal cause of which was the substantial increase in loads of sediments/nutrients that occurred as a result of urban and agricultural developments along the coast of Queensland (18, 31, 32).

In the ETM analysis, it was noted (4, 5, 17) that the magnitude of the proposed NTCs corresponded to many reported values for the half-saturation constants (K_S) for the Monod model (33) or saturation constants ($C_S \sim 2 \times K_S$) for the threshold/saturation model (34, 35) for phytoplankton growth, and, hence, variations around these concentrations will significantly affect the rate of growth of the phytoplankton. Other independent work (16) demonstrated that the extent of macroalgal growth along a natural nutrient-enriched gradient in

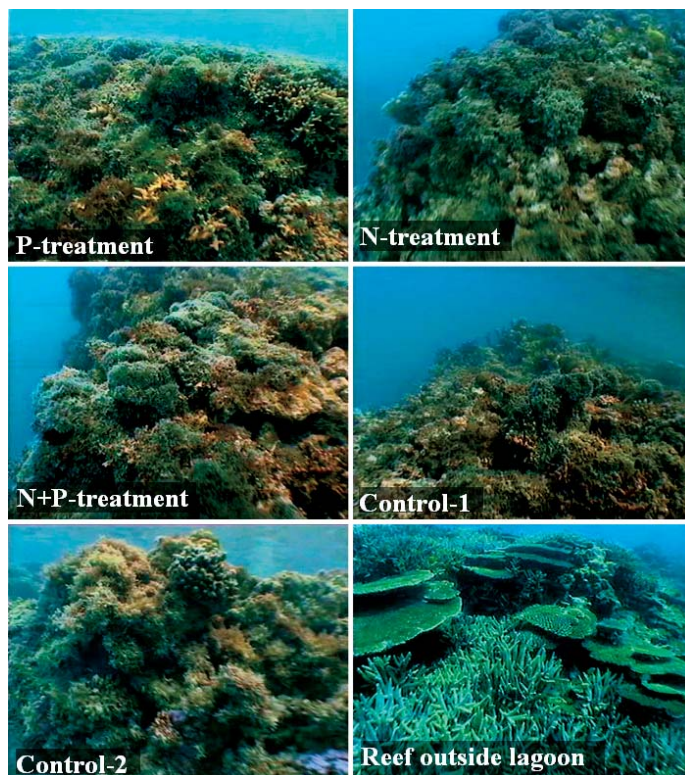


Figure 2. Images of macroalgae and hermatypic corals on walls/crests of ENCORE control (Control 1) and treatment microatolls within OTIR lagoon and on a site further away (Control 2) but still within the lagoon, January 1996; image of corals outside OTIR lagoon also shown. Images captured from BE Lapointe video January 1996.

a seagrass/coral habitat (16) correlated with the NTCs, and data from continuous culture laboratory studies (36) showed that maximal growth rates for various macroalgae occur in the range of $DIN \sim 0.5\text{--}1.0 \mu\text{M}$ (i.e., $\sim TC_N$). Recent laboratory studies (37, 38) with the filamentous N_2 fixing cyanobacteria *Lyngbya majuscula* and *Trichodesmium* sp., which are common to many coral-reef regions, including OTIR, show that maximum growth and N_2 fixation rates occur at $\sim 0.2 \mu\text{M}$ DIP (i.e., $\sim TC_P$). A similar range of values for the nutrient limitation of phytoplankton growth in various coral-reef regions has been noted by other workers (39–41).

Overall, these results suggest that a fundamental ecological property of coral reefs represented by the ETM is that the growth rates of algae are significantly affected at concentrations around the NTCs. Indeed, as illustrated below, relatively small variations (\sim parts per billion [ppb]) in nutrient concentrations around the NTCs can lead to large changes in the algal growth rates. It needs to be recognized that the relatively small magnitude of the NTCs, in comparison with the nutrient concentrations in wastewater discharges and even runoff, means that large nutrient discharges (e.g., rivers) can affect reefs over vast distances, and even very small discharges can affect nearby reefs.

The suggestion that the impact of nutrient enrichment on a coral-reef system is directly linked to the concentrations of nutrients that control algal growth rates should not be all that surprising when one considers that

- the biomass of a coral reef is dominated by algae, and hence, the overall productivity and the reef-building calcification processes are driven principally by algal growth (42).
- the waters that bathe coral reefs in relatively unimpacted regions are characteristically low in nutrients, and in general,

