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Plant community dynamics in a chain of lakes: principal factors in the decline of rooted macrophytes with eutrophication

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Abstract

Shoe Lake and East Graham Lake, part of a small chain of lakes in southeastern Michigan, USA, differ in nutrient loading and in the structure and productivity of their aquatic plant communities. A comparative study of species frequency and biomass distributions, nutrient contents, and responses to experimental nutrient enrichment and shading, was conducted to determine the principal factors controlling the macrophyte dynamics. A central objective was to address the question of why rooted macrophyte growth declines with eutrophication, and to test existing models designed to explain this phenomenon. In the more eutrophic Shoe Lake, diversity and productivity of rooted macrophytes were relatively low, restricted primarily by combined shading of phytoplankton, periphyton, and non-rooted macrophytes (principally *Ceratophyllum demersum*, along with *Utricularia vulgaris* and *Cladophora fracta*). In the less eutrophic East Graham Lake, lower nitrogen availability restricted the growth of all of these shading components, resulting in clearer water and higher productivity and diversity of rooted macrophytes. The macrophytes did not allelopathically suppress the phytoplankton in East Graham Lake. The results supported a direct relationship between nutrient loading, increasing growth of phytoplankton, periphyton and non-rooted macrophytes, and decline of rooted macrophytes.

Introduction

It is well known among aquatic plant ecologists that the environmental and biotic interactions involved in macrophyte community structure and dynamics are highly complex and have long challenged the efforts of the relatively few workers who have attempted to elucidate them. In recent years there have been some efforts to understand the interactions responsible for differences in macrophyte communities at different (or changing) levels of nutrient availability, especially relative to phytoplankton and periphyton growth. The influence of dissolved nutrient content on macrophyte growth and distribution largely as mediated by light availability was described in a synthesis of literature and experience by Wetzel and Hough (1973; further refined by Wetzel 1979; reviewed in Wetzel 1983). Nutrient-induced dominance of phytoplankton and periphyton was viewed as leading to reduced submersed macrophyte growth, with eventual dominance of emergent macrophytes and periphytic and eulittoral algae. A different synthesis was developed by Phillips *et al.* (1978), who emphasized references to allelopathic suppression of phytoplankton by macrophyte organic secretions, and hypothesized that macrophyte decline with eutrophication more specifi-

cally results from periphytic shading, and that phytoplankton dominance is a later consequence of macrophyte decline as the allelopathy declines. Several subsequent studies have been concerned with this issue and have provided some relevant data (see Discussion), but both models remain inadequately tested (Wetzel and Grace, 1983).

The present study evolved from observations of varying macrophyte distributions in a chain of lakes in which there are differences in nutrient content and phytoplankton productivity. Because the water flowing through them is primarily from a common upstream source, and watershed geology is similar throughout, variables in the water are developed within the system largely as a function of metabolic fluxes. A lake near the head of the chain is eutrophic with abundant phytoplankton, periphyton, and non-rooted macrophytes, but with a poorly developed rooted submersed macrophyte community. Subsequent lakes in the chain have reduced nutrient concentrations and lower abundance of phytoplankton, periphyton, and non-rooted macrophytes, but there is greater development of rooted macrophytes. Within this de-eutrophication (oligotrophication) process, the macrophyte-eutrophication relationship appears to reverse itself as well.

The model of Phillips *et al.* (1978) would predict that the phytoplankton abundance in the less eutrophic lakes, kept lower by macrophyte allelopathy, would not respond to nutrient enrichment at levels present in the more eutrophic lake, and that shading inhibition of rooted plants in the more eutrophic lake is primarily a function of periphyton. The Wetzel and Hough (1973) model would predict that phytoplankton in the less eutrophic lakes can be stimulated by nutrient enrichment to levels present in the more eutrophic lake, and that submersed macrophytes are limited in depth and productivity by phytoplankton turbidity as well as that from periphyton. Neither model addresses non-rooted (free-floating) macrophytes as a specific functional component; our observations led us to hypothesize that *Ceratophyllum* and *Utricularia* populations are a major factor, and to predict that they respond to nutrient availability and act as a shading factor as do phytoplankton. The purpose of this study is to contribute to the testing of these hypotheses, and to provide additional data and perspective on macrophyte community ecology generally.

