

Chapter 8

THE PHYSIOLOGICAL ECOLOGY OF NUISANCE ALGAE IN AN OLIGOTROPHIC LAKE

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ABSTRACT

Periphyton growth in oligotrophic Lake Tahoe appears to be regulated by nutrient input and provides additional evidence of cultural eutrophication. A stalked diatom community, *Gomphonema herculeana*, dominates the biomass in the eulittoral (splash) zone, and it is the luxuriant growth of this alga which has caused algal biofouling problems in this pristine lake. ¹⁵N-labelled nitrate and ammonium uptake experiments showed that this community had a greater affinity for these nutrients than did the sublittoral periphyton community which depended on nitrogen fixation to meet its cellular demands. The rates of nitrogen uptake at natural substrate levels, measured under no flow (static) conditions were too low to account for this community's N-demand. We suggest that water movement (e.g., wave action) is an important mechanism which acts to increase the bio-availability of nutrients and therefore allows these algae to achieve high rates of growth even though ambient substrate concentrations are low.

8.1 INTRODUCTION

Long term measurements of productivity in oligotrophic Lake Tahoe (California-Nevada) have clearly demonstrated that the rate of pelagic algal growth has more than doubled over the last two decades (Goldman 1985). Nutrient limitation, particularly nitrogen, appears to be the most important factor regulating phytoplankton growth (Arneson 1979; Goldman 1974, 1981). Further evidence which supports the observation that the overall fertility of the lake is increasing comes from studies of nearshore periphyton (Goldman and de Amezaga 1975; Goldman et al. 1982; Loeb and Reuter 1984). The results of these investigations indicate that the amount of growth of attached algae is well correlated with land disturbance in the adjacent watershed and therefore, is most likely regulated by nutrient availability (see Loeb manuscript in this symposium). The importance of nutrient availability to periphyton growth in Lake Tahoe has been experimentally verified using algal bioassay techniques. Dissolved inorganic nitrogen (DIN) as both nitrate and ammonium, and to a lesser extent ortho-phosphorus, significantly stimulated the assimilation of ¹⁴C-labelled inorganic carbon, and increased the chlorophyll *a* content per unit biomass and the percentage chlorophyll *a* to total pigments (Eloranta 1983; Loeb 1986).

The contribution of allochthonous sources (surface water and ground-water) to the nutrient budget of Lake Tahoe is considered significant, and therefore it is not uncommon to find that the waters of the littoral zone contain higher concentrations of nutrients relative to the open water (Goldman 1974; Goldman et al. 1982). Since the attached algal and littoral phytoplankton communities occupy this nearshore region, they have the first opportunity (vis-a-vis the pelagic phytoplankton) to use nutrients derived from the watershed. Indeed, in Lake Tahoe the periphyton community has provided the most visually striking evidence of cultural eutrophication. The luxuriant growth of an attached diatom community in the eulittoral, or splash zone of this lake is considered a nuisance from both an aesthetic point of view and a water quality perspective. These organisms occupy a unique niche in the lake ecosystem; in addition to living in a region of higher nutrient loading, they inhabit an area of the lake which is constantly under the influence of turbulent water movements (i.e. breaking waves). These two factors appear to be critical in determining the availability of nutrients for this community.

In this paper we will first, examine the physiological characteristics of nitrogen uptake by the splash zone diatom community, second, explain why biomass accumulations in this region are so high despite the fact that these organisms live in a nutrient deficient system and, third, hypothesize why these algae are restricted to the eulittoral zone. We would like to stress that this paper is, in part, an overview of previous and ongoing periphyton research at Lake Tahoe. In addition, we consider some of our conclusions regarding the importance of water movement to nutrient uptake and growth of this community as preliminary. However, given the overall lack of information concerning the functional role of freshwater periphyton communities in nutrient cycling, we hope that other researchers will be encouraged to test the hypotheses we present here.

8.2 METHODS

Nitrate and ammonium (DIN) uptake were determined independently by measuring the rate of incorporation of the stable isotope ^{15}N into the periphyton particulate fraction. These experiments were conducted during the spring of 1980, a period of active biomass accrual approximately midway between the minimum and maximum annual production for that year. Since senescence and the typical summer sloughing off of biomass did not occur until late August we assumed that the experimental results obtained were representative of the period of active growth.