EFFECT OF NUTRIENT CONCENTRATIONS ON ALGAL GROWTH RATES

It is generally accepted that the growth rate of algae is a function of the cellular content of the limiting nutrient and that the uptake of nutrients from solution is a strong function of the external nutrient concentrations (33). However, it needs to be recognized that, in a steady-state system, there is a direct relation between the algal growth rate and the external nutrient concentrations (33, 55–57). Under such conditions, the uptake rate of the limiting nutrient corresponds to the utilization rate of that nutrient. Also, it is generally found that algal growth rates approach, or actually reach, a maximum value (μ_{\max}) at relatively low concentrations of nutrients. The relation between algal-specific growth rates on the limiting nutrient concentration is often modeled by using the hyperbolic Monod relation (33):

$$\mu = \frac{C}{K_S + C} \mu_{\max} \quad \text{Eq. 1}$$

where μ = specific algal growth rate (d^{-1}); C = ambient concentration of nutrient (μM); K_S = half-saturation constant for growth for the limiting nutrient (μM); and μ_{\max} = maximum specific algal growth rate (d^{-1}).

It is interesting to note that some workers (37, 58, 59) found that the growth rates of algae plateau at their maximum value at relatively low-nutrient concentrations rather than approaching such a value asymptotically, as predicted by the Monod model. In these cases, a linear threshold or saturation model (34, 35) is more appropriate:

$$\mu = \frac{C}{C_S} \mu_{\max} \quad C < C_S \quad \text{Eq. 2}$$

$$\mu = \mu_{\max} \quad C \geq C_S \quad \text{Eq. 3}$$

where C_S = saturation/threshold constant (μM).

The key parameter in the Monod model is the half-saturation constant K_S (i.e., equivalent to the concentration of the limiting nutrient that causes half the maximum growth rate). It is important not to confuse this K_S with the K_S' in the Michaelis-Menton equation that is used to relate nutrient uptake rates to the nutrient concentrations; K_S has been shown to be a function of K_S' but is generally much smaller (33, 55, 57). The key parameter in the threshold model is C_S (i.e., the concentration at which the growth rate is maximized, $\sim 2 \times K_S$).

A comparison of variations in algal growth rates as a function of limiting nutrient concentration as predicted by the above models for P and N limited conditions is illustrated in Fig. 3. These results show that algal growth rates are sensitive to relatively small changes in nutrient concentration in the low concentration region. For example, if we assume the background concentration for a system is $\sim 0.1 \mu\text{M}$ DIP (typical of various regions in GBR lagoon [5, 43]) and that the threshold model results shown in Fig. 3 are applicable, then for a DIP limited case (e.g., for *Trichodesmium* growth), an increase of only 1 ppb DIP (i.e., $1 \mu\text{g L}^{-1}$ or $0.03 \mu\text{M}$) would increase the algal growth rate by 33%. It is important to note that for systems characterized by lower DIP values (e.g., those in the wider Caribbean [17, 19, 28]), the relative increase in growth rate would be far greater for an increase of 1 ppb DIP. These simple examples not only demonstrate the potential sensitivity of coral-reef systems to increased nutrient concentrations but also the need for highly sensitive analytical techniques for the measurement of nutrient concentrations.

It is generally found that, for a given species, μ_{\max} would vary with environmental variables, such as light and tempera-