Methods

Study area

The chain of lakes is located in the Bald Mountain State Recreation Area, Oakland County, southeastern Michigan, USA (Fig. 1). These small glacial lakes lie in a narrow outwash plain among moraine bands. The West Branch of Stoney Creek emanates from Bunny Run Lake and flows at discharge rates of 0.2–0.3 m^3 sec^{-1} between lakes, providing the principal water source for them. Wetlands are contiguous to the stream and lakes throughout. The upland soil consists of lacustrine sands and clays overlying till; wetland soils and lake sediments include mucks and peats. Shoe Lake has a surface area of 1.9 ha and maximum depth of 5.5 m, and East Graham Lake has a surface area of 4.5 ha and maximum depth of 11 m; both are dimictic, and both are protected from wind by the uplands, woodlands, and fringing cattail and rush communities. They are colonized by submersed macrophytes substantially below the depth of effective turbulence, a circumstance in which light availability is considered to be a paramount factor (Spence 1982). Although of somewhat different size, the lakes are similar in morphometry, including steepness of slope of littoral zone bottom.

Limnology

Mid-lake depth profiles of temperature (Whitney TC5 UW thermometer), light penetration (Secchi disc; LI-COR LI-185A UW quantum meter), and dissolved oxygen (unmodified Winkler titration) were measured biweekly in Shoe Lake in 1976 – 1978, and monthly in Shoe and East Graham Lakes in 1979 and 1982.

Water was collected by Van Dorn sampler at midlake (surface and depth intervals) and at

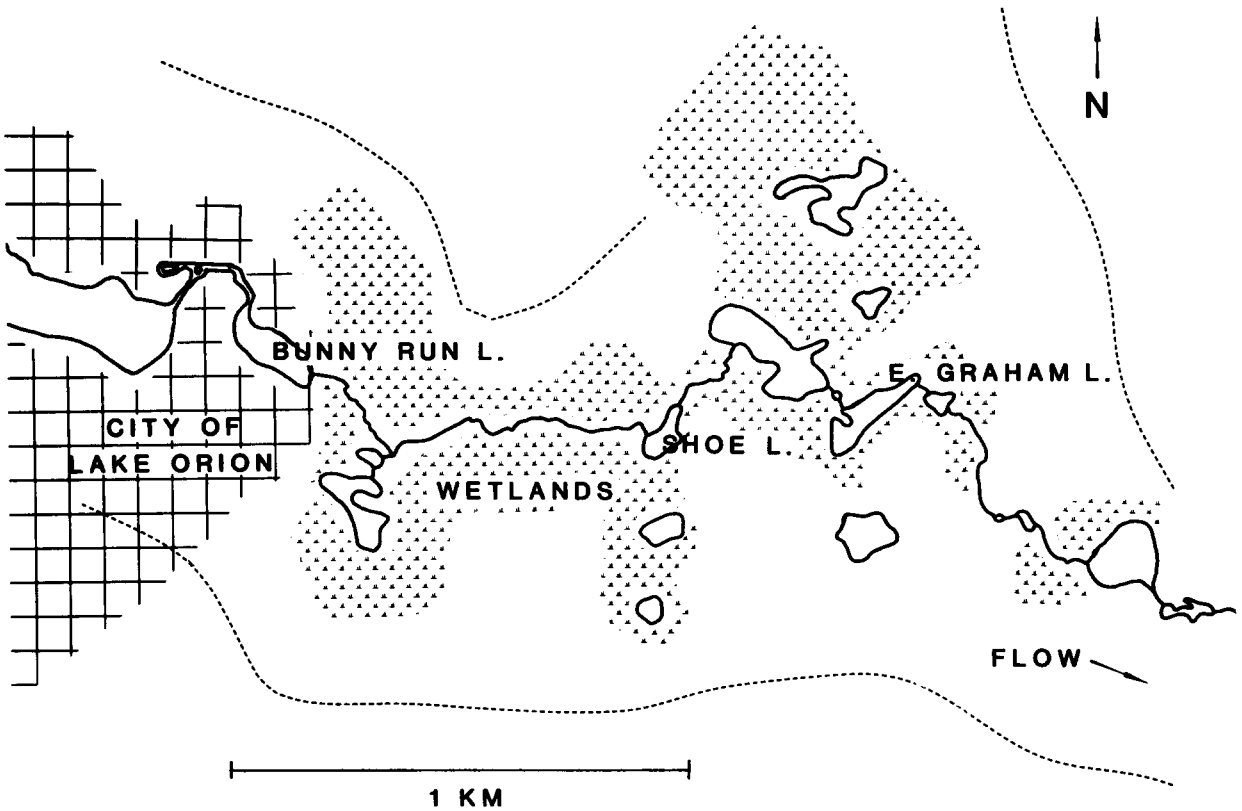

Fig. 1. Stoney Creek (West Branch) chain of lakes, Oakland County, Michigan USA.

