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Effect of nutrient enrichment in the field on the biomass, growth and calcification of the giant clam *Tridacna maxima*

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Abstract Nutrients were added separately and combined to an initial concentration of 10 μ*M* (ammonium) and/or 2 μ*M* (phosphate) in a series of experiments carried out with the giant clam *Tridacna maxima* at 12 microatolls in One Tree Island lagoon, Great Barrier Reef, Australia (ENCORE Project). These nutrient concentrations remained for 2 to 3 h before returning to natural levels. The additions were made every low tide (twice per day) over 13 and 12 mo periods for the first and second phase of the experiment, respectively. The nutrients did not change the wet tissue weight of the clams, host C:N ratio, protein content of the mantle, calcification rates or growth rates. However, ammonium (N) enrichment alone significantly increased the total population density of the algal symbiont (*Symbiodinium* sp.: C = $3.6 \cdot 10^8$ cell clam^{-1}, N = $6.6 \cdot 10^8$ cell clam^{-1}, P = $5.7 \cdot 10^8$ cell clam^{-1}, N + P = $5.7 \cdot 10^8$ cell clam^{-1}; and C = $4.1 \cdot 10^8$ cell clam^{-1}, N = $5.1 \cdot 10^8$ cell clam^{-1}, P = $4.7 \cdot 10^8$ cell clam^{-1}, N + P = $4.5 \cdot 10^8$ cell clam^{-1}, at the end of the first and second phases of the experiment, respectively), although no differences in the mitotic index of these populations were detected. The total chlorophyll *a* (chl *a*) content per clam but not chlorophyll *a* per cell also increased with ammonium addition (C = 7.0 mg chl *a* clam^{-1}, N = 13.1 mg chl *a* clam^{-1}, P = 12.9 mg chl *a* clam^{-1}, N + P = 11.8 mg chl *a* clam^{-1}; and C = 8.8 mg chl *a* clam^{-1}, N = 12.8 mg chl *a* clam^{-1}; P = 11.2 mg chl *a* clam^{-1}, N + P = 11.3 mg chl *a* clam^{-1}, at the end of the first and second phases of the experiment, respectively). The response of clams to nutrient enrichment was quantitatively small, but indicated that small changes in inorganic nutrient levels affect the clam–zooxanthellae association.

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Introduction

Coral reefs are typified by low concentrations of inorganic nutrients (Crossland 1983; D'Elia 1988), yet they are also known to be highly productive ecosystems (Muscatine and Porter 1977; Lewis 1981). At the heart of the success of the reef-building corals and clams that make up coral reefs is the symbiosis between these organisms and dinoflagellate algae (genus *Symbiodinium*) known as zooxanthellae. These microalgae, like all primary producers, require inorganic nutrients (e.g. nitrogen and phosphorus) to sustain normal levels of growth and productivity. These nutrients are obtained from host metabolism and from the surrounding water (Muscatine and Porter 1977). It is expected, therefore, that changes in the concentration of inorganic nutrients in the water should influence properties of symbioses that involve zooxanthellae (Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989; Muller-Parker et al. 1994 a, b).

The growth of clams in hatcheries has been found to be enhanced by short-term increases in nutrient concentrations. The growth rate of *Hippopus hippopus* in aquaria with elevated levels of nitrate was three times faster than that of clams in control aquaria (Solis et al. 1988). The growth of two size classes of *Tridacna gigas* (1.2 and 17.0 cm shell length) significantly increased when they were grown in seawater with an ammonium concentration of 20 μ*M* (Braley et al. 1992). Increasing DIN (dissolved inorganic nitrogen: 0.2 to 50 μ*M*) in water for 16 h d^{-1} during a 60 d experiment increased clam weight by 288 to 375% compared to untreated *T. derasa* (Hastie et al. 1992). Furthermore, increases in the concentration of some inorganic ions can also affect the biomass and shell structure of the clams. The addition of ammonium (40 μ*M*) increased the population density of zooxanthellae in *T. gigas* (cell g^{-1} clam; Braley et al. 1992). Belda et al. (1993 a, b) also reported that