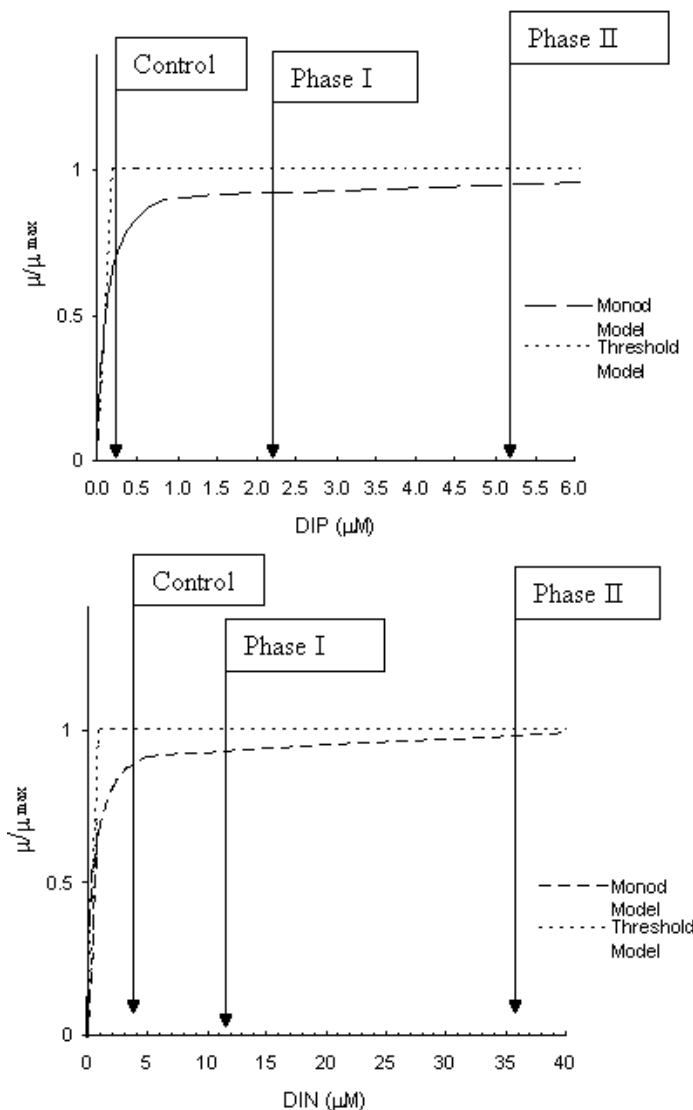


Figure 3. Comparison of relative specific algal growth rates as predicted by the threshold model ($C_{SN} = 1 \mu\text{M}$; $C_{SP} = 0.2 \mu\text{M}$) and the Monod model ($K_{SN} = 0.5 \mu\text{M}$; $K_{SP} = 0.1 \mu\text{M}$). Concentrations of DIP and DIN for the ENCORE Control sites and PHASE I and PHASE II treatments are also shown.

at least one of $\overline{\text{DIN}}/\overline{\text{DIP}}$ is less than the suggested NTCs (19, 26, 40, 42–45).

The ability to define such threshold concentrations is crucial to the management of such regions. Indeed, it is noted that one of the main aims of ENCORE was to define such levels (12). It would appear though that many workers do not understand and/or have misinterpreted the basic relations between nutrient concentrations and the growth rates of algae. Since the misinterpretations by Hughes (46) and Hughes et al. (47) that the macroalgal overgrowth of the Jamaican Reefs was caused principally by a lack of grazing (i.e., they adopted the “top down” model) and not related to the chronically high nutrient concentrations (36, 48, 49), many coral-reef scientists (50–54) have tended to downplay the importance of elevated nutrient concentrations on the promotion of algal growth. Indeed, some workers (52) have even suggested that there is no need to use sensitive analytical techniques for the measurement of nutrients. It would appear that these workers have a very different view of the effects of nutrient concentrations on algal growth rates, and, therefore, these effects obviously need some clarification.

ture (60). Because K_S and C_S were found (55) to be dependent on uptake rates of nutrients and on the cellular content of the limiting nutrient they too would probably vary with temperature and light to some extent and, probably, because of mass transfer effects, on hydrodynamic conditions. It is important to note that in modeling studies (60, 61) K_S' , K_S , and C_S are usually taken to be constants and their variations with environmental conditions are implicitly handled in the variations of μ_{\max} . Strictly speaking, the above model equations (Eqs. 1–3) are only applicable to steady-state systems that have a constant concentration of limiting nutrient. However, here we implicitly assume, as others (62) have for the basic equations based on cell content in cyclostat studies, that the overall functional relations are also applicable to the average growth rate and average concentration of a nonsteady/oscillatory system.

The applicability of such an averaged model can be seen from the following example for DIP limited growth by using the threshold model (Fig. 3): if the water-quality variations are such that the maximum value for DIP $< C_{SP}$, then the algal growth rate for that region would always be $< \mu_{\max}$. Alternatively, if the DIP were always $> C_{SP}$ then the average algal growth rate would be μ_{\max} . Now, if the water-quality variations are normally distributed and the \overline{DIP} for a given sampling station is $< C_{SP}$, then the average algal growth rate for that region will most probably be $< \mu_{\max}$. Alternatively, if the \overline{DIP} is $> C_{SP}$, then the average algal growth rate would most probably be $\sim \mu_{\max}$. The level of confidence in these determinations would depend on the variations in the measured DIP values. Another factor, which provides relevance of the average approach, is that many algae, and particularly macroalgae, tend to take up nutrients in luxury amounts whereby the cellular content of the nutrients exceeds that necessary to maintain the maximum growth rate. Thus, the algae themselves tend to average out the effects of varying nutrient concentrations.

As noted above, it is to be anticipated that the C_S and K_S values will depend to some extent on the environmental conditions and would also vary somewhat from species to species. For example, it has been found (60) that typical K_S' values for DIN uptake, and, hence, K_{SN} for growth, of many oligotrophic oceanic phytoplankton species are usually much smaller than those of phytoplankton characteristic of more nutrient-rich coastal waters. Overall, such variations suggest that algae with higher K_S values will become more competitive in nutrient-enriched conditions. The same types of variations could be expected for K_S and C_S values for the benthic algal species. Indeed, Lapointe, Littler, and Littler (63) showed that the calcareous alga *Halimeda opuntia*, growing in the oligotrophic waters of Curlew Cay, Belize, did not respond to DIP additions, whereas, the fleshy frondose algae, namely *Acanthophora spicifera* and *Dictyota divaricata*, did. These results suggest that the C_{SP} and K_{SP} are significantly lower for *H. opuntia* than for the fleshy frondose algae, and, hence, one would expect that DIP discharges to such systems would favor the competitive development of fleshy frondose algae at the expense of the *H. opuntia*. Another important point is that many of the fleshy algae are less palatable for many grazers, and, hence, with time, these less palatable algae will tend to dominate in the long term, even if their growth rates are relatively slow (e.g., *Lyngbya* spp. and *Sargassum* spp., which now dominate many of the inshore reefs of the GBR).

