

General host metabolism

Biomass changes. There was no effect of nutrient enrichment on the wet tissue weight of *T. maxima* (g cm^{-1} shell length) during either the first or second phase of nutrient enrichment ($p > 0.05$). The C:N ratio of the mantle of clams from the different treatments ranged from 4.11 to 4.83, and was also not influenced by nutrient enrichment ($p > 0.05$). The protein content per gram mantle of control clams did not change during the first six months of the first phase of the experiment ($p > 0.05$). Significant differences were found in the protein content per gram mantle after 13 months of nutrient enrichment ($p < 0.036$). The mean values revealed a trend whereby the protein content per gram mantle with +N-treated clams had the highest value, followed by +N+P-treated, then +P-treated clams, and finally by clams from control patch reefs. There were no differences in the protein content per gram mantle of the clams during the second phase of nutrient enrichment ($p > 0.05$).

The total number of zooxanthellae per clam (cells clam^{-1}) was significantly higher in all nutrient treatments than in controls six months after the beginning of nutrient enrichment during the first phase ($p = 0.044$) and after 13 months ($p = 0.037$).

Haemolymph. The haemolymph is the main conduit for both the supply of nutrients to the animal and zooxanthellae, and also the transfer of photosynthate from the zooxanthellae to the host. Therefore, assuming nutrients are absorbed and they have impact on the symbiosis, haemolymph composition has the potential to be used as a monitor for nutrient perturbations in the water surrounding the clam. The inorganic constituents of the haemolymph approximate those found in seawater and appear to be in equilibrium with that medium (Rees *et al.*, 1993). Therefore changes in seawater nitrogen and phosphorus or any response by the clam and its zooxanthellae to that change may be reflected in haemolymph composition.

Monitoring of phosphate, total phosphorus and ammonium levels in haemolymph showed no significant difference after both one and 3 months in the initial, low-loading phase of ENCORE. Ammonium levels were surprisingly high ($>30 \mu\text{M}$) while phosphate was very low ($< 0.1 \mu\text{M}$). These results are significantly different from those previously obtained with *T. gigas* in experiments at Orpheus Island (Fitt *et al.*, 1995). In contrast to *T. gigas*, *T. maxima* has unexpectedly high levels of ammonium in its haemolymph. Grice (1999) has since confirmed these high levels in *T. maxima*.

With the exception of glycine concentrations increasing with N-enrichment, the free amino acid pool in haemolymph did not vary significantly with nutrient treatment. In *T. gigas* the glutamine:glutamate ratio is dramatically affected by the availability of N (Shepherd *et al.*, 1999). However, this ratio was not influenced in *T. maxima*. This, combined with the high ambient

concentration of ammonium in the haemolymph of *T. maxima*, indicates there are significant qualitative and quantitative differences between the two clams.

Zooxanthellae

The effect of nutrient enrichment on the mutualistic zooxanthellae population from both corals and clams is a fundamental parameter in determining the impact of nutrient loading on coral reefs.

Population density and mitotic index. A variety of zooxanthellar responses were seen in the ENCORE project. Again, these differences depended on the coral species, colony size and on the nutrient loading. No differences were reported for zooxanthellae from *P. damicornis* (Hoegh-Guldberg and Moreno unpub. data) during the initial, low-loading phase of ENCORE. Similarly, Takabayashi (1996) did not detect differences among nutrient treatments for the population density of zooxanthellae in small colonies of *S. pistillata* during the second high-loading phase. However, in a set of larger coral colonies (approximately $10 \times$ larger) used in a study of the photophysiological responses of *S. pistillata* to nutrient increases, significant differences between treatments were seen (Fig. 21). In this case, the population density of zooxanthellae resident in the coral sub-colonies was significantly greater in the +P and the +N treatments compared with corals from control patch reefs ($F_{3,8} = 7.13$, $p < 0.01$; Fig. 21). In the high-loading phase zooxanthellae densities of large colonies of *A. longicyathus* were significantly higher in +P treatments. In *A. aspera* the highest densities were in the +N+P but +P was also elevated with respect to controls.