stream outflow and inflow sites at the above described times and monthly during 1984 and 1985. Samples were subjected to analyses (Wetzel and Likens, 1979) as follows: In filtered water (Whatman GF/F 0.7 micron glass fiber), measurements of soluble reactive phosphorus (SRP) were by acid molybdate spectrophotometry (Beckman 25 UV-VIS), nitrate + nitrite by cadmium reduction and diazotization spectrophotometry, ammonia by phenol-hypochlorite spectrophotometry, silicate by acid molybdate spectrophotometry, and dissolved organic carbon (DOM) by persulfate oxidation and infrared CO_2 analysis (Beckman 215A IR absorption meter). The glass filters were used to determine particulate organic carbon (POC) by wet dichromate-sulfuric acid oxidation spectrophotometry, and corrected chlorophyll *a* by alkaline acetone extraction spectrophotometry. Unfiltered water was used to measure total P by persulfate digestion and acid molybdate spectrophotometry, pH (Corning 7), total alkalinity by sulfuric acid titration to methyl red-brom cresol green endpoint, and conductivity (Beckman RC-16B2).

Littoral zone sediments were sampled by plastic corer in Shoe and E. Graham Lakes near the stream inflows and outflows and midway between these locations, and near the stream outflow from Bunny Run lake. Samples were analysed for particle size distribution, organic matter content, and total P, nitrate + nitrite, and ammonia content as described in Fornwall (1986).

Macrophyte distribution

Species distribution of macrophytes in the littoral zones of Shoe and East Graham Lakes was first surveyed qualitatively by plant hook sampling in early summer, 1979. Samples were taken at 1 m depth intervals along transects perpendicular to the shore to maximum depth of plant growth.

Transects were located 15 m apart around the circumference of each lake, similar to the transect method in Dubois *et al.* (1984). Samples also were collected at a depth of 1/2 m on most transects. In Shoe Lake, 41 transects provided 180 samples, while in E. Graham Lake 108 transects provided 324 samples. Plants in each sample were identified according to Fassett (1957) and Gleason and Cronquist (1963). Distribution data (presence or absence) were used to group species into associations. Associations were identified using cluster analysis (MIDAS statistical package; Fox and Guire, 1976). Clustering was done on species which occurred in over 33% of the samples from each lake. The specific algorithm used to estimate distances was Jaccard's coefficient of similarity (Sneath and Sokal, 1973).

Subsequently, quantitative distribution of macrophytes in terms of whole plant ash-free dry mass was measured in both lakes at monthly or biweekly intervals during a calender year in 1980–1981. Sampling was done with a steel corer designed and constructed by Fornwall (1986), cutting and retaining a sediment core of 127 cm^2 area and 30 cm depth, with overlying plant material. On each sampling date, 5 replicate samples were taken within associations established from the previous qualitative survey, at locations according to a stratified random design. Samples were washed, separated according to species, and weighed after drying at 60 °C and again ashing at 550 °C. Data were subjected to a multivariate analysis of variance (MANOVA) with particular attention to comparison of rooted submersed species vs. non-rooted and floating species.

Macrophyte tissue nutrient content

Species of rooted submersed and non-rooted macrophytes were sampled randomly from both lakes during June, July, and August of 1983 and rinsed, freeze-dried, weighed, and analyzed in quadruplicate for phosphorus and nitrogen (as percent of dry mass) as in Gerloff and Krombholz (1966). Total nitrogen and total phosphorus were determined from micro-Kjehdahl digestates using SRP and ammonia methods described above. Tissue nutrient comparisons were made (MANOVA) for species and growth habit groups (rooted vs non-rooted) over time and within and between lakes. For growth habit groups, *Ceratophyllum* and *Utricularia* were pooled as non-rooted; the rest were pooled as rooted with the exceptions of *Myriophyllum* spp., which are weakly rooted here, and *Chara*, which is not a vascular plant.