IMPORTANCE OF NUTRIENTS AND THE STRUCTURE OF CORAL REEFS

It is generally accepted that the functioning of a coral-reef ecosystem depends on its natural distribution of algae and their productivity, as well as the symbiotic interactions between the

algae and the various animals inhabiting the coral reef (26, 42). Overall coral-reef systems exhibit high gross productivity, whereas, the net import of N and P is usually low to negligible, and, in the case of N, is often negative because of N_2 fixation (42, 44, 45). The maintenance of the high gross productivity, therefore, requires high rates of supply of recycled nutrients. The recycling of nutrients is achieved by various symbiotic relations within the reef system, which promote the efficient recycling of the nutrients within particular sectors and between sectors. For example, the zooxanthellae residing within the coral polyps recycle nutrients within their local habitat, grazers of benthic algae deposit nutrients in small pulses in the algal-dominated regions, and some grazers (e.g., fish) deposit such pulses in other regions of the reef (e.g., in the hermatypic coral-dominated regions) (26, 42). These pulses provide localized higher concentrations of nutrients that would be quickly scavenged by the various algal biota.

The available evidence suggests that the maintenance of the overall complex interactions between the various components of coral-reef systems and, hence, ultimately their structure, actually depends on the maintenance of the existing nutrient-recycling pathways (26). Indeed, Falkowski et al. (26) suggest that the maintenance of a balanced coral/zooxanthellae symbiotic association would require low ambient nutrient concentrations ($< 1 \mu\text{M}$ DIN, i.e., $< \text{TC}_N$). The external addition of nutrients to such complex systems will increase the concentrations of nutrients in areas/zones where they are normally low and, in doing so, will increase algal growth rates/productivity in those zones. We propose, as previous work suggests (26), that this increased availability of nutrients will tend to break down the necessity for the natural symbiotic/recycling processes and, in doing so, will lead to a reduction in the stability of the system, thus leaving it poised in a relatively unstable state of equilibrium and thus prone to sudden phase shifts.

Typical triggers for such phase shifts would be events that lead to the physical destruction of the coral matrix (e.g., hurricanes/cyclones, bleaching events, attacks by crown of thorns). If the system were not eutrophic, then the corals and the associated complex structure would eventually reestablish overtime (i.e., the system could be considered robust). However, if the system is eutrophic, then there would be increased competition for space by other organisms (e.g., algae, including coralline algae, filamentous algae, macroalgae; and filter-feeders, including octocorals, sponges, bivalves) that can now flourish in the more fertile waters. Under such conditions, it is less likely that the hermatypic corals will reestablish, and, hence, the eutrophic system should be considered fragile (18). There are many examples of the changing of robust coral-reef systems to fragile systems because of eutrophication over time (e.g., the fringing reefs of Jamaica [36, 48, 49], Florida [28–30, 64, 65], Hawaii [22–24, 66], Barbados [17, 19–21, 67], Indonesia [68, 69], and the GBR [5, 18, 68]), yet, as noted above, the overall importance of eutrophication has been misunderstood/undervalued by many coral-reef scientists. We suggest that this misunderstanding contributed significantly to the ineffective monitoring, evaluation, and remediation protocols/procedures now generally adopted in coral-reef regions (68).

EVALUATION OF ENCORE RESULTS IN THE LIGHT OF NTCs

A principal aim of ENCORE was to investigate the paradigm that increases in nutrient supply would increase algal productivity (12). The fertilization experiments were conducted in 12 small patch reefs (microatolls) located within OTIR lagoon (11, 12). Three atolls were chosen at random for each of the

following 4 treatments: *i*) P (added as $\text{PO}_4\text{-P}$); *ii*) N (added as $\text{NH}_4\text{-N}$); *iii*) P + N; and *iv*) control, no added nutrients. In PHASE I (September 1993 to December 1994), nutrients were added into the microatolls at each low tide to produce concentrations of $11.5 \mu\text{M}$ DIN and $2.3 \mu\text{M}$ DIP (i.e., at concentrations an order of magnitude greater than TC_N and TC_P). Because essentially no effects of these treatments on algal growth/productivity and, indeed, on most coral-reef processes, were obtained, the nutrient loads were increased in the PHASE II experiment (January 1995 to February 1996) to produce concentrations of $36.2 \mu\text{M}$ DIN and $5.1 \mu\text{M}$ DIP. A summary of the principal findings of ENCORE that are related to eutrophication and, in particular, to the effects on algal growth/productivity and closely related processes (e.g., calcification) will now be discussed in the light of the proposed NTCs. It is noted that in contrast to the PHASE I results some mixed effects on some coral-reef processes were recorded for the PHASE II high loading period, but, because of the very high exposure levels, these results are not relevant to the assessment of the ETM and, hence, are largely ignored in the discussion below.