The cell density of zooxanthellae in clams in nutrient treatment versus control patch reefs showed trends after three and six months, but these did not become statistically significant until 13 months when significantly

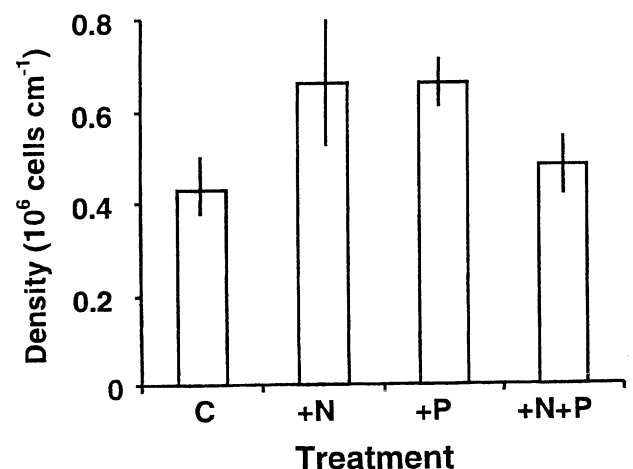


Fig. 21 Population density of zooxanthellae in *S. pistillata* after exposure to +N, +P and +N+P during the second phase of the ENCORE experiment.

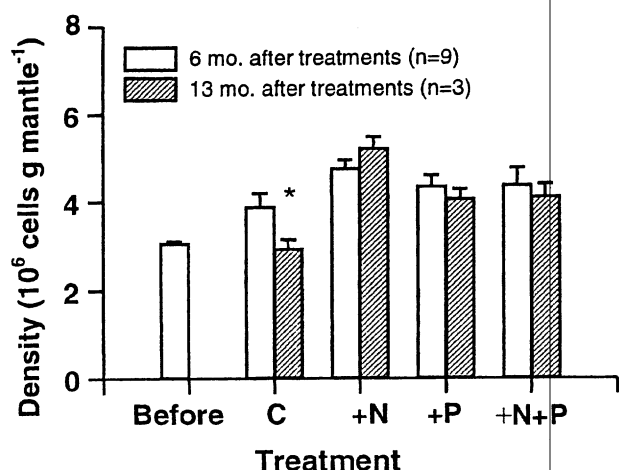


Fig. 22 Population density of zooxanthellae in the clam *T. maxima* as a function of ENCORE nutrient treatments during the first low dose phase.

higher numbers of zooxanthellae were recorded in clams from all three nutrient treatments (Fig. 22). During the second, high-loading phase the increase in cell density was statistically significant after five months in all nutrient treatments.

Changes in density of zooxanthellae have been observed previously in both corals and tridacnids as a result of nutrient enrichment (Hoegh-Guldberg and Smith, 1989; Belda *et al.*, 1993). This can be attributed either to increases in the mitotic index or the fact that the animal can retain and support larger numbers of zooxanthellae.

Experiments to examine the mitotic index (MI) of zooxanthellae of clams showed that maximum division occurred at 03:00 h and minimum at 15:00 h. However it was not until the 13th month that the MI increased statistically over the control. This was in the low-loading phase. Little change was observed in the second, high-loading phase.

Marked decreases in the cell diameter of zooxanthellae in giant clams (*T. maxima*) were seen in nutrient treatments, particularly the +N treatment compared with the control. This may be indicative of a higher division rate and the consequent increase in zooxanthellae density observed in these tridacnids.

Chlorophyll content. A major determinant of productivity within symbiotic organisms like corals and clams is the concentration of the primary photosynthetic pigment chlorophyll. Chlorophyll has been found to be highly responsive to changes in the concentration of nutrients like ammonium (e.g. Hoegh-Guldberg and Smith, 1989). Few significant changes in chlorophyll content of zooxanthellae in any organisms were detected during the initial, low-loading phase (Hoegh-Guldberg unpub. data). The exception was in giant clams. Here the total chlorophyll *a* content of the clams from all nutrient treatments was significantly higher than that of

control clams after 6 and 13 months of nutrient enrichment during the low-loading phase ($p < 0.001$ and 0.048 in February, 1994 and November, 1994, respectively) (Ambariyanto and Hoegh-Guldberg, 1996).