Enrichment experiments

Macrophytes – During June, 1982, non-rooted macrophytes *Ceratophyllum demersum* and *Utricularia vulgaris* from both lakes, and the rooted submersed macrophyte *Najas flexilis* from East Graham Lake, were tested in the laboratory for photosynthetic response to enrichments of P and N, and in the case of East Graham Lake plants, to exposure to Shoe lake water. Filtered (Millipore HA 0.45 micron membrane) surface water samples from each lake were used as control growth media, and for experimental treatments they were enriched with K_2HPO_4 (10 μgL^{-1} final added P), or KNO_3 (10 μgL^{-1} added N) plus NH_4Cl (10 μgL^{-1} added N), or all three together. Five replicate plant sprigs or shoots were acclimated to each control or treatment medium (400 ml) for 48 h in a controlled environment chamber at 20 °C with 12 h photoperiod of 200 μEinst m^{-2} s^{-1} photosynthetically active radiation (PAR). In the case of *Najas flexilis*, the plant roots were kept separate from treatment media in adjacent flasks of control media; exposed stem areas crossing the flask rims were protected from desiccation with wet paper pads. Media were renewed in the flasks halfway through the acclimation period.

To determine photosynthetic capacity, during late morning of their photoperiod the plants were placed in fresh medium of appropriate control or treatment content (with known pH and total inorganic carbon content; normal for, and identical within, samples from each lake) at 20 °C and under illumination of 600 μEinst m^{-2} s^{-1} PAR. Additions of aqueous $NaH^{14}CO_3$ were made to give 1.3 kBq ml^{-1}; after 30 min of photosynthesis with slow stirring by magnetic bars, plants were rinsed, freeze-dried, weighed, and radioassayed

by extraction in DMSO and liquid scintillation spectrometry (Beckman 3801) according to procedures in Filbin and Hough (1984). Photosynthetic rate as carbon uptake per unit dry mass per L were calculated from measured ^{14}C plant extract radioactivity and known ^{14}C and ^{12}C availabilities, pH, and temperature, according to Saunders *et al.* (1962). Photosynthetic rates were compared in a MANOVA.

Phytoplankton – In July, 1983, phytoplankton in the epilimnion of East Graham Lake were tested for their growth response to fractional enrichments of N ($10\,\mu gL^{-1}$ added as KNO_3 and $10\,\mu gL^{-1}$ added as NH_4Cl), P ($10\,\mu gL^{-1}$ added as K_2HPO_4), and C ($10\,mgL^{-1}$ added as $NaHCO_3$). Of eight flasks each containing 3L of lake water, one served as a control, and the others received the enrichments singly or in combinations. All were maintained in a controlled environment chamber at 20 °C with a 12 h photoperiod of $200\,\mu Einst\,m^{-2}\,s^{-1}$ PAR, lightly stirred by magnetic bars, for a total of 23 days. Nutrient concentrations and pH were monitored at five day intervals, and final phytoplankton biomass was measured as corrected chlorophyll *a* by filtration (GF/F glass fiber) and acetone extraction as described above.

Epiphyton – During the summer of 1984, the growth of epiphytic algae on submersed macrophytes of East Graham Lake was tested for its response to exposure to Shoe Lake water. Two 40-L tanks were established with East Graham Lake littoral zone sediment, and *Nitella flexilis* and *Ceratophyllum demersum* plants from East Graham Lake. One tank was filled with filtered East Graham Lake water (littoral zone), and the other with filtered Shoe Lake water (littoral zone). The tanks were maintained in the laboratory at 25 °C with a 14 h photoperiod of $65\,\mu Einst\,m^{-2}\,s^{-1}$ PAR, with weekly slow replacement of water in each with freshly collected and filtered lake water. At the end of six weeks, plants from each tank were treated for epiphyte removal by vigorous squeeze-bottle rinsing. The collected rinsings were filtered and analysed for epiphyte biomass by chlorophyll *a* measurement. The host plants were freeze-dried and weighed, so that epiphyte biomass per plant could be expressed as chlorophyll mass per unit dry mass of host plant.