Periphyton was removed from natural rock surfaces at a depth of 0.5 m at a location adjacent to a fertilized lawn. The biomass was returned to the laboratory, and transferred to flasks containing 100 ml of lake water. To measure DIN uptake, a kinetics approach was used in which each set of treatment

flasks (n=3) was inoculated with $^{15}\text{NH}_4\text{Cl}$ or $\text{Na}^{15}\text{NO}_3$ (99.5 atom-%, ICN Biomedicals Inc.) to achieve a final substrate concentration which ranged from 10-2,000 $\mu\text{g N liter}^{-1}$. Samples were incubated in the laboratory for ~6 h under conditions of ambient temperature (10-15°C) and a light intensity of 200-250 $\mu\text{E m}^{-2} \text{sec}^{-1}$. Studies on DIN uptake by other periphyton communities in Lake Tahoe have shown that substrate depletion is linear over time (2-8 h) and that non-biological uptake is insignificant (Reuter 1983). Following the incubation, the periphyton biomass was removed from the treatment flasks, rinsed 6-8 times with lake water, oven dried (60°C), and frozen (-20°C). A mass spectrometer (Consolidated Engineering Systems) was used to determine the final ^{15}N enrichment and samples were prepared for analysis using a Kjeldahl digestion and steam distillation procedure (Fiedler and Proksch 1975). The fraction of ^{15}N in the gas phase was calculated according to Neess et al. (1962) and Pavlou et al. (1974). Final enrichment values ranged from 0.1-6.0 atom-% ^{15}N with substrate depletion generally less than 25%.

The Michaelis-Menten equation was used to model the kinetics of DIN uptake (Dugdale 1967):

$$V_N = V_{\max} \frac{S}{K_t + S} \quad (1)$$

where V_N is the rate of uptake, S is the external substrate concentration, V_{\max} is the maximum rate of uptake (i.e. at saturation levels of S), and K_t is the half-saturation constant (at which $V = V_{\max}/2$). The kinetic parameters K_t and V_{\max} , along with their standard deviations, were calculated directly from a rectangular hyperbola fitted to the data points by a least squares analysis (Cleland 1967).

Rates of nitrogen fixation were measured using the acetylene reduction technique (Stewart et al. 1967; Flett et al. 1976). The factor 4.6, used to convert moles of ethylene to moles of nitrogen was experimentally determined using $^{15}\text{N}_2$ (Reuter et al. 1983).

Particulate nitrogen was used as an estimate of standing crop for the kinetics experiments and was measured immediately following the steam distillation procedure using 1.04N H_2SO_4 as the titrant (APHA 1981). Chlorophyll *a* (corrected for phaeophytin) was also used as a biomass indicator and was measured according to Strickland and Parsons (1972) using 90% acetone as the extracting solvent. *In situ* and experimental concentrations of nitrate ($\text{NO}_3^- + \text{NO}_2^-$) were determined using the hydrazine reduction method described by Mullin and Riley (1955) and Kamphake et al. (1967) while ammonium was measured according to Solorzano (1969).

Water movement was measured using an *in situ* current meter (Kahlsico #232WA240) equipped with an electro-mechanical, digital counter. This meter was chosen because it detects two-directional flow (180°) and therefore measurements were more representative of the surge-type flow which occurs in the splash zone. Measurements were taken on the bottom along a transect away from the shoreline. The final readings are presented as a percent of surface flow and not as actual velocities.



Figure 8.1. Luxuriant growth of the stalked diatom *Gomphonopsis herculeana* in the eulittoral zone. Biomass accumulation represents a single year's growth. Production begins as early as January and by mid-late summer this community has sloughed off the rocks. This unattached biomass may accumulate in the littoral zone, be washed up on the beaches, or be transported away from shore by lake currents. Photograph was taken at the study site at a depth of ~1m.

8.3 RESULTS AND DISCUSSION

In Lake Tahoe, natural rock surfaces provide the major substratum for algal attachment. The vertical (depth) distribution of periphyton can be broadly divided into two zones delineated primarily by the annual changes in lake level and by wave action. Each of these zones is characterized by a separate algal flora with distinct taxonomic and physiological differences. The eulittoral or splash zone is restricted to the area located between annual periods of low and high water levels (i.e. 0-2 m) and is the most affected by water movement. Substrata within this region desiccate during the summer period of reduced precipitation (June-September) and each year, periphyton biomass must recolonize when the lake level rises again in the spring (February-June). The biomass of this community is totally dominated by the stalked diatom *Gomphonema herculeana*. The luxuriant growth of this species can be seen in Figure 8.1. In contrast, the second, deeper sublittoral zone remains constantly submerged and extends from 2 to over 150 m in depth. The algae in the upper sublittoral (2-80 m) are dominated by heterocystous, filamentous blue-green algae.