During the second phase of the project, however, a number of research teams found that chlorophyll levels did respond to nutrient enrichment. The areal concentrations of chlorophyll *a* in *S. pistillata* were higher in the +N and +N+P treatments than in controls (Fig. 23), (Takabayashi, 1996). The concentrations of chlorophyll *a* per zooxanthella in the +N and +N+P treatments, however, were not significantly different from those of the control (Fig. 24). The increase in the areal concentration of chlorophyll was thus due to an increased population density of zooxanthellae, especially in the +N treatment. These results are consistent with other studies within the project and the scientific literature (Hoegh-Guldberg and Smith, 1989; Muller-Parker *et al.*, 1994; Stambler *et al.*, 1991, 1994). Ambariyanto and Hoegh-Guldberg (1996) also found significantly higher total chlorophyll *a* content in ammonium-treated clams 5 months after the beginning of the high-loading phase of nutrient enrichment ($p < 0.015$). Just as was found in the coral studies, the chlorophyll *a* content per zooxanthella was not affected by nutrient enrichment during the first or second phase of nutrient enrichment.

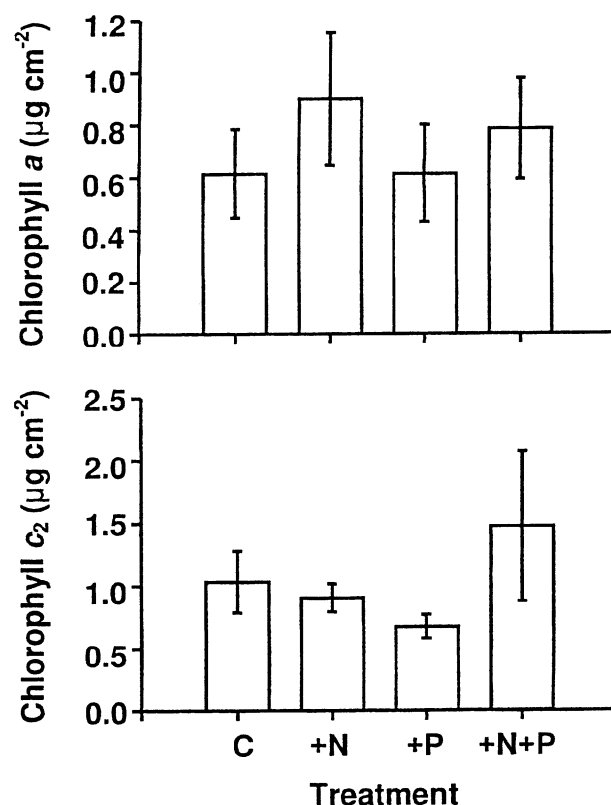


Fig. 23 Concentration of chlorophyll as a function of surface area in the coral *S. pistillata* exposed to the second high dose ENCORE nutrient treatments.

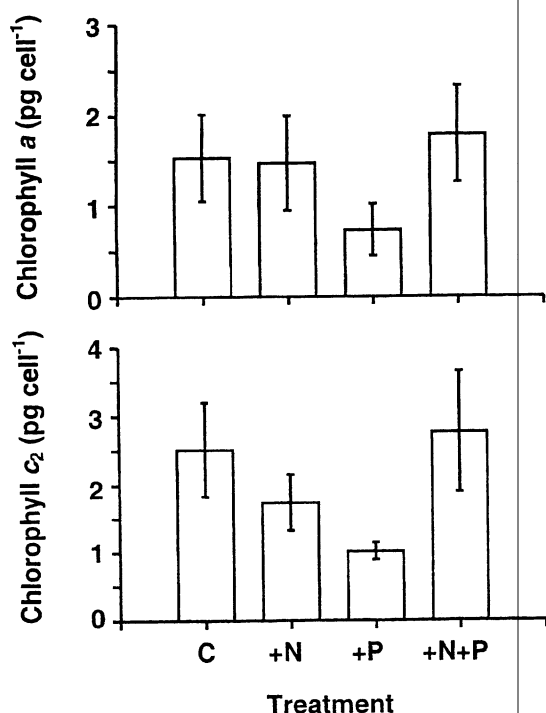


Fig. 24 Concentration of chlorophyll per zooxanthella in the coral *S. pistillata* exposed to the second high dose ENCORE nutrient treatments.

