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Benthic algal response to N and P enrichment along a pH gradient[1]

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Abstract

Nutrient enrichment and its effect on benthic algal growth, community composition, and average cell size was assessed across two sites of differing pH within a single habitat. Nutrients were added using *in situ* substrata, which released either N, P, or no additional nutrients (controls) at each site for 21 days. Upon collection, chlorophyll and biovolume standing stocks of the attached algal microflora were measured. Chlorophyll concentration was different among all treatments, accumulating greatest on P, followed by N, and the least on C substrata ($P < 0.001$) and was highest at site-2 ($P < 0.001$), while total algal biovolume was highest on P compared to both N and C substrata ($P < 0.05$) and did not vary between sites. Increased growth on P substrata was due to the enhanced biovolume of filamentous green algae, although the affected taxa varied between sites. Biovolume to cell density ratios (as a measure of average cell size) were highest on P substrata over both N-enriched and control substrata ($P < 0.05$) and this pattern was similar between sites. Progression towards a community composed of larger cells following P enrichment observed along this pH gradient, seems to be related to the dominance of larger celled filamentous green algae. Thus, nutrients exhibited greater control on benthic algal growth than did changes in hydrogen ion concentration.

Introduction

Studies assessing the relationship between nutrients and algal growth have focused almost entirely on the phytoplankton (e.g. Tilman, 1982). This fact is unfortunate, in that benthic algae do play a significant role in the trophic status of some lakes (Cattaneo & Kalff, 1980; Wetzel, 1983; Strayer & Likens, 1986).

In addition to nutritional factors, physicochemical parameters such as hydrogen ion concentration (and common covariants, e.g. alkalinity) are strong selective factors in aquatic habitats (Wetzel, 1983), and can influence the distribution of algal species (Lowe, 1974). Historical changes in lake pH are often correlated with characteristic alterations in the algal assemblage (e.g. Charles & Norton, 1986). Furthermore, hydrogen ion gradients within a single habitat can have a discernable and predictable effect on algal community composition (Bruno & Lowe, 1980).

The response of benthic algae to nutrient perturbation is less well understood than that of the phytoplankton, and has not been readily quantified. A very positive correlation exists between

phytoplankton biomass and total-P concentration (Dillon & Rigler, 1974), whereas benthic algal community biomass does not always correlate as strongly with total-P (Cattaneo, 1987), although certain groups of algae (i.e. green algae) often do (Auer *et al.*, 1982). Also, several studies suggest that increasing trophy leads to an increase in the individual cell size of phytoplankton (Watson & Kalff, 1981). This idea has not been adequately addressed for benthic algal communities, although a similar pattern is suggested for benthic algae collected from Canadian lakes of higher trophy (Cattaneo, 1987). Here we quantify alterations in the size structure and community composition of benthic algae following *in situ* fertilization with N and P under two pH regimes.

This study addresses the following questions: (1) Does enrichment with N and/or P promote benthic algal growth in a northern Michigan Bog Lake? (2) How do pH differences within a single habitat alter the response of algae to nutrient enrichment? (3) Does nutrient enrichment alter community composition predictably (i.e. P-enrichment stimulate green algal growth)? and (4) Do increased nutrient levels promote the development of communities with increased cell size?

