Review article
Are Natural Populations of Zooxanthellae Ever Nutrient-Limited?

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Abstract

Symbiotic zooxanthellae in coral reef ecosystems have two general sources of "new" nutrients: those derived from host feeding, and those derived from inorganic nutrients dissolved in seawater. Zooxanthellae biomass may therefore be limited by these nutrient supplies. It is generally assumed in the literature that the intracellular host milieu is a nutrient-rich one that supplies the alga with a surfeit of nitrogen and phosphorus; however, published data are consistent with the notion that natural populations of zooxanthellae are generally nutrient-limited.

a. Zooxanthellae exist in enormous densities in host tissue, far surpassing any nuisance algal bloom. This implies a huge demand for nutrients and may result in very low internal concentrations of inorganic nutrients in host cells to support further algal growth.

b. *In situ* growth rates of zooxanthellae from hosts in coral reef environments are less than those at log phase in culture and in hosts in more nutrient-rich environments. Growth rates are less in starving than in fed hosts.

c. Sea anemones and corals deprived of particulate food sources support smaller algal populations than well fed ones.

d. Intact symbioses take up dissolved inorganic nutrients from seawater at very low concentrations. The kinetics of uptake processes imply low concentrations of nutrients (e.g. ammonium, phosphate, and nutrient analogues such as methylamine) within host tissues. Nutrient uptake declines sharply in the intact symbiosis and by freshly isolated zooxanthellae from well fed hosts.

e. Uptake of nitrate by some corals may indicate ammonium limitation, as nitrate uptake is characteristic of N-starved algae.

1. Introduction

"Research on nitrogen acquisition in algal-invertebrate symbiosis has progressed in the shadow of work on marine phytoplankton... symbiotic algae offer a more accessible experimental system that ought to be exploited in a way that would lead related phytoplankton research rather than follow it" — D.L. Taylor, 1983, p. 693.

Most research dealing the biology of marine algae-invertebrate symbioses has examined benefits accruing to the host, rather than the algae. Thus, research has focused on the nutritional value of the symbiosis from the host's perspective. How the host's metabolic processes affect the growth of the algae is less often considered. In this paper, we examine the question of possible nutrient limitation in endosymbiotic zooxanthellae. This question has been raised for the hydra – *Chlorella* symbiosis (Muscatine and Pool, 1979; Muscatine and Neckelmann, 1981; McAuley, 1985). To our knowledge, the question has not been raised for symbioses involving zooxanthellae, although Taylor (1980) suggested that nutrient limitation is a significant factor in the competition between potential symbionts in the acoel turbellarian *Amphiscolops langerhansi*. By considering the issue of possible nutrient limitation of zooxanthellae within host cells, we hope to develop insights into the biology of zooxanthellae, and to draw attention to Taylor's (1983) comments that these unialgal populations offer unique advantages to examine questions of broad interest to phytoplankton ecologists.

2. The Association of Zooxanthellae with Nutrient-Poor Waters

Zooxanthellae generally occur in environments such as coral reefs which are characteristically low in dissolved inorganic nutrients, especially nitrogen and phosphorus (reviewed by D'Elia, in press). For example, Bermuda is situated in the Sargasso Sea; dissolved nutrient concentrations in surface waters are typically close to detectable limits throughout the year, as are waters over reefs and lagoons (Morris et al., 1977). The Sargasso Sea has been a classical model of oligotrophic waters, with very low annual productivity (Menzel and Ryther, 1961). Phytoplankton biomass in the region is low, with cell concentrations (less than 5 μm diameter) generally under 10^4 liter^{-1}. Despite the low overall productivity of these waters, surprisingly high (albeit conflicting) rates of cell division have been reported (Table 1; see also Eppley, 1980). The contradiction between low nutrient availability and apparently high relative growth rates has been explained by analogy with a chemostat: high nutrient turnover and rapid removal of algae by predation and other routes would

Table 1. Densities and growth rates of phytoplankton populations in the Sargasso Sea off Bermuda

(a) Cell densities ($> 5\ \mu m$):	(Hulburt et al., 1959)	
Group	Density (cells·ml^{-1})	
Diatoms	0.1–0.5	
Coccolithophores	4–10	
Dinoflagellates	< 0.1	
(b) Estimates of growth rates:		
Source	Doubling time (days)	μ (day^{-1})
Riley et al. (1949)	3.8	0.18
Swift and Durbin (1972)	7.1–20	0.097–0.035
Sheldon and Sutcliffe (1978)	0.3–0.8	2.31–0.87

maintain low standing stocks (Sheldon and Sutcliffe, 1978; Goldman et al., 1979). By this argument, despite high rates of turnover, biomass would be proportional to the concentration of a limiting nutrient, and low nutrient levels would probably select for slower growing species that utilize nutrients efficiently.