Increases in chlorophyll and concentration per unit area in +N and +N+P treatments were related to the increase in number of zooxanthellae (and hence biomass) rather than increases in chlorophyll per cell. This is consistent with the conclusions of previous laboratory or raceway studies (Hoegh-Guldberg and Smith, 1989; Dubinsky *et al.*, 1990; Stambler *et al.*, 1991; Ambariyanto, 1996).

Ammonium uptake by zooxanthellae. After one month of nutrient enrichment there was no significant change in the capacity for ammonium uptake by zooxanthellae in large giant clams (*T. gigas*) although a trend was evident. After three months exposure to nutrient additions, zooxanthellae from +N-treated clams had a significantly lower ammonium uptake capacity (down-regulated), while zooxanthellae from +P-treated clams had a significantly greater ammonium uptake capacity (up-regulated) than control clams. However, zooxanthellae from +N+P treated clams had N-uptake rates similar to control clams. In the +N+P treatment it is likely that there was an interaction between the two nutrients cancelling out the effect of each in isolation. Results obtained with zooxanthellae freshly isolated from the coral *P. damicornis* showed a similar trend after three months (Fig. 25).

Zooxanthellae ultrastructure. Using electron microscopy, Ambariyanto and Hoegh-Guldberg (1996) demonstrated that in the +N and +N+P treatments there

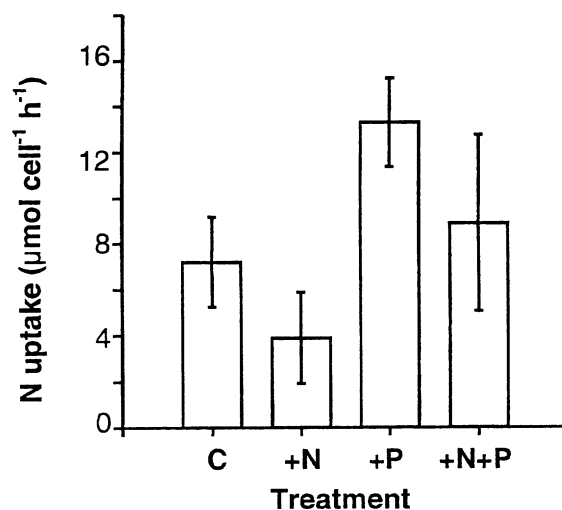


Fig. 25 Effect of nutrient enhancement on the ammonium uptake capacity of freshly isolated zooxanthellae from the coral *P. damicornis*.

was a decrease in cell size and in the amount of starch in the sheath surrounding the pyrenoid of the zooxanthellae chloroplast in giant clams. This was not evident in either the control or phosphate treatment. These results are consistent with the fact that zooxanthellae are nitrogen limited. The zooxanthellae under enriched ammonium conditions are capable of mobilizing starch reserves for the synthesis of amino acids. In a similar study of zooxanthellae from the branching coral *S. pistillata* the zooxanthellae were sectioned and examined using a similar set of methods (Takabayashi, 1996). In contrast to changes observed in clams, zooxanthellae in *S. pistillata* were the same size in all treatments and had similar amounts of starch surrounding their pyrenoid stalks suggesting that, perhaps, the zooxanthellae in *S. pistillata* were not nitrogen limited.

DMSP in zooxanthellae

Studies in the Great Barrier Reef have shown that coral zooxanthellae contain abundant amounts of dimethylsulphoniopropionate (DMSP) (Jones *et al.*, 1994; Broadbent *et al.* unpub. data). The exact role and function of DMSP in algae and coral zooxanthellae is not known, although in algae it has been suggested that DMSP acts as an osmolyte (Kirst, 1989). Recent work suggests that the concentration of DMSP in certain species of algae may be an adaptation to a low nutrient environment (Liss and Galloway, 1993). Nitrogen has been suggested as the most energy efficient preference for the synthesis of osmolytes. During nitrogen limitation, it has been suggested that sulphur can replace some nitrogen-containing osmolytes of similar structure (e.g. glycine betaine), so that nitrogen can be utilized for the more important process of amino acid and protein synthesis. During ENCORE the effect of nutrient enrichment by +N and +P on the synthesis of DMSP was examined in the coral *A. palifera*.