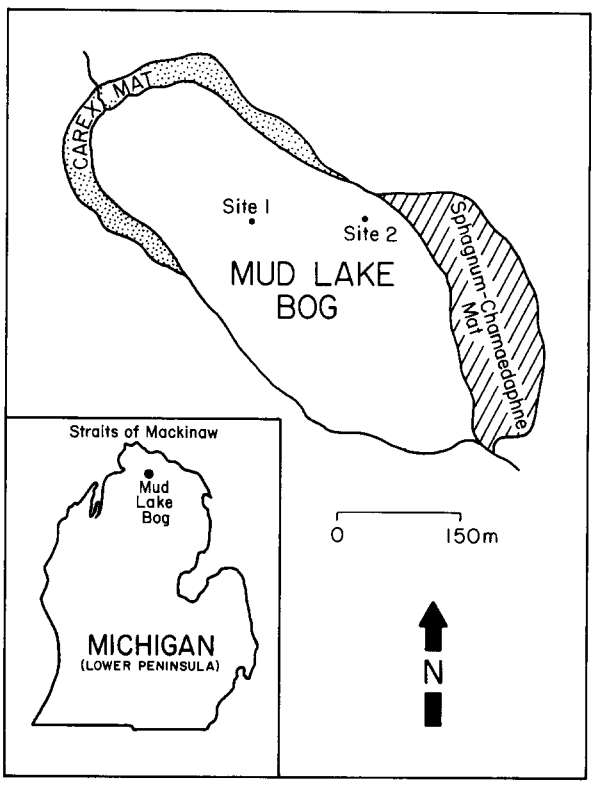

Fig. 1. A map of Michigan's lower pennisula, with Mud Lake Bog enlarged to indicate the location of the two experimental areas of differing pH and the orientation of aquatic vegetation (after Goe *et al.*, 1924).

Materials and methods

Study area

This study was conducted in Inverness Mud Lake Bog located in the Inverness Township, Cheboygen County, Michigan (Fig. 1). This fairly large bog lake (surface area = 104,190 m^2) has remained relatively unchanged from earlier descriptions (Goe *et al.*, 1924; Welch, 1936). Mud Lake possesses an inherent pH gradient, where waters are alkaline in the centre of the lake (site-1) and become more acidic in the vicinity of the *Sphagnum–Chamaedaphne* mat (site-2). The unusual alkaline pH, characteristic of much of the open water zone, has been attributed to the buffering capacity of substances produced by decaying vegetation (i.e. sedge bog forest) present in the peat formation (Welch, 1936). The lake is bordered by a *Carex*-fern mat at the northern portion of the bog, and the *Sphagnum–Chamaedaphne* mat is located along the southeastern perimeter. The entire bog-complex is surrounded by a *Thuja–Picea* swamp.

Experimental design

Eighteen nutrient-releasing substrata were constructed for field experiments from clay flowerpots (internal volume = 245 ml^3) according to the methods of Fairchild & Lowe (1984). Briefly, the large opening of each pot was sealed with a plastic petri dish and aquarium sealant. Nutrient additions to substrata were administered by filling six replicate flowerpots through a second smaller opening with a 2% hot agar-distilled water solution containing one of three treatments (0.1M $NaNO_3$, N substrata; 0.1M Na_2HPO_4, P substrata; and no nutrient addition constituted experimental controls, C substrata). Once filled,

the smaller aperture was closed by inserting a #000 neoprene stopper. Three replicate substrata of each treatment were placed within each site by gently inserting a wooden dowl, attached the base of each substratum, into the peat bottom. Substrata were situated 30 cm apart in a square random matrix at a depth of 1 m. In addition, both N and P are released from these substrata for several weeks in relation to the internal nutrient load (Fairchild *et al.*, 1985).

After 21 days of incubation, substrata were collected from a boat by encasing each substratum within a 400 ml tricorner beaker, while *in situ*, in an attempt to collect the intact algal assemblage. The encased substratum was lifted into the boat and the beaker's contents were transferred to a one-liter field jar. The attached algae were immediately removed from the surface of the substratum and washed into the same field jar.

Subsequently, all samples were diluted to a constant volume, and subsamples were removed, preserved with glutaraldehyde (2% final concentration), and enumerated in a Palmer–Maloney nanoplankton counting chamber using a A.O. Micro-Star Light Microscope. The 'soft' algae (all algae excluding diatoms) were enumerated at 450× magnification, while the diatoms were enumerated at 1000×. Cell densities were converted to biovolume using the geometric formula that best defined each species shape, and then scaling it to measured cell dimensions. Diatom reference slides were prepared from a second subsample to confirm species identifications (Patrick & Reimer, 1966). A third subsample was filtered onto membranes (Millipore^R, 0.45 μm), sonicated, and extracted in 90% buffered acetone (saturated with $MgCO_3$). Chlorophyll-*a* fluorescence was then assayed with a Turner 111 fluorometer and determined a second time following acidification to correct for phaeopigments (Strickland & Parsons, 1972).