Shading experiments

A transplant experiment was conducted to test the relative roles of light attenuation due to water turbidity (from the combined presence of dissolved organic matter and particulate matter including phytoplankton), periphyton, and non-rooted macrophytes, in the growth and distribution of rooted submersed macrophytes. Early in the growth season of 1980, entire *Potamogeton pectinatus* plants were collected from East Graham Lake with roots and sediment intact in perforated plastic tubs (3 plants per tub). Six plants were transplanted in this way randomly at 1 m depth in the littoral zone within East Graham Lake as controls, and the rest were taken to Shoe Lake and placed as follows (all at 1 m depth): six plants in open littoral areas with stems and leaves cleaned of periphyton biweekly (by gentle hand stripping); six plants (untreated) in open littoral areas; and six plants beneath existing mats of *C. demersum*. At the end of the growth season, plants were collected and their apparent growth success was described on the basis of physical appearance (color and apparent health) and reproductive potential (quantity of new vegetative shoots or flowers) as compared to the controls transplanted in East Graham Lake.

In another experiment, two floating mats of *C. demersum* in Shoe Lake were placed in floating wood and screen frames (surface area $2.5\,m^2$) anchored over existing submersed macrophyte beds. Plants densities within the transplanted mats were kept similar to natural mats in the lake. Percent cover of submersed macrophyte species under the transplanted *C. demersum* mats were recorded at the beginning and at the end of the growth season (1980). Percent cover of submersed species near the transplanted mats (with similar species and cover) also were recorded at the beginning and end of the growth season and were used as control areas. At the sites from which floating mats were removed for transplanting, initial percent cover of species beneath

the natural mat were determined before removal and again at the end of the growth season, to determine the extent of additional colonization in the absence of the mat.

The mat transplant experiments were repeated in 1981 at different locations in the littoral zone of Shoe Lake. In this case light intensities at the underside of the naturally occurring mats (averaging 20 μEinst m^{-2} s^{-1} at mid-day) were replicated beneath the transplanted mats by adjusting *C. demersum* plant densities. In addition, the growth of macrophytes in experimental and control areas was determined by ash-free dry mass measurements from triplicate plant corer samples at the beginning and end of the growth season.

Results

Limnology

Both Shoe Lake and East Graham Lake are dimictic and undergo summer thermal stratification typical of temperate zone lakes. Stratification of physical, chemical and biological factors develop accordingly (detailed data and figures are presented in Fornwall (1986)). In the past decade of observations both lakes have exhibited depth profiles reflecting relatively active trophic systems, but with consistently higher intensity in Shoe Lake than in East Graham Lake. The influence of the higher degree of eutrophy of Shoe Lake on relative light availability within the lakes is shown by the summer-long conditions of water transparency, where Secchi depth is 20 to 80% greater in East Graham Lake (Table 1) and the light extinction coefficient is 20 to 70% greater in Shoe Lake (Table 2).

Table 1. Depths of Secchi disc visibility (metres).

Date	Shoe Lake	East Graham Lake
28 May	2.8	3.4
18 June	3.8	5.2
9 July	2.7	4.1
30 July	2.4	4.3
23 August	2.7	3.7
10 September	3.4	4.4

Table 2. Light extinction coefficient per metre depth.

Date	Shoe Lake	East Graham Lake
31 May	0.90	0.70
6 July	0.90	0.75
5 August	1.25	1.75
24 September	0.90	0.65

The flow of nutrients through the system and response of phytoplankton production can be seen in Figure 2. The stream water flowing between Bunny Run Lake and Shoe Lake receives enrichments of P and N, especially the latter, such that maximal concentrations are at the Shoe Lake inflow. The P and N levels then fall as the water flows through the lakes in the chain. The most dynamic flux in this system is in the nitrogen compounds. A major portion of the removal of N occurs in Shoe Lake itself, consistent with the phytoplanktonic chlorophyll *a* biomass accumulation there.

Sediment analysis data are presented in detail in Fornwall (1986). The lake sediments are fine to coarse silts with varying content of organic matter. In both lakes the silts are finest with highest organic content at the inflows, and coarsest with lowest organic content at the outflows. Overall, Shoe Lake contains finer silts with higher organic content than those in East Graham Lake. In general, the sediment nutrient content (N and P) is high in both lakes.