The association of zooxanthellae with heterotrophic hosts is usually thought to represent an adaptation to nutrient-poor environments that allows tight nutrient recycling between the partners and the accumulation of biomass (Muscatine and Porter, 1977; Muscatine and D'Elia, 1978). On one hand, the endosymbionts' ability to acquire and recycle inorganic nutrients provides the host with an alternate source of nitrogen and phosphorus. On the other, metabolic products from host feeding are probably available to the algae, as has been indicated in tracer studies (Cook, 1971; Taylor, 1984; Steen, 1986). Conventional wisdom suggests that host metabolism produces a surfeit of nutrients for zooxanthellae that results in high internal nutrient concentrations resulting in photosynthetic and growth rates that are never nutrient-limited. Although no critical experimental work directly addresses this question, our survey of data from the literature indicates that nutrient limitation in populations of symbiotic zooxanthellae is more plausible than conventional wisdom suggests.

3.   Indicators of Nutrient Limitation in Zooxanthellae

A. Densities of natural populations vs. nutrient supply

Perhaps the most striking comparison between the phytoplankton of oligotrophic tropical waters and populations of symbiotic zooxanthellae is cell densities in host tissue. Cell concentrations in surface waters are in the range

Table 2. Estimated densities of *in situ* populations of zooxanthellae

Source	Est. density (cells·ml^{-1})	Reference
Montastrea annularis	2.5×10^6 *	Smith and Muscatine, 1986
Stylophora pistillata	$1.6 - 1.7 \times 10^6$ *	Falkowski and Dubinsky, 1981
S. pistillata	3.6×10^6 *	Smith and Muscatine, 1986
Aiptasia pallida (fed daily in lab)	1.2×10^6	Cook, Muller-Parker and D'Elia, in prep.

*Calculated from areal data, assuming tissue thickness of 1 cm.

of $10 \cdot ml^{-1}$ (Table 1). In contrast, populations of zooxanthellae within host tissue exist in enormous densities. Muscatine (1980a) summarized data for corals which show counts per cm^2 in excess of 10^6; more recent measurements are summarized in Table 2. If such corals have a tissue height of 1 cm, then cell concentrations are in excess of $10^6 \cdot ml^{-1}$. Our calculations of densities in fed sea anemones (*Aiptasia pallida*) are of the same order of magnitude. However, the veneer of algae in the symbiotic organism is so thin that light limitation seems unlikely especially in organisms found in shallow water.

Such concentrations exceed those in oligotrophic waters by 5 orders of magnitude, and exceed by an order of magnitude densities of nuisance plankton blooms. This implies that an enormous, localized potential demand for nutrients exists for these algae. There is, however, little information on the actual nutrient demand involved: it seems likely to exceed the rates at which host catabolism provides nutrients (D'Elia, 1977).

B. Rates of cell division

Relative population growth rates (μ/μ_{max}) less than 1.0 may be indicative of nutrient limitation (Goldman et al., 1979; $\mu =$ doublings·day^{-1} · 0.693). Unlike relative growth rates of tropical oceanic phytoplankton which may be close to 1.0, recent measurements of the *in situ* division rate of zooxanthellae based on 24 hr observations consistently show that rates are less than those of log-phase zooxanthellae *in vitro* (Table 3).