Separate whole water samples were collected with a 2–1 Van Dorn bottle from sites 1 and 2 to determine concentrations of CO_2, hardness, and dissolved oxygen following the methods of Wetzel & Likens (1979). Also, concentrations of NO_3-N an soluble reactive phosphorus (SRP) were determined using the sulfanilamide–cadmium reduction and antimony potassium tartrate–ammonium molybdate colormetric reactions, respectively, and analyzed using a Technicon II autoanalyzer (Davis & Simmons, 1979). Hydrogen ion concentration was measured with a standard pH probe.

Statistical analyses

Data were analyzed using a two-way analysis of variance (ANOVA), with nutrient treatments and sites considered fixed factors. Data were log transformed to meet assumptions of homoscedasicity and the 'Student' Newman–Keuls range test ($P < 0.05$) was used to test for pairwise differences among treatments (Zar, 1983). In addition, values of five biomass estimates (total biovolume, total cell density, chlorophyll-a concentration, green algal biovolume, and green cell density) were averaged over all treatments ($n = 18$) and correlated amongst themselves. These and all subsequent analyses were preformed using Statistical Analysis Systems, SAS-82 (SAS Institute 1982).

Table 1. Average (top value) and standard error (bottom value) estimates for five physiochemical parameters measured on 3 July, 1983 from duplicate water samples taken at a depth of 0.5 m from two sites in Mud Lake Bog.

Site	CO_2 mg l^{-1}	Hardness mg l^{-1}	O_2 mg l^{-1}	NO_3-N μg l^{-1}	SRP μg l^{-1}
1 (alkaline)	12.5	85.3	8.3	20.0$^+$	1.0$^+$
	(2.5)	(0.3)	(0.3)	–	–
2 (circumneutral)	12.5	77.0	7.2	20.0$^+$	1.0$^+$
	(2.5)	(8.6)	(0.2)	–	–

$^+$ Single measurement taken.

Table 2. Hydrogen ion concentration (pH) and temperature (°C) determined from two sampling sites on five dates during the experiment.

Date	Site-1		Site-2	
	pH	Temp	pH	Temp
6-22-83	8.0	27.4	7.1	28.9
6-25-83	8.3	26.7	7.1	28.9
6-27-83	8.0	27.0	6.5	27.0
6-30-83	8.9	23.5	6.0	23.5
7-03-83	8.3	30.0	7.2	30.0
Mean	8.3	26.9	6.8	27.7
SE	0.2	1.0	0.2	1.1