After 65 days DMSP (nmol/polyp) decreased in colonies enriched with +N and +P compared with controls. After 273 days, however, this trend had been reversed, with a significant increase in DMSP in +N+P, and +P enriched colonies, indicating an effect on DMSP from P enrichment. At the cellular level, however, nutrient enrichment showed no clear trend in zooxanthellar DMSP (fmol/cell).

Bioerosion

Bioerosion consists of internal boring by macro- and micro-organisms, and external erosion by grazing organisms such as scarids and molluscs. In many reef situations, dead coral substrata are not only subjected to bioerosion but are added to by calcareous algae and various encrusting fauna including serpulid worms, bryozoans and bivalve molluscs. Thus substrata may experience net gains or net losses of calcium carbonate. Kiene and Hutchings (1994) have discussed the relationships between these two processes.

Gektidis (1997) identified six species of cyanobacteria/cyanophyta, of which three are possibly new species, three genera of green algae each represented by a single species and a rhizoid of a green alga, in his samples of *Tridacna*, calcite and limestone from One Tree Island patch reefs. Differences in the species composition and abundance of these communities could not be related to the various nutrient treatments. While no treatment effect was observed, differences in the structure of these communities varied over time, and hence did rates of bioerosion. Vogel *et al.* (1996) suggest that the position of the patch reefs within the One Tree lagoon is a major factor controlling these communities. Kiene (1994) recorded the highest and lowest average rates of micro-boring (7.56 and $43.44 \text{ g m}^{-2} \text{ yr}^{-1}$) on patch reefs with both N and P added. There was a trend for average microboring rates to increase from east to west through the lagoon. In contrast, Kiene (1994) found no differences related to position of the patch reefs in the lagoon with regard to grazing or macroborers after 26 months of exposure and no effects of nutrients. However, he stressed that perhaps a 2-year study period was insufficient to investigate the effects of nutrient addition on macroborers. Complementary studies were done by Hutchings (unpub. data) to investigate rates and agents of macroborers, losses of calcium carbonate due to grazers and gains by accretion, in the control sites, as well as the +N+P sites. To date only substrata exposed for 2 years have been analysed and substrata exposed for a further 2 years are currently being analysed. After 2 years, no significant differences were found between control and nutrient-enriched patch reefs, with all sites experiencing net losses (ie grazing and boring exceeded gains by accretion) of substrata of between 1.57 ± 0.24 and $2.83 \pm 1.06 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$. This is in contrast to Kiene (1994) who found that the dry weight of the samples increased at most sites, indicating that net accretion was generally higher than net erosion. The ap-

parent difference in results is probably due to the methods used. Kiene (1994) used dry weight of blocks before and after exposure, whereas Hutchings (unpub. data) measured loss and gains of calcium carbonate from digitized sections of the blocks (see Pari *et al.*, 1998). In summary all studies of bioerosion and accretion showed that the addition of nutrients had no significant effects on rates, at least over a 2-year period. No attempt was made to distinguish between the low and high-loading phases. Throughout the 2 years, the infauna boring organisms were characterized by relatively few species, with vermetid molluscs and the polychaete *Dodecaceria* dominant, with increasing exposure time, a more diverse boring community has developed (Hutchings unpub. data).

Conclusions

A summary of all results from the ENCORE study is presented in Table 13.

The study demonstrated a number of important effects of inorganic nutrients on coral reef organisms and biochemical and ecological processes. On the other hand it did not reveal some of the effects generally expected from nutrient impacts.

(1) Nutrients caused considerable effects at the level of the organism (e.g. increased mortality, reduced reproduction of corals) but did not cause coral reefs to convert from coral communities to seaweed-dominated reefs as has been recorded elsewhere (Smith *et al.*, 1981). We did not observe a stimulation of primary productivity of epilithic algal communities (EAC), and only saw minor increases in larger macroalgae. In the lagoon of One Tree Island, the fastest growing component of the algal community, the EAC, is not nutrient limited.