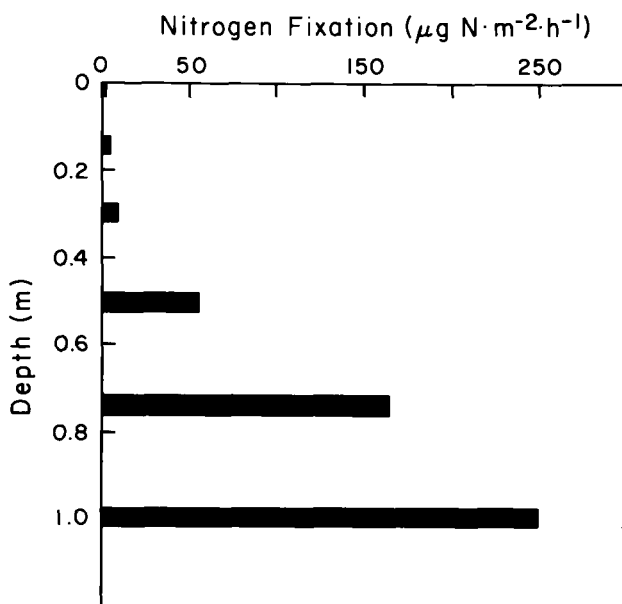


Figure 8.2. Vertical profile of periphyton nitrogen fixation in the eulittoral zone of Lake Tahoe. At the time of sampling the transition depth between the eulittoral diatom community and the sublittoral blue-green algal community was visually apparent at approximately 0.5 m. For each depth $n=3$.

The vertical distribution of benthic nitrogenase activity was measured from 0-1 m and clearly showed that nitrogen fixation was virtually non-existent in the eu littoral zone relative to the sublittoral zone, and was not important as a source of nitrogen for the splash zone community (Fig. 8.2). This was not unexpected since the algal biomass in this region was dominated by diatoms. At the time the samples were taken (July), the lake level was declining and the transition between the eu littoral and sublittoral was located between 0.4 and 0.6 m. At and below this depth heterocystous blue-green algae (i.e. *Tolypothrix*, *Calothrix*, and *Nostoc*) dominated the biomass and studies have shown that this community depends on nitrogen fixation as the major pathway of nitrogen assimilation (Reuter et al. 1986). Occasional, isolated patches of nitrogen fixing species existed beneath the *Gomphonema* community and accounted for the positive, albeit minimal, rates of nitrogen fixation observed at 0, 0.15 and 0.30 m.

Rates of nitrate and ammonium uptake were dependent on the external substrate concentration and these data agreed well with the curves generated by the Michaelis-Menten model (Fig. 8.3). The half-saturation constants were very

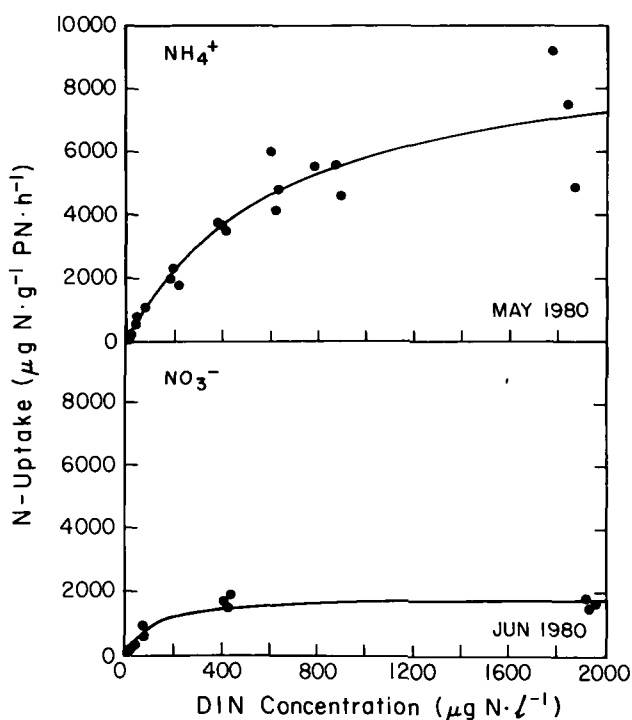


Figure 8.3. Ammonium and nitrate uptake as a function of substrate concentration for eu littoral (splash zone) epilithic periphyton. These experiments were conducted during the period of active spring growth.