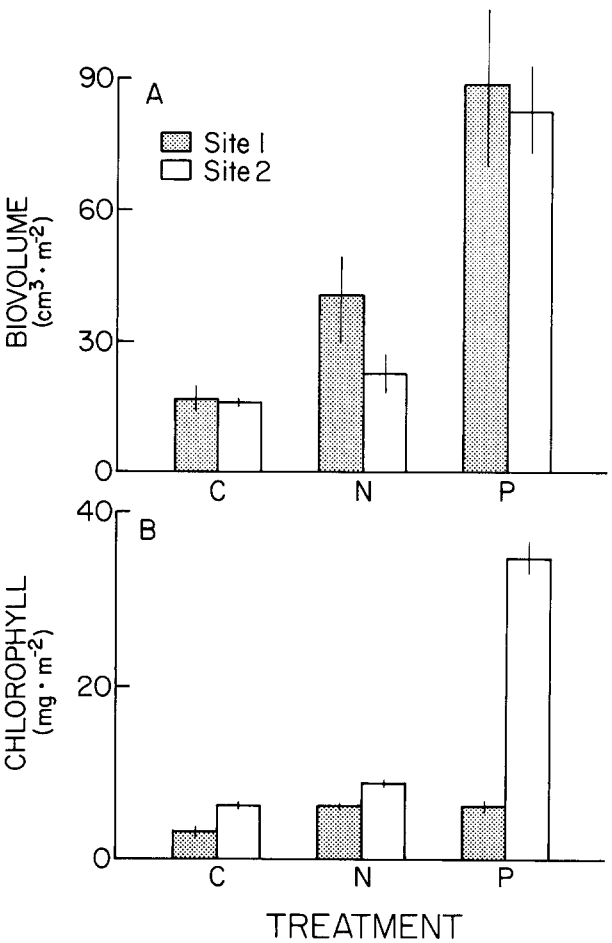

Fig. 2. Average (A) biovolume estimates and (B) chlorophyll-*a* concentrations for three nutrient treatments (C, control; N, nitrogen-enriched; and P, phosphorus-enriched substrata) incubated within two sites of differing ambient pH (site-1, alkaline; site-2, circumneutral). Vertical bars denote one standard error from the mean.

Results

Sites-1 and -2 had similar physical and chemical parameters (Tables 1 and 2), whereas the pH in site-1 (alkaline) was higher than that in site-2 (circumneutral) throughout the study (Paired t-test; $t = 6.54$, $P < 0.001$). Both chlorophyll-*a* and total biovolume varied among nutrient treatments ($F = 13.24$, $P < 0.001$ and $F = 4.72$, $P < 0.05$, respectively), while only chlorophyll-*a* concentrations varied between sites, being highest on site-2 substrata ($F = 21.62$, $P < 0.001$, Fig. 2). Chlorophyll-*a* accumulation was greatest on P, followed by N, and least on C substrata. Total algal biovolume was highest on P compared to N and C substrata; however, only the difference between P and C substrata was statistically significant.

The biovolume contribution of major algal divisions varied similarly among nutrient treatments in both sites (Fig. 3). Enrichment with P prompted a 5-fold increase in green algal biovolume ($F = 5.09$, $P < 0.05$). Diatom biovolume increased following N enrichment; however, this difference was not significant. Additionally, blue-green algal biovolume did not vary significantly among treatments.

Increased biovolume on P substrata in both sites-1 and -2 was mainly due to several species of filamentous green algae and one diatom species (Table 3). In site-1, the biovolume of *Mougeotia varians* and *Spirogyra affinis* was enhanced 11.5- and 30.7-fold on P relative to C substrata, while *Hyalotheca dissiliens* only grew following P enrichment in this site. Collectively, these three taxa accounted for 64% of the algal biovolume on the P treatment. On site-2 P substrata, the biovolume of *Chaetophora pisiformis, Mougeotia* sp., and the diatom *Gomphonema parvulum* was enhanced 72.8-, 106.6, and 3.5-fold, respectively, whereas *Oedogonium* sp. was only present on P substrata at this site. The combined biovolume of the four taxa contributed more than 67% to algal biovolume on this treatment.

Enhancement of algal biomass on N substrata can be attributed to increases in the abundance of but a few dominant taxa (Table 3). The biovolume

of *Achnanthes minutissima, Gomphonema gracile, Spirogyra* sp., and *Zygnema* sp. increased between 1.8- and 17.6-fold on N relative to C substrata in site-1, and accounted for 76% of total biomass. In site-2, five algal taxa (*A. minutissima, Mougeotia* sp., *Oscillatoria sancta, Oscillatoria splendida*, and *Zygnema* sp.) represented 42.7% of the algal standing stock and underwent from 1.6- to 15.4-fold increases in biovolume on N substrata.

The relative size of algae among each nutrient treatment was determined by calculating ratios of

Table 3. Average biovolume ($cm^3 \cdot m^{-2}$) and standard error estimates (in parentheses) for fifteen dominant taxa (>5% of total biovolume on at least one treatment) occurring on each of three nutrient treatments incubated under two pH regimes.