(2) One of the most important observations of this project was the impact of nutrients on coral reproduction. While growth and mortality increased in some species of corals, other species were unaffected. The production of viable gametes and successful fertilization were reduced by the addition of both inorganic nitrogen and phosphorus. This may be a factor contributing to the observed decline of reef-building corals close to developed sections of coastline. Further investigation of these sub-lethal impacts on coral reef organisms is recommended.

The Direct Effect of Increased Nutrient Availability on Coral Reef Organisms

Increasing concentrations of nutrients had a number of direct effects on the organisms living within the ENCORE patch reefs. While many organisms showed subtle responses at biochemical levels (e.g. increased nitrogen storage in macroalgae, decreased starch storage in zooxanthellae, shifts in the activity of assimilation enzymes within the zooxanthellae of clams), some

TABLE 13

Summary of major responses of organisms studied during the low (September 1993–December 1994) and high (January 1995–February 1996) loading phases.^a

Parameter	Treatment					
	Low			High		
	+N	+P	+N+P	+N	+P	+N+P
<i>Plants</i>						
<i>Phytoplankton</i>	No data	No data	No data	0	0	0
<i>Zooxanthellae (clam)</i>						
• Mitotic index	↑	↑	↑	0	0	0
• Cell diameter (clams)	↓	↓*	↓*	No data	No data	No data
• Ultrastructure (size, pyrenoid starch)	↓	0	↓	No data	No data	No data
• Ammonium uptake	↓	↑	0	No data	No data	No data
• Chlorophyll per cell	0	0	0	0	0	0
<i>Zooxanthellae (coral)</i>						
• Mitotic index (<i>Stylophora pistillata</i>)	0	0	0	0	0	0
• Cell diameter (<i>S. pistillata</i>)	No data	No data	No data	0	0	0
• Ultrastructure (size, pyrenoid starch)	No data	No data	No data	0	0	0
• Chlorophyll per cell	0	0	0	0	0	0
• Ammonium uptake	No data	No data	No data	↓	0	0
• DMSP (per zooxanthella)	0	0	0	No data	No data	No data
<i>Incrusting algae and Rhodoliths</i>						
• Buoyant weight	0	0	0	0	0	0
• Growth rates	0	0	0	0	0	0
• Calcification (alkalinity)	0	0	0	0	0	0
• Carbon production	No data	No data	No data	0	0	0
<i>Epilithic algae community</i>						
• Nitrogen uptake	0	0	No data	No data	No data	No data
• Carbon production	0	0	0	0	0	0
• Growth	0	0	0	0	0	0
• Chlorophyll <i>a</i>	0	0	0	0	0	0
• Alkaline phosphatase	0	0	0	0	0	0
<i>Filamentous algae</i>						
• Carbon production	0	0	0	No data	No data	No data
• Alkaline phosphatase (<i>Laurencia intricata</i>)	0	0	0	0	0	0
• Amino acid content (citrulline)	↑	0	↑	No data	No data	No data
• Total amino acid content	0	0	0	No data	No data	No data
• Total tissue N	0	0	0	No data	No data	No data
• C:N ratio (<i>Laurencia intricata</i>)	0	0	0	No data	No data	No data
• Chlorophyll <i>a</i> (<i>Laurencia intricata</i>)	0	0	0	No data	No data	No data
• Growth (<i>Laurencia intricata</i>)	0	0	0	0	0	0
• Nitrogen fixation (community on <i>Laurencia intricata</i>)	No data	No data	No data	↓	↓	↓
<i>Animals</i>						
<i>Reef-building corals</i>						
<i>Symbiont population density</i>						
• <i>Pocillopora damicornis</i> (nubbins)	0	0	0	No data	No data	No data
• <i>Stylophora pistillata</i> (nubbins)	No data	No data	No data	0	0	0
• <i>Stylophora pistillata</i> (large)	No data	No data	No data	0	0	No data
<i>Total chlorophyll content</i>						
• <i>Stylophora pistillata</i> (nubbins)	No data	No data	No data	↑	0	↑
<i>Mortality</i>						
• <i>Pocillopora damicornis</i> (nubbins)	0	0	0	0	↑	↑
• <i>Acropora longicyathus</i> (nubbins)	0	0	0	↑*	↑*	0
• <i>Acropora longicyathus</i> (large)	No data	No data	No data	0	0	0
• <i>Acropora aspera</i>	No data	No data	No data	0	0	0
<i>Growth</i>						
<i>Linear extension</i>						
• <i>Acropora palifera</i>	0	0	0	↓	↑	↑
• <i>A. longicyathus</i>	0	0	0	↓	↑	↑
<i>Buoyant weight</i>						
• <i>Acropora longicyathus</i> (large)	No data	No data	No data	↑	↑	↑
• <i>Acropora aspera</i> (large)	No data	No data	No data	0	↓	0
• <i>Acropora palifera</i> (large)	No data	No data	No data	↓	↑	0
• <i>Acropora longicyathus</i> (nubbins)	0	0	0	↓*	0	0
• <i>Pocillopora damicornis</i> (nubbins)	0	0	0	↓	0	↓
• <i>Stylophora pistillata</i> (nubbins)	No data	No data	No data	↓*	↓*	0