high relative to ambient levels of DIN. These k_t values were 113 ± 26 $\mu\text{g N liter}^{-1}$ ($\bar{X} \pm \text{SD}$) and 634 ± 158 $\mu\text{g N liter}^{-1}$ for nitrate and ammonium, respectively. The ambient lake concentrations of NO_3^- and NH_4^+ at the time of these experiments were less than 5 $\mu\text{g N liter}^{-1}$; i.e. near the analytical limit of detection. The maximum rate of ammonium uptake was calculated to be 9540 ± 1047 $\mu\text{g N g}^{-1}\text{PN h}^{-1}$ which was more than five times greater than the V_{max} for nitrate uptake (1864 ± 108 $\mu\text{g N g}^{-1}\text{PN h}^{-1}$). At ecologically relevant DIN concentrations (≤ 25 $\mu\text{g N liter}^{-1}$), however, the rates of uptake for these two forms of nitrogen were similar ($V\text{-ammonium}/V\text{-nitrate} = 1.6$). These results suggest that when DIN levels are low the organisms in this eulittoral periphyton community appear to be adapted to use either substrate equally. This conclusion is supported by field studies of Reuter et al. (1985) who found that in Castle Lake, California, at ammonium concentrations less than 45 $\mu\text{g N liter}^{-1}$, epilithic periphyton was able to use NH_4^+ and NO_3^- simultaneously without an apparent preference for either substrate. In addition, evidence from batch culture studies has shown that if external ammonium levels are insufficient to saturate internal-N pools, simultaneous NH_4^+ and NO_3^- uptake is likely (McCarthy 1981).

The magnitude of the kinetics parameter, K_t , is often interpreted as an indication of an organism's ability to use a nutrient when available in low concentrations. A low K_t value implies that an organism has a high biological affinity for a specific nutrient, presumably an adaptive advantage in environments where that nutrient was scarce (Dugdale 1976; Raymond 1980). Previous studies of marine and freshwater phytoplankton have shown that the magnitude of half-saturation constants of these natural algal communities for nitrate and ammonium uptake are often directly related to substrate availability (e.g. MacIsaac and Dugdale 1969; Eppley et al. 1969; Murphy 1980; Axler et al. 1982, 1983; Priscu and Priscu 1984). Therefore, we hypothesized that the eulittoral periphyton community would have a low K_t (≤ 20 $\mu\text{g N liter}^{-1}$) in order to survive in a nutrient deficient system.

Since the measured k_t value was much greater, we re-evaluated the uptake kinetics data by examining the ratio of V_{max}/K_t . This value represents the initial slope of the Michaelis-Menten equation (dV/dS), and provides a more realistic interpretation of biological affinity in cases where V_{max} values are different (Healey 1980; Zevenboom 1980). When uptake was normalized to the amount of chlorophyll *a* (i.e. metabolically active algae), the V_{max}/K_t values for NO_3^- and NH_4^+ were nearly identical, 3.8 and 3.4 respectively. These V_{max}/K_t values for eulittoral algae were 20 times greater than those ratios calculated for the sublittoral community which depends on nitrogen fixation and not DIN for nitrogen (Reuter unpubl. data). This suggested that the Gomphonis community had a greater affinity for DIN than the cyanophycean sublittoral community even

though the K_t values for each community were similar (Reuter 1983). A similar relationship between the V_{max}/K_t ratios has also been demonstrated for the *Zygnema* dominated eulittoral periphyton and the nitrogen-fixing cyanophycean sublittoral communities in N-deficient Castle Lake, California (Reuter and Axler in press).