Epilithic Algal Community Productivity and Growth

Epilithic algal community (EAC) productivity and growth were measured (12, 70). No differences between treatments were discernible during PHASE I and PHASE II. Additional experiments (12) showed that incubations of EAC in very high nutrient concentrations ($80 \mu\text{M}$ and $200 \mu\text{M}$ DIN and DIP, both individually and combined) also had no effect. The overall conclusion of this work was that the productivity and growth of EAC at the control sites were not nutrient limited. We basically agree with this conclusion, and we suggest that the principal reason for no significant effects of the added nutrients on algal growth is that all sites, including the control sites, had elevated levels of DIN and DIP that were equal to or exceeded the proposed NTCs (Fig. 3). In particular, it is noted that the $\overline{\text{DIN}}$ for the control sites (12) was $\sim 3.6 \mu\text{M}$ (i.e., $3 \times \text{TC}_\text{N}$), and the $\overline{\text{DIP}}$ was $\sim 0.2 \mu\text{M}$ (i.e., equal to the upper bound of the proposed TC_P). The elevated nutrient concentrations in the control sites suggest that the whole lagoon was nutrient saturated during the ENCORE experiment.

Larkum and Koop (70) note that "the results (from ENCORE) are contrary to the widely held view that enhanced levels of nutrients cause the rapid growth of the EAC on reefs, thereby causing problems for associated biota." These results prompted one of the principal overall conclusions of ENCORE (12), namely, that the addition of nutrients did not cause coral reefs to convert from coral communities to seaweed-dominated reefs. However, these conclusions are not supported by the historical evidence on the algal productivity of the OTIR, nor by the fact that macroalgal growth was prolific on the walls and crests of the microatolls (Fig. 2) by the end of ENCORE. Indeed, it is reported that Larkum (13) found significant increases in algal productivity at OTIR, with additions of $20 \mu\text{M}$ DIN and $2 \mu\text{M}$ DIP during the first fertilization experiment, and Kinsey and Domm (13) found that the gross productivity (P) of the experimental atoll had increased by about 30% by the end of the first fertilization experiment. These earlier results demonstrate that the OTIR lagoon was not saturated with nutrients during 1971–1972.

Kinsey and Domm (13) note the DIP concentrations in the OTIR lagoon were variable, with a maximum of $0.3 \mu\text{M}$, which is consistent with a mean value $\sim 0.2 \mu\text{M}$; this value agrees with the inference of Kinsey and Davies (71) that the added P- PO_4 (i.e., $2 \mu\text{M}$) was 10 times that normally found in the area. Kinsey and Davies (71) also note that the background concentration of

DIN was always very low with the nitrate well below $0.5 \mu\text{M}$. A comparison of these data with the proposed NTCs suggests that the algal productivity in the OTIR lagoon would have been somewhat N limited before the first fertilization experiment and that the increased productivity observed by Kinsey and Domm (13) and by Larkum during the first fertilization experiment was probably because of the added N. If we assume a $\overline{\text{DIN}}$ of $\sim 0.5 \mu\text{M}$ for the lagoon before the first fertilization experiment and compare that with the background levels found during ENCORE (12) (i.e., $\sim 3.6 \mu\text{M}$), we could conclude for OTIR lagoon that $0.5 < \text{TC}_\text{N} \leq 3.6 \mu\text{M}$, which is consistent with the $\text{TC}_\text{N} \sim 1.0 \mu\text{M}$ proposed by the ETM.

Coral Calcification and Growth

The impact of nutrient enrichment on coral calcification and growth was also investigated (12, 72). The overall conclusion of the PHASE I work was that the nutrient addition had little or no effect on coral calcification and growth when integrated over a full year. It is suggested that a valid conclusion that could be drawn from this work is the following: the results support the ETM in the enhancement of nutrient levels well above the proposed NTCs for both N and P did not cause any significant changes in the growth and calcification rates of the hermatypic corals tested. However, it should be noted that other work (27) showed that significant reductions in calcification of corals does occur for DIN at $\sim \text{TC}_\text{N}$. Kinsey and Davies (71) reported inhibition of calcification during the first fertilization experiment, which also supports the conclusion that the OTIR lagoon was not nutrient saturated before that time. They attributed the reduced calcification to the effects of DIP, but the results of Marubini and Davies (27) and the noted probable N limitation of the OTIR system before the first fertilization experiment suggest that it could well have been because of the effects of DIN.