Taxon	Treatment		
	C	N	P
	Site-1 (Alkaline)		
Bacillariophyta:			
Achnanthes minutissima Kütz.	2.55 (1.00)	4.82 (2.11)	0.94 (0.14)
Gomphonema gracile Ehr.	0.49 (0.49)	2.26 (1.00)	0.45 (0.06)
Nitzschia palea (Kütz) W.Sm.	0.21 (0.05)	0.38 (0.07)	0.73 (0.16)
Chlorophyta:			
Hyalotheca dissiliens (Sm.) Bréb.	0	0	7.33 (7.33)
Mougeotia varians (Willr.) Cz.	0.69 (0.69)	0.28 (0.28)	21.06 (6.74)
Mougeotia sp.	0.09 (0.09)	0	0
Oedogonium sp.	0.04 (0.03)	0.27 (0.20)	0.85 (0.44)
Spirogyra affinis (Hass.) Petit	1.71 (0.89)	0.50 (0.50)	19.60 (16.00)
Spirogyra laxa Kütz.	7.99 (4.54)	28.00 (26.80)	5.00 (4.30)
Zygnema sp. 1	0	1.15 (0.64)	0.48 (0.28)
Cyanophyta:			
Oscillatoria sancta (Kütz.) Gomont	0.09 (0.03)	0.17 (0.06)	0.27 (0.21)
	Site-2 (Circumneutral)		
Bacillariophyta:			
Achnanthes minutissima Kütz.	1.87 (0.74)	2.96 (0.41)	0.68 (0.06)
Gomphonema gracile Ehr.	1.58 (0.56)	1.08 (0.28)	2.26 (0.17)
Gomphonema parvulum Kütz.	0	0.06 (0.06)	1.24 (0.24)
Nitzschia palea (Kütz) W.Sm.	0.10 (0.55)	0.30 (0.08)	0.21 (0.08)
Chlorophyta:			
Chaetophora pisiformis (Roth) Ag..	0	1.31 (0.62)	34.84 (21.99)
Mougeotia varians (Willr.) Cz.	2.19 (1.10)	1.10 (0.73)	25.75 (17.48)
Mougeotia sp.	0.09 (0.09)	2.92 (2.44)	9.62 (6.30)
Oedogonium sp.	0	0.35 (0.35)	4.14 (4.14)
Spirogyra affinis (Hass.) Petit	0	8.72 (8.72)	0
Spirogyra laxa Kütz.	1.06 (1.06)	0	0
Spirogyra sp.	3.98 (3.75)	0	0
Zygnema sp.	0.23 (0.23)	1.01 (1.01)	0
Cyanophyta:			
Oscillatoria sancta (Kütz.) Gomont	0.04 (0.04)	0.23 (0.08)	0
Oscillatoria splendida Greville	0	0.66 (0.51)	0.05 (0.03)

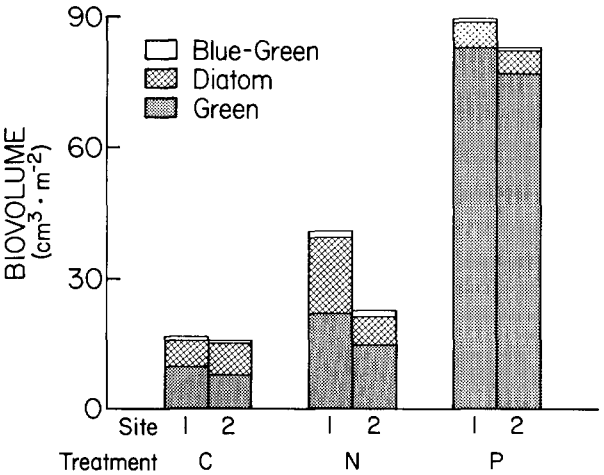

Fig. 3. The contribution of three divisions of algae (blue-green, diatom, and green) to the total algal biovolume existing on three nutrient treatments incubated in two sites of differing pH (codes as in Fig. 2).

algal biovolume to cell density (Table 4). This ratio was highest for P substrata ($F = 5.32$, $P < 0.05$) and the pattern was similar between sites.