TABLE 13 (CONTINUED)

<i>Photophysiology</i>						
<i>After 3 months</i>						
• Gross Photosynthetic rate (per cm ²)	No data	No data	No data	0	↑	0
• Net Photosynthetic rate (per cm ²)	No data	No data	No data	0	↑	0
• Photosynthetic Efficiency	No data	No data	No data	0	0	0
• Respiratory rate (per cm ²)	No data	No data	No data	0	↑	0
<i>After 9 months</i>						
• Gross Photosynthetic rate (per cm ²)	No data	No data	No data	↓	0	0
• Net Photosynthetic rate (per cm ²)	No data	No data	No data	0	0	0
• Photosynthetic Efficiency	No data	No data	No data	↓	0	0
• Respiratory rate (per cm ²)	No data	No data	No data	↓	0	0
<i>Acropora longicyathus (skeletal)</i>						
• Bulk density	No data	No data	No data	↑	↓	?
• Microdensity	No data	No data	No data	↑	↑	?
• Mucus cell density	No data	No data	No data	0	↓	?
• Free body wall thickness	No data	No data	No data	0	↑	?
<i>Stylophora pistillata (skeletal particle size)</i>						
	No data	No data	No data	0	↓	0
<i>S. pistillata (Density of symbionts)</i>						
	No data	No data	No data	0	0	0
• DMSP (per polyp, <i>Acropora palifera</i>)	0	↑	↑	No data	No data	No data
<i>Reproduction/Recruitment</i>						
<i>Egg numbers</i>						
• <i>Acropora longicyathus</i>	↓	0	↓	↓	0	↓
• <i>Acropora aspera</i>	↓	0	↓	↓	0	↓
<i>Egg size</i>						
• <i>Acropora longicyathus</i>	↓	↓	↓	↓	↓	↓
• <i>Acropora aspera</i>	↓	↓	↓	↓	↓	↓
<i>Testes total</i>						
• <i>Acropora longicyathus</i>	↓	↑	↓	0	↑	↓
• <i>Acropora aspera</i>	↓	↑	↓	0	↑	↓
<i>Fertilization rates</i>						
• <i>Acropora longicyathus</i>	↓	↓	↓	↓	↓	↓
• <i>Goniastrea aspera</i>	0	0	↓	0	0	↓
<i>Occurrence of irregular embryos</i>						
• <i>Acropora longicyathus</i>	↑	↑	↑	↑	↑	↑
• <i>Goniastrea aspera</i>	↑	↑	↑	↑	↑	↑
<i>Settlement success</i>						
• Spawning species	↓	0	↓	↓	0	↓
• Brooding species	↓	0	↓	↓	↑	↑
<i>Lipids</i>						
• <i>Acropora longicyathus</i>	↓	↑	↓	↓	↑	↓
• <i>Acropora aspera</i>	↓	↑	↓	↓	↑	↓
• <i>Acropora bushyensis</i>	↓	↑	↓	↓	↑	↓
<i>Soft corals</i>						
• C:N:P	No data	No data	No data	0	0	0
• Terpene production	No data	No data	No data	0	0	0
• Lipids (fatty ester)	No data	No data	No data	0	0	0
• Stress (terpenes/lipids)	No data	No data	No data	0	↑	0
<i>Giant clams</i>						
<i>Growth</i>						
• Shell length	0	0	0	↑	↑	0
• Buoyant weight	0	0	0	0	0	0
• Wet tissue weight	0	0	0	0	0	0
• Protein content per gram mantle	↑	↑	↑	0	0	0
• C:N (clam only)	0	0	0	0	0	0
• N:P	No data	No data	No data	↑	↓	0
• Haemolymph (N,P)	0	0	0	No data	No data	No data
• Glycine (free amino acid pool)	↑	↑	↑	No data	No data	No data
• Uptake of dissolved free amino acids	No data	No data	No data	0	No data	No data
• Respiration	0	0	0	0	0	0
• Photosynthesis	0	0	0	0	0	0
<i>Density of symbionts</i>						
	↑	↑	↑	↑	↑	↑
<i>Total chlorophyll content (per clam)</i>						
	↑	↑	↑	↑	0	0
<i>Stomatopod recruitment</i>						
	No data	No data	No data	↓*	0	↓
<i>Fish</i>						
• Grazing rate	0	0	0	0	0	0
• <i>Pomacentrus wardi</i> fecundity	0	0	0	0	0	0