Calcifying Algae: Rhodoliths

The effects of the nutrient additions on calcification and growth of the rhodolith, *Lithophyllum kotchyanum*, was examined (12). The overall conclusion of this work was that the addition of nutrients had no effect on growth and calcification rates. Again, the results support the ETM in the enhancement of nutrient levels above the proposed NTCs for both N and P did not cause any significant changes in the growth and calcification rates of *L. kotchyanum*. These are useful data in that these are the first to verify the NTCs for calcifying algae.

Coral Photophysiology and Effects on Zooxanthellae

The experiments on coral photophysiology showed no significant effects of the nutrient enrichment on the photosynthetic performance during PHASE I (12). Also, no significant differences between the treatments were noted in the population density of the symbiotic zooxanthellae and the mitotic index. Again, overall, we can conclude that these results support the proposed NTCs.

Endolithic Community Colonization and Bioerosion

The results of this work (12, 73) showed that the N and P treatments had no effect on the colonization of the endolithic community, nor on the rates of erosion by macroborers and grazing organisms. It was suggested that this could be because the concentrations of nutrients in the substrates are normally higher than those in the water column. This is a valid point; one would expect that, even in a noneutrophic system, the algal growth rates in the solid substrata would normally be far less



Heron Is lagoon



Wistari Reef lagoon

Figure 4. Macroalgal overgrowth of hermatypic corals in Heron Island lagoon and Wistari Reef Lagoon, January 1996. Images captured from BE Lapointe video January 1996.

limited by nutrients than those by relying on the water column for their nutrient supply.

Overall, the above analysis supports the conclusion that the algal productivity in OTIR lagoon was nutrient saturated during ENCORE but that it was not so before the first fertilization experiment. The question is when and how did the nutrient enrichment occur? The most obvious answer is that it occurred during ENCORE. However, as discussed below, the available data suggest that the OTIR lagoon was probably significantly enriched with nutrients before ENCORE and that an expansion of macroalgal growth had occurred since the first fertilization experiment, i.e., the OTIR system had become eutrophic in the intervening period between the first fertilization experiment (i.e., 1971) and ENCORE (i.e., 1993).

EVIDENCE OF EUTROPHICATION IN OTIR LAGOON BEFORE ENCORE

Observations during January 1996 (i.e., toward the end of PHASE II of the ENCORE experiment) showed that the corals on the outer walls and on the “pie-crust” tops of the nutrient-enriched and unenriched microatolls were in a very poor state of development, with much of the coral substrata covered by macroalgae, principally *Caulerpa* spp., *Laurencia* spp., *Chlorodesmis fastigiata* (Fig. 2). Significant growth of macroalgae (*C. fastigiata*) was also occurring on the moorings of nutrient supply robots. Nowhere in the summary report on ENCORE (12), nor in any of the subsequent publications, is there any mention of the excessive macroalgal growth in the OTIR lagoon. These observations suggest that, if the OTIR lagoon was indeed relatively pristine at the beginning of ENCORE, then the ENCORE study had essentially destroyed a pristine coral-reef environment. However, further investigation of the literature suggests that the OTIR lagoon was not relatively pristine before ENCORE; it was, in fact, using the proposed ETM at advanced stages of eutrophication (i.e., high nutrient levels and excessive macroalgal growth occurred in the OTIR lagoon before ENCORE). For example, studies (44, 74) conducted between the first fertilization experiment and ENCORE showed that the mean DIN of waters outside the OTIR lagoon was $\sim 0.34 \mu\text{M}$ and the mean DIN of waters within the lagoon was $\sim 3.8 \mu\text{M}$ (i.e., $\sim 4 \times \text{TC}_\text{N}$); the investigators suggest that N_2 fixation is probably an important source of the DIN, and they note that a seasonal (winter) benthic algal bloom (*Laurencia obtusa*) occurs within the