We have arbitrarily divided the data of Table 3 into categories of "high" and "low" nutrient environments. These nutrients include both dissolved sources and particulate food which is available for hosts. "High nutrient environments" include both temperate coastal waters (Washington State, California, southern Australia) and the "jellyfish lakes" of Palau, which are categorized by a nitrogen-rich chemocline (Hamner et al., 1982). "Low nutrient" environments would refer to coral reef waters. The data suggest that

Table 3. Growth rates of zooxanthellae (from various sources):

Host Source	Doubling time, days, (log phase)	μ (day^{-1})	Reference
(a) *in vitro*			
*Aiptasia tagetes**	3.5	0.22	Fitt and Trench, 1983
Cassiopeia xamachana	2.9	0.24	Fitt and Trench, 1983
Zoanthus sociatus	2.9	0.24	Domotor and D'Elia, 1984
(b) *in situ*: "High nutrient environments"			
Mastigias papua	6.9	0.10	Wilkerson et al., 1983
Anthopleura elegantissima			
(Friday Harbor)	6.9	0.10	Lerch, 1979, cited in Wilkerson et al., (1983)
(Los Angeles)	11.2	0.062	Lerch, 1979, cited in Wilkerson et al., (1983)
Pteraeolidia ianthina (low density)	2.5	0.28	Hoegh-Guldberg et al., 1986
Pteraeolidia ianthina (high density)	10.0	0.069	Hoegh-Guldberg et al., 1986
(c) *In situ*: "Low nutrient environments"			
Aiptasia pallida (lab, fed daily)	11.0	0.063	Cook et al., 1987
A. pulchella (lab, fed 2/week)	28.0	0.025	Muller-Parker, 1985
A. pulchella (field collected)	42	0.016	Wilkerson et al., 1983
Aulactinia stelloides (juvenile, low density)	7.4	0.094	Smith, 1986
Aulactinia stelloides (adult, high density)	14.4	0.048	Smith, 1986
Palythoa variabilis	40.8	0.017	Steen and Muscatine, 1984
Zoanthus sociatus	53.0	0.013	Steen and Muscatine, 1984
Stylophora pistillata (light-adapted)	53.3	0.013	Muscatine et al., 1984
S. pistillata (dark-adapted)	73.7	0.009	Muscatine et al., 1984

A. tagetes and *A. pallida* may be synonyms (Sterrer, 1986, p. 175)

growth of *in situ* zooxanthellae from "high nutrient" environments are inter-
mediate between that of log phase cultured algae and those from hosts living
in coral reef waters. Within the "low nutrient" group there appears to be
a relationship between growth and the nutritional status of the host. The
fastest growth rates are reported from sea anemones fed in the laboratory,
while the slowest rates have been reported from scleractinian corals, which

are likely to be less effective predators than anemones (cf. Porter, 1976). However, given that zooxanthellae from various host species are genetically different (Blank and Trench, 1985), and that *in situ* growth rates may have a genetic basis, there may have been selection for zooxanthellae with low μ_{max} in corals.

We have found that growth rates and biomass of zooxanthellae in the sea anemone *Aiptasia pallida* decline with starvation of the host, and that algal division rates in starving anemones can be increased by the addition of dissolved inorganic N and P (Cook, D'Elia and Muller-Parker, 1987). This observation provides evidence that growth of zooxanthellae, at least in unfed anemones, is limited by nutrient availability. Obviously other factors may influence the growth rate of algae within animal cells, such as putative host-produced inhibitory substances (reviewed by Smith, 1980). Growth rate is probably density-dependent, as growth rates of zooxanthellae *in situ* appear to be greatest in conditions of low population density. This has been observed both in natural hosts with different population densities (Hoegh-Guldberg et al., 1986; Smith, 1986, Table 3) and in experimental infections of algae-free hosts (reviewed in Cook, 1985, p. 178). While one interpretation is that more "space" is available, we propose that host catabolism provides a greater relative supply of nutrients for symbionts at low population densities. Moreover, as Wilkerson has pointed out (pers. comm., to CFD), the achieveable algal biomass of the symbiosis will depend on the supply of "new" nutrients to the symbiosis (sensu Dugdale and Goering, 1967).

Thus, although several possibilities exist for the "regulation" of populations of symbiotic algae, the correlation between growth rate and nutrient supply carries the strong implication that natural populations of symbiotic algae are nutrient-limited.

C. Standing crops of zooxanthellae in host tissue

Several reports show that in addition to enhancing endosymbiont growth rate, feeding hosts can support a larger standing crop of zooxanthellae than starved ones. This has been demonstrated in sea anemones (Clayton and Lasker, 1984; Cook et al., 1987), and in the temperate coral *Astrangia danae*, in which fed colonies have higher algal densities than starved ones (Szmant-Froelich and Pilson, 1984). In contrast to thse studies, Muller-Parker (1985), working with anemones maintained in a nutrient rich aquarium, found that densities of zooxanthellae in *Aiptasia pulchella* increased with feeding. Meyer and Schultz (1985) reported increased symbiont densities in corals which were

exposed to elevated nutrient loads in the form of fish excreta.