Discussion

Benthic algal growth in Mud lake, as estimated by total biovolume and chlorophyll-*a* accumulation, was enhance to the greatest extent by enrichment with phosphorus. Nitrogen fertilization did enhance algal biomass, although these differences were not consistent among both biomass determinations. It is quite possible that additions of both N and P together may have promoted greater algal accumulation than fertilization with either N or P alone.

Table 4. Average (one standard error) estimates of algal size (biovolume expressed in μm^3) for algal communities exposed to three nutrient treatments under two pH regimes (codes as in Fig. 2).

Site	Treatment		
	C	N	P
site-1	398.1 (61.9)	784.6 (548.2)	2524.6 (1217.4)
site-2	646.3 (271.8)	400.7 (86.2)	1405.3 (561.8)

Between-site differences in the response of algae to nutrient enrichment were variable, depending upon the biomass estimate analyzed. Chlorophyll-*a* concentrations were higher under circumneutral pH conditions (site-2), while total biovolume was not different between sites. This discrepancy may be related to inherent biases in the two biomass estimates and to differences between sites with respect to the abundance of individual algal populations.

All biovolume estimates used here are estimates of total cell volume and did not correct for vacuolar space and/or inert portions of the cell. This can place emphasis on larger taxa (Strathmann, 1967; Bellinger, 1974; Sicko-Goad *et al.*, 1977), or taxa with small portions of living matter relative to vacuolar cell space (Lohman, 1908). Although treatments between sites were similar in terms of total biovolume, chlorophyll-*a* accruelment was higher at site-2 and correlates better with green algal cell density compared with total or green algal biovolume (Table 5). Thus, ultrastructural differences between individual populations (e.g. chlorophyll per unit cell volume) may have been

Table 5. Correlation coefficients (r) among five estimates of algal biomass. Correlations are based upon pooled biomass estimates (n = 18 for each).

	Chlorophyll-*a*	Cell density	Total biovolume	Green density	Green biovolume
Chlorophyll-*a*	1.000	0.417	0.425	0.780***	0.426
Cell density	–	1.000	0.202	0.606**	0.154
Total biovolume	–	–	1.000	0.380	0.997***
Green density	–	–	–	1.000	0.384
Green biovolume	–	–	–	–	1.000

** $P < 0.01$.
*** $P < 0.0001$.

a source of error between the two biomass measures, and can account for discrepancies of this type (Strathmann, 1967). Furthermore, the greater biovolume contribution of diatoms: green algae in site-2 may have inflated chlorophyll-*a* estimates in this site, because the fluorometric technique used here can underestimate the biomass of algae containing chlorophyll-b (i.e. green algae).

Population dynamics

This experiment was designed to ascertain population-level responses to nutrient additions, as well as, alterations in this response attributable to between-site differences (i.e. pH). This information can provide valuable insights about the nutrient requirements of benthic algae and characterize shifts in species composition associated with such perturbations.

Green filamentous algae generally responded strongly to P-enrichment under both pH regimes. Species belonging to the genera *Mougeotia* and *Spirogyra* were dominant on P treatments in both sites, and characteristically have broad tolerances to nutrient enrichment and pH (Prescott, 1962; Morgan, 1987); hence their pattern of response seems reasonable. The growth of some affected green algal taxa following P fertilization was restricted to a single pH regime. For example, *Chaetophora pisiformis* responded very strongly to P enrichment at circumneutral pH. *C. pisiformis* thrives in circumneutral waters (Sheath & Burkholder, 1985), and its nutritional characteristics may be similar to other species belonging to the order Chaetophorales, which grow well under P-rich conditions (Gibson & Whitton, 1987a, 1987b). Also, the growth of *Mougeotia* sp., *Spirogyra laxa*, and *Zygnema* sp. was enhanced by N-enrichment under alkaline pH. However, comments concerning the autecology of affected taxa are speculative without knowing their subgeneric identity.