lagoon. Hatcher and Larkum (75) also noted these macroalgal blooms and demonstrated that the growth of EAC was not limited by DIN during the spring. These observations support the conclusion that, although OTIR lagoon was not DIN saturated before the first fertilization experiment (i.e., 1971), it had become so by the time of this later work (i.e., by ~ 1980). The question is, how did this nutrient enrichment occur? A possible answer to this question is that, in addition to loads of nutrients added during the first fertilization experiment and the resultant increase in organic matter, there could have been significant loads of nutrients discharged to the lagoon as a result of the operation of the research station, which was established at OTIR in 1971. However, although it is expected that these inputs were significant, it is noted that some other microatoll formations and coral mounds located in the less well flushed regions of nearby lagoons (e.g., those of Heron Island, Sykes Reef, and Wistari Reef) (Fig. 1) are also often covered by macroalgae (Fig. 4), whereas those in better flushed regions of the same lagoons exhibit little or no macroalgal cover. Although the nearshore reefs in the Heron Island lagoon are most probably subjected to significant loads of nutrients from the leaching of ground waters (which are impacted by sewage discharges from the resort and research station, and from birds [76]), the observed extensive macroalgal growth at more remote locations (e.g., Sykes Reef, Wistari Reef, outer Heron Island lagoon) suggests that this southern GBR region as a whole is now nutrient rich. Indeed, the SeaWiFS images (Figs. 1 and 5) and field data (77) ($\overline{\text{Chl } a}$ for this region, 1993–1995, was $0.62 \mu\text{g L}^{-1}$ i.e., $>\text{TC}_{\text{Chl } a}$) support this finding. A closer look at the SeaWiFS images shows that the pigment concentrations often increase significantly downstream of the reef complexes, which suggests that the reefs themselves are contributing to the observed increased growth of phytoplankton. This increase in the downstream growth of phytoplankton is attributed to the export of DIN from the reefs. Such export of DIN from reefs has been documented for many such systems, including OTIR, and has been attributed to the N_2 fixation that naturally occurs in reef systems and to the breakdown of imported organic matter (42, 44, 45, 74, 75, 78).

It is noted that, in the OTIR region and, in fact, in the Queensland coastal region as a whole, the winds tend to be predominantly from the SE/SW direction for much of the year. During the autumn-winter-spring period, these SE/SW winds generate significant along-shore swells to the NW/NE (12, 77). The SeaWiFS images suggest that the enrichment of the wind-

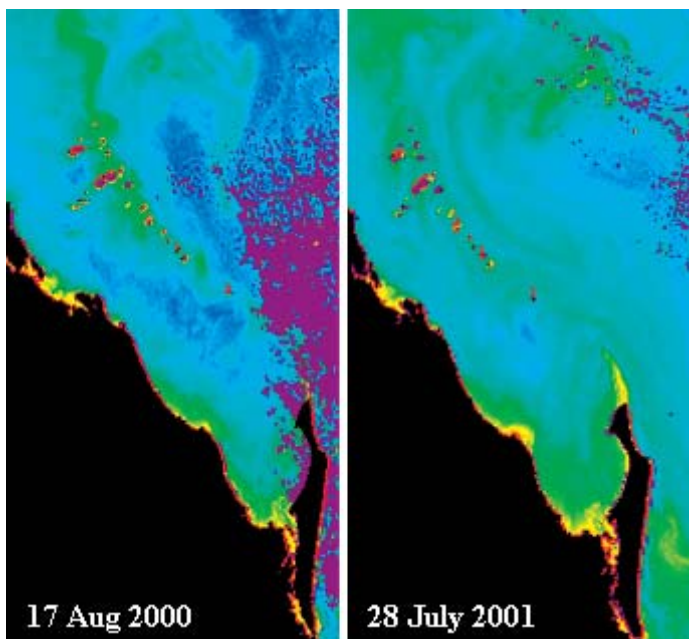


Figure 5. SeaWiFS images illustrating NW directional flow (driven by SE winds) through the OTIR region and enhanced enrichment effects of reefs (see Fig. 1 for pigment concentration scale).

driven northerly flowing plumes in the OTIR region occurs not only from the reef matrix but also from the adjacent coastal regions and from those well to the south of OTIR. The historical evidence discussed above suggests that DIN within the OTIR lagoon and, hence, the N_2 fixation production of DIN within the lagoon, together with the import of organic matter to the lagoon, increased significantly since the first fertilization experiment (i.e., 1972). We hypothesize that similar increases occurred in this GBR region as a whole and that such increases were promoted by the increased loads of nutrients/pollutants entering the nearby coastal regions and those to the south (Hervey Bay to Brisbane and beyond). These regions have not only seen unprecedented growth in population over the past 4 decades, but have also, during this time, been connected to sewerage systems that discharge into the predominantly northerly flowing nearshore coastal waters (Fig. 1).

