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Influence of field-based nutrient enrichment on the photobiology of the giant clam *Tridacna maxima*

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Abstract Nutrients were added to 12 microatolls in One Tree Island lagoon every low tide for 13 mo to an initial concentration of 10 μM (ammonium, N) and 2 μM (phosphate, P). These concentrations remained above background for 2 to 3 h after addition. The addition of ammonium (N and N + P but not P alone) significantly increased P_g (gross photosynthesis) P_n (net photosynthesis) and R (respiration) per unit wet-tissue weight and α (photosynthetic efficiency) in *Tridacna maxima* after 3 mo nutrient enrichment. These responses to small and transient changes in ammonium concentrations suggest that symbiotic clams are not nutrient-replete, and that even subtle changes in nutrients can have a measurable effect on photosynthesis. The same clams did not show significant differences in photosynthetic parameters 6 mo after the beginning of nutrient enrichment, suggesting that their previous responses had either been seasonal or that symbiotic clams such as *T. maxima* are able to adjust their photophysiology following external changes in nutrient concentrations.

Introduction

The effect of nutrient enrichment on the photosynthetic and respiratory rates of symbiotic marine invertebrates has only been explored to a small extent, and only a few studies have been published (Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989; Stambler et al. 1994). Upon exposure to increased nutrient concentrations, the corals *Seriatopora hystrix* and *Stylophora pistillata* increased their photosynthetic rates. This was presumably related to observed increases in chlorophyll *a* and total zooxanthellae numbers (Hoegh-Guldberg and Smith 1989). The respiratory rates of the same corals tended to increase, but differences were not significant. Stambler et al. (1994) also reported an increase in the concentration of photosynthetic pigments per unit area of *Pocillopora damicornis* and *Montipora verrucosa* in response to ammonium enrichment, although this trend was also not statistically significant. The respiratory rate of N-enriched corals did not change relative to that of untreated corals (Stambler et al. 1994). Nutrient enrichment has also been reported to increase the C:N ratio of zooxanthellae (Muller-Parker et al. 1994), the surface density of the thylakoids, the starch content of the cells (Berner and Izhaki 1994), and the glutamine:glutamate ratio of the cells (McAuley 1994). The effect of ammonium enrichment on giant clams in past studies has included increases in the population density of zooxanthellae, total chlorophyll content, and clam growth rate (Braley et al. 1992; Hastie et al. 1992; Belda et al. 1993a,b; Fitt et al. 1993), and changes in the ultrastructure of the zooxanthellae (Ambariyanto and Hoegh-Guldberg 1996). None of these studies, however, investigated the photosynthetic and respiratory responses of the clams.

Most of the previous studies on nutrient enrichment of giant clams have been carried out under laboratory or hatchery conditions for short periods (< 3 mo). This paper set out to investigate the long-term impact of relatively subtle changes in nutrient concentrations on the photobiology of giant clams (*Tridacna maxima*) growing under field conditions. This was done as part of the ENCORE experiment (Enrichment of Nutrient on COral Reefs) which was undertaken at One Tree Island on the southern Great Barrier Reef, Australia (Steven and Larkum 1993).

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