Diatom growth was enhanced by N-fertilization under both pH regimes (with the exception of *G. parvulum*) and corresponds well with the autecology of the affected taxa. Populations of *A. minutissima* and *N. palea* respond to high levels of N (Pringle & Bowers, 1984; Lowe, 1974, respectively) and have broad pH requirements (Lowe, 1974). *Gomphonema parvulum* was the only diatom that responded to P-enrichment; it inhabits nutrient-rich waters with a pH ranging from 7.8 to 8.2 (Cholnoky, 1968).

In general, blue-green algal biovolume was not significantly affected by nutrient enrichment. However, two species of *Oscillatoria* (*O. splendida* and *O. sancta*) were stimulated by N-enrichment. As observed here, both taxa have high requirments for N (Van Landingham, 1983), but differ in their pH optima. *O. splendida* is more commonly observed in habitats of circumneutral pH, while *O. sancta* occurs at higher pH (Van Landingham, 1983).

Relationships between cell size and nutrient enrichment

The observed progression towards a community composed of larger cells following P enrichment seems to be attributable to the positive response of the larger celled green algae. This pattern is similar to that observed in many Canadian lakes, where benthic algal cell size increased with increasing lake trophy, owing to the enhanced standing stock of filamentous green algae in more eutrophic waters (Cattaneo, 1987). Moreover, this pattern is consistent with increases in the size structure of phytoplankton with higher lake trophy (e.g. Watson & Kalff, 1981).

Results from manipulations of natural assemblages of organisms can be confounded by experimentally induced artifacts (Venrick *et al.*, 1975). Although this *in situ* experiment controlled for many environmental variables, the results obtained still require careful interpretation. First, the supply of nutrients from a substratum design similar to the one used here, can vary temporally, mediated in part by the attached microflora (Pringle, 1987). The influence of the attached microflora on the release of N and P from our substrata was not determined. Based upon release rates measured under laboratory conditions (Fairchild *et al.*, 1985; G. W. Fairchild, unpubl. data), we assume that the supply of nutrients (following an initial pulse) was linear throughout the

experiment (Carrick & Lowe, 1988). Second, the form of nutrients provided and their finite supply pool may lead to algal responses that differ from other modes of enrichment (i.e. water column fertilization, Pringle, 1987). Lastly, alterations in the local N:P ratios associated with the single nutrient fertilizations used here might have created nutrient micro-environments characterized by a relatively high N:P ratio (condition on N substrata) and a low N:P ratio (condition on P substrata), compared to that measured in the water column. Such conditions may have been selective and predispose the species able to thrive under such conditions.

Conclusions

Green algal dominance increased with increasing P abundance along a gradient spanning nearly to pH units. Thus, within the context of this study, nutrient 'controls' on benthic algal growth and community composition in Mud Lake tended to override differences in pH.

The positive response illicited by green filamentous algae exposed to nutrient perturbation may be a reoccurring pattern in benthic assemblages (Cattaneo, 1987). The reasons for this are potentially numerous. Low N:P ratios have been shown to favor the growth of green and blue-green benthic algae (Schindler, 1975). Thus, low N:P ratios associated with our P substrata cannot be ruled out as a factor which might have prompted the observed taxonomic shifts. Also, because algal biovolume on P substrata is fairly high compared with levels common in many Canadian lakes (Cattaneo, 1987), the observed increase in filamentous algal growth may be an adaptation to increasing spatial constraints. Under such conditions filamentous algae might be favored, in that their physiognomy allows them to capture more light by elevating themselves from the light and space limited environment of the substratum (Hudon & Bourget, 1983; Hudon & Legendre, 1987).

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