TABLE 13 (CONTINUED)

Community responses						
• N-fixation		0				
• Denitrification (sediments)	↓ No data	0 No data	↓ No data	↓ ↑ No data	↑ ↑ No data	↓ ↑ No data
• Bioerosion	0	0	No data	No data	No data	No data

^a Arrows indicate direction of significant changes. Asterisks indicate strong but not significant responses. No data indicate that measurements were not performed. There may have been minor seasonal differences in cases where measurements were repeated over the year – summary indicates the most common type of response in these cases.

organisms showed quite substantial changes. Of these, reef-building corals showed some of the most dramatic changes. The direct effect of nutrients on reef-building corals ranged from slower growth (in many species) to higher mortality rates (up to threefold higher than those growing in control patch reefs). Significant effects on coral reproductive capacity were also observed. In particular, corals exposed to elevated ammonium produced significantly smaller and fewer eggs and contained significantly less testes material than unexposed corals. Gametes exposed to ammonium with or without phosphate had very low fertilization rates. Phosphorus on its own dramatically reduced fertilization rates and also significantly increased the incidence of irregular embryos. In many cases, development was arrested at the first cleavage stage.

These observations suggest that the changes in the abundance of corals associated with eutrophication of tropical coastlines may also be related to more subtle effects such as those on coral reproduction in addition to direct effects on survivorship. It also suggests that a closer study of the reproductive behaviour of corals and their recruitment in areas affected by increased nutrients levels should be done.

Bioindicators of Nutrient Stress

ENCORE research focused on the biochemical, physiological and ecological changes that occur in coral reefs exposed to increased levels of inorganic nutrients, nitrogen and phosphorus. One of the possible outcomes of this type of work is that it can identify organisms and processes that might be useful as biological indicators of nutrient stress. A number of parameters were initially identified as potential bioindicators but did not reveal consistent responses or had responses that were complicated by species-specific behaviour. Notably, the primary production and phosphatase activity of EAC and macroalgae, buoyant weight (= growth) and skeletal structure of reef-building corals and sediment chemistry (e.g. dissolved free amino acid concentrations) did not show the consistent responses necessary for use as bioindicators. Our results did, however, show promise with a number of parameters that had clear and marked responses. These were:

1. Gametogenesis in reef-building corals (Ward and Harrison, 2000).
2. Ultrastructure of zooxanthellae (Ambariyanto and Hoegh-Guldberg, 1997).

3. C:N ratios in coral and zooxanthellae tissue (Hoegh-Guldberg *et al.*, unpub. data).

4. Nitrogen fixation in sediments and algal/cyanobacterial communities and sediment denitrification (O'Neil *et al.*, unpub. data).

Clearly further development work will be necessary to develop these into useful tools. Specifically, it will be necessary to investigate how a measured change in a particular indicator can be interpreted in ecosystem terms. ENCORE has put a number of parameters on the agenda, which warrant further investigation. With increasing pressure on the world's coral reefs, and the recognized limitations of the much-used physico-chemical parameters as indicators of ecosystem health, developing relevant biological indicators is of supreme importance.

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