Estimates of net carbon production were used to calculate the nitrogen demand of this community. Eulittoral algal productivity was taken as the difference between the seasonal minimum and maximum levels of standing crop total carbon. During the period of spring maximum growth from 1981-1983 this rate was 122 ± 29 mg C m⁻² day⁻¹ ($X \pm SD$). This value represents net carbon productivity and will underestimate the actual daily nitrogen demand of this community to the extent that metabolic and mechanical losses occur (i.e. release of nitrogenous extracellular products, death and decomposition, grazing and sloughing due to wave action). The maximum, short term (30 day) rate of production was calculated to be 231 ± 47 mg C m⁻² day⁻¹. Since the rate of biomass accumulation during short time periods is more likely to reflect gross production, the 30-day rate was used to estimate nitrogen demand. Assuming a C/N uptake of 8:1 (a value which was always greater than the C/N biomass composition ratio) and that N-uptake occurred at equal rates over the entire day, the estimated nitrogen demand of this community was calculated to be ~ 1200 ug N m⁻² h⁻¹. This value is believed to be an underestimate of the actual nitrogen demand because of the two assumptions made above. Based on the rates of N-uptake measured during the kinetics experiments, the concentration of total DIN that would be necessary to support eulittoral algal growth would be ~ 70 ug N liter⁻¹. Since the maximum concentrations of nitrate in the euphotic region of Lake Tahoe never exceed 15-20 ug N liter⁻¹ (Paerl et al. 1975) and concentrations of ammonium rarely exceed 5 ug N liter⁻¹, the maximum available concentration of DIN cannot be greater than 20-25 ug N liter⁻¹.

Based on these calculations, other nitrogen sources and/or mechanisms which enhance the bioavailability of this nutrient must exist to enable these algae to meet their nitrogen demand during periods of maximum growth. Groundwater seepage and overland runoff could be important sources of nitrogen to the littoral zone. Preliminary data on the chemical composition of interstitial water sampled from the eulittoral zone in Lake Tahoe shows that DIN concentrations are high (generally greater than 100 ug N liter⁻¹) relative to the values routinely measured in the overlying water (Loeb and Palmer 1985). It is therefore possible that the periphyton community is also exposed to these elevated DIN levels. We believe that a more important factor which may regulate the rate of DIN uptake by the eulittoral community is related to the physical rigor of the habitat of these organisms. The splash zone is a region

of the lake where there is constant water movement and water movement per se can enhance nutrient transport into cells. Whitford (1960) presented theoretical evidence to suggest that at velocities greater than 15 cm sec^{-1} the rate of periphyton growth could be increased by maintaining a steep nutrient concentration gradient at the cell boundary which would in turn facilitate diffusion from the surrounding water. Lock and John (1979) observed that even a minimal flow velocity stimulated phosphorus uptake by river periphyton. Wheeler (1982) examined nitrate and ammonium uptake by mature blades of the marine macroalga Macrocystis pyrifera as a function of current speed and showed that at velocities greater than 5 cm sec^{-1} the uptake rates were 5-10 times greater than those measured under static conditions. We hypothesize that the nitrogen demand of the natural eulittoral algal community can be accounted for at low ambient substrate levels because water flow will augment nutrient uptake rates.

The velocities of breaking waves in lakes range from 50-500 cm sec^{-1} (Boyce 1974) and therefore should be more than sufficient to maintain an elevated nutrient concentration gradient at the cell boundary. The water flow measurements taken in the eulittoral zone at Lake Tahoe showed that water movement at the rock-water boundary decreased exponentially with depth on a transect away from the shoreline, and at a depth of 2 m the current was reduced to 7% of that measured at the surface at the lakeshore boundary. We suggest that the luxuriant growth of eulittoral periphyton community is restricted to the upper 2-3 meters of the littoral zone because below this depth wave flow is insufficient to sustain the required rates of nutrient uptake. Loeb (unpubl. data) found that Gomphonoidis ^{14}C primary productivity was reduced at the surface relative to more intermediate depths (2-30 m). This suggests that this community is not restricted to the eulittoral zone on the basis of its light requirements. As suggested long ago by Ruttner (1926), the movement of water allows attached algae to live in a "physiologically rich" environment even though the nutrient concentration in the surrounding water may be low.

8.4 CONCLUSIONS

Periphyton biomass accumulation in the eulittoral zone in Lake Tahoe is much greater than that measured for the sublittoral community. We believe that the luxuriant growth of this nuisance algal community is related to the following:

1. The Gomphonoidis community has a greater biological affinity for nitrogen as compared to the sublittoral algae.
2. Increased water movement in this zone probably enhances the rate of uptake of DIN, as well as other important nutrients.
3. Additional sources of nutrients are greater at the lakeshore boundary, particularly from groundwater seepage and overland runoff.

Furthermore, we hypothesize that the vertical distribution of the eulittoral algae is also related to nutrient availability as regulated by water movement.

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