The standing stock of zooxanthellae within a host will be the balance between increases in algal biomass, and losses through expulsion (Steele, 1975) and cell death (either via senescence or digestion). Whether the effects of feeding and nutrient supply on numbers of zooxanthellae within host tissue are due to changes in growth or losses (or both) is at present unclear.

Any consideration of the dynamics between symbiotic algae and hosts would be incomplete without some discussion of green hydra, which are often used as models of host-symbiont interactions. However, this symbiosis appears to differ from zooxanthellar associations with regard to how host feeding affects symbiont standing crop. Cessation of feeding usually results in increased numbers of symbiotic *Chlorella* (Douglas and Smith, 1984; McAuley, 1985), although Muscatine and Neckelmann (1981) showed that zoochlorellae density in hydra increased following the addition of dissolved inorganic nutrients.

D. *Uptake of dissolved nutrients by intact associations*

The uptake and assimilation of dissolved inorganic nitrogen and phosphorus at low environmental concentrations are among the major features of symbioses involving zooxanthellae (Muscatine, 1980b). Host tissue alone lacks the capability to effect active uptake of these nutrients from solution, even though it may possess enzyme systems for assimilation (e.g., glutamine synthetase; Rees, 1987). As carrier-mediated uptake of nutrients is typical of isolated symbionts, the most plausible mechanism of uptake by intact associations is the diffusion-depletion hypothesis mechanism proposed by D'Elia et al. (1983). According to this model, uptake is effected by the algae, presumably following diffusive passage into the host cell (D'Elia, 1977; Muscatine and D'Elia, 1978; Webb and Wiebe, 1978). The model implies that host cell concentrations of these nutrients must be lower than ambient, and that algal uptake rate exceeds host regeneration rate. The conclusion to be drawn from these observations is that the pool of host metabolites that could be available to algae is very small.

Some intact symbioses and freshly isolated zooxanthellae take up nitrate at low natural concentrations (Webb and Wiebe, 1978; D'Elia et al., 1983; Domotor and D'Elia, 1984; Wilkerson and Trench, 1985). This would be unexpected if there is an ample supply of catabolically derived NH_4^+ in host tissues. One particularly interesting observation is that intact *Aiptasia* do not take up nitrate (Wilkerson and Muscatine, 1984), while cultured sym-

bionts from this anemone do so only under conditions of nitrogen deprivation (Wilkerson and Trench, 1985). The implication is that the available N supply in tissues of corals and other symbioses which take up nitrate must be vanishingly small.

4. Test of Hypothesis

As an approach to determining the nutrient sufficiency of zooxanthellae, we have begun a series of experiments to evaluate the physiological and growth responses of zooxanthellae to nutrient supply. For example, well-fed individuals of the sea anemone *Aiptasia pallida* were starved in glass-fiber filtered (0.45 μm pore size) seawater from the Sargasso Sea. Zooxanthellae harvested from these anemones exhibited classical signs of nutrient limitation, including decreased growth rate, decreased chlorophyll *a* content and elevated ratios of carbon to nitrogen (Cook, D'Elia and Muller-Parker, 1987).

We are also investigating the relationship between host holozoic nutrition and the uptake of the ammonium analogue ^{14}C-methylamine (D'Elia and Cook, in prep.). The data suggest that the rate of uptake of ammonium by zooxanthellae from *Aiptasia pallida* is affected greatly by host nutritional history, being greatest in starved anemones; moreover, in well-fed anemones, internal levels of ammonium are elevated enough to inhibit competitively the uptake of the ammonium analogue.

5. Conclusions

In this speculative paper, we have pointed out a number of lines of evidence that are consistent with the view that *in situ* zooxanthellae, viewed from the perspective of natural populations of algae, may be nutrient-limited. Clearly much relevant research to answer this question lies ahead. Many useful techniques exist that are routinely used to determine the nutrient sufficiency of natural phytoplankton populations. The application of these approaches should provide the answer. Such work presents a useful comparison with similar studies of phytoplankton, as such techniques can rarely be applied in the field to unialgal populations.

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