IMPACTS OF ENCORE ON CORAL-REEF SCIENCE AND MANAGEMENT

The principal negative impact that resulted from the misinterpretation of the ENCORE results is that it added to the confusion that already permeates through the coral-reef science community in relation to quantitative aspects of nutrient dynamics on coral reefs and, in particular, whether *i*) increases in nutrient loads and the resultant eutrophication are important factors in the demise of coral reefs and *ii*) the concentration of nutrients are a useful indicator of eutrophication on coral reefs. As suggested by the comments of Szmant (50, 54, 79) and ably demonstrated by Hughes et al. (47), Miller et al. (80), and McCook (81), quantitative aspects of nutrient dynamics on coral reefs are poorly understood by many coral-reef scientists; the published ENCORE results have done little to elucidate such aspects of nutrient dynamics. Indeed Szmant (54) used the results of ENCORE in arriving at her conflicting conclusions, namely that *i*) nutrient enrichment does not play a major role in promoting increased algal growth in coral-reef regions and, paradoxically, but correctly, that *ii*) even low-level nutrient enrichment can lead to algal growth problems after events that led to coral death and/or damage the structure of coral reefs. Of

particular concern is the major conclusion of ENCORE (12, 70), namely, that the addition of nutrients had no effect on algal growth/productivity within the pristine OTIR coral-reef system, was used (54, 80, 81) to support the flawed top-down control model (36, 46–48) to explain the widespread replacement of reef-building corals by algae.

It is noted that, in the top-down control analysis (46, 47), it was argued that macroalgal blooms on reefs in Jamaica and south Florida were promoted exclusively by a decline in herbivory that resulted from overfishing and the die-off of the echinoid *Diadema antillarum* and that nutrient enrichment did not play a significant role. This analysis ignored the extensive amount of data that has accumulated on the demise of other coral-reef systems in the wider Caribbean before the die-off of *D. antillarum* and of other reefs around the world (5, 17–24, 28–30, 64–69). For example, the data available for the decline of reefs in Barbados (17, 67) demonstrate that many of the reefs were highly degraded by the early 1960s. The degree and the extent of that degradation correlates with the reduction in water quality and increased eutrophication because of the expansion of tourism and industrial developments. These reefs, which were once covered by $\geq 75\%$ hermatypic corals, were reduced in a relatively short time to coralline-algal reefs, not macroalgal covered reefs. Such a phase shift was also recorded by Littler (66) in Hawaii, and it was hypothesized that this change was partly because of eutrophication. The relative dominance model (49, 82), which considers both the effects of eutrophication and grazing, actually predicts such changes, i.e., as eutrophication progresses and grazing pressure remains relatively high, the corals will eventually be replaced by coralline algae. The top-down herbivory model cannot predict such a change.

Prolific macroalgal growth also occurs in the inner GBR lagoon, but it is important to note the available evidence suggests (5, 18) that many, if not most, of the shallow-water reefs of the inner lagoon were, until relatively recent times, dominated by hard corals, not algae. It is known that there are far fewer grazing fish on the nearshore macroalgal dominated reefs (83), and this observation led McCook, Price, and Klumpp (53) to adopt the simplistic top-down model (i.e., the prolific growth of the macroalgae results simply from the lack of grazers); the alternative hypothesis that the low grazing-fish populations are a direct result of the changed habitat that was brought about by the nutrient enrichment/eutrophication of the inner GBR was not considered (84, 85).

This promotion of the top-down model by scientists supported the managers of the Florida Keys National Marine Sanctuary (FKNMS) to downplay the importance of nutrient discharges in the Florida Keys and, in doing so, supported their acceptance of another flawed model, namely the hypersalinity model for Florida Bay (29). Their acceptance of the hypersalinity model supported the decision to flood Florida Bay with N-rich waters from agricultural developments (29, 30). Thus, indirectly, the misinterpretation of ENCORE supported actions that led to the N enrichment of Florida Bay ($\overline{DIN} \gg TC_N$) and regional mass coral extinction via increased diseases and algal overgrowth (28–30).

CONCLUDING REMARKS

The results from ENCORE provide strong support for the proposed ETM for coral reefs and the associated NTCs and thus support the ecological principle that algal productivity, and, hence, the functioning of coral reefs are sensitive to very small changes in the background concentrations of nutrients. The observed algal overgrowth of the OTIR reefs and of other reefs in the nearby GBR region suggest that the region as a whole is eutrophic, and these observations, together with field

data and satellite images of the region, support the proposed TC_{Chlor}. Overall, the ETM/NTC concept was never accepted by senior executives of the Great Barrier Reef Marine Park Authority, who largely funded ENCORE, nor by managers of the FKNMS, because it would have meant that they were the managers of degraded systems, and was ignored by most of the coral-reef science community, because it was too simple an answer to a problem in a very complex system. For example, as noted by Dennison (86) in his support for the PHASE I ENCORE results: "The GBR is too large and complex . . . and too little degraded (fortunately), to hope for simple answers to the question whether or not it is eutrophied." It is ironic that the ENCORE study provided good support for the ETM and the proposed NTCs. Once one accepts the ETM and that the productivity of coral reefs is fundamentally driven by algal growth rates, i.e., "bottom-up" driven, it is not difficult to accept that small changes in nutrient concentrations in the water column can lead to major changes in the structure of coral reefs.

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