Macrophyte distribution

The collection frequencies of macrophyte species in plant hook samples from both lakes are summarized in Table 3, in which species are grouped as those which 1) tend to predominate in Shoe Lake, 2) are of roughly equal frequency in both lakes, 3) tend to predominate in East Graham Lake, or 4) were found only in East Graham Lake. The most frequently collected species in Shoe Lake were non-rooted species, while the most frequently collected plants in East Graham Lake were submersed rooted plants. Fewer species were collected in Shoe Lake as a whole, and of those, a relatively small number were

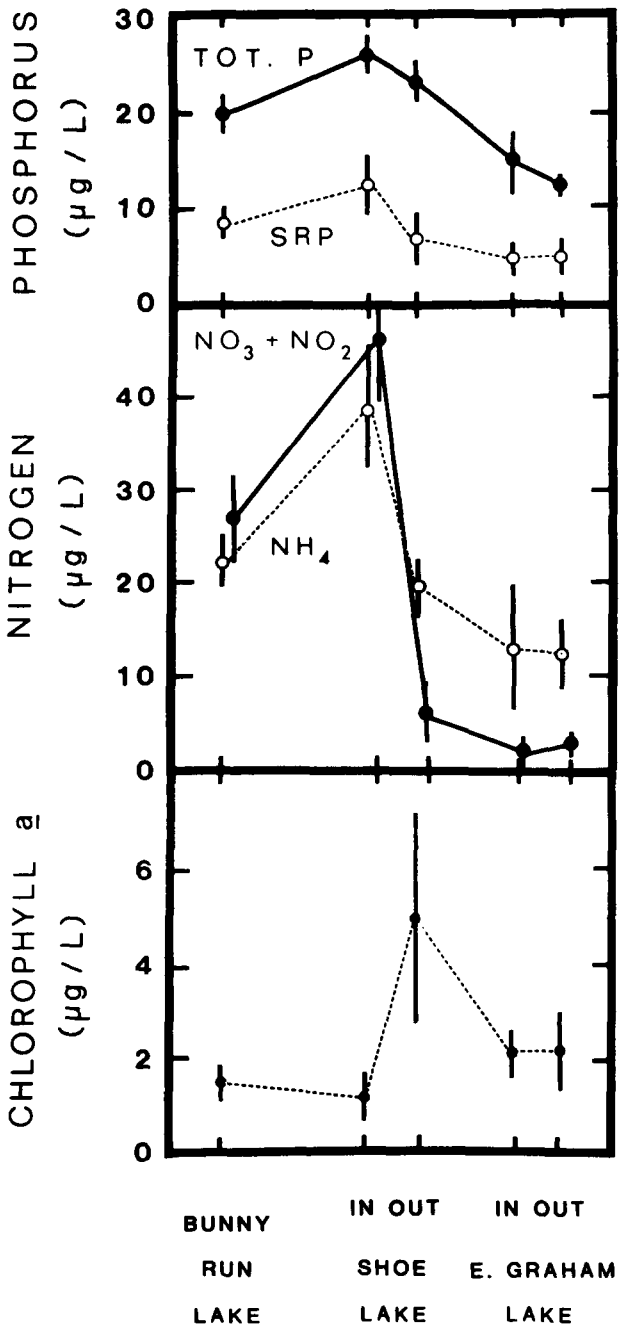

Fig. 2. Concentrations of total and soluble reactive phosphorus, nitrate + nitrite and ammonia nitrogen, and chlorophyll *a* (corrected) in Stoney Creek at inflow and outflow locations of lakes during the summer (mean + SD, n = 5).

collected at high frequencies; in East Graham Lake more species were found, and the collection frequencies were more uniform among them. Maximum depths at which the more prevalent species were collected in both lakes is shown in Table 4, indicating generally greater depths of growth in East Graham Lake for many of the species common to both lakes.

Cluster analyses of sampling frequency data identified several hydrophyte associations within each lake. Detailed descriptions are in Fornwall (1986); they are summarized in the abbreviated dendrograms in Figures 3 and 4 and with depth distributions in Table 5. It is clear that the associations are quite different in the two lakes, both in composition and depth distribution.

The data from the series of macrophyte standing crop biomass analyses were grouped according to plant growth habit such that rooted submersed plant growth could be compared with non-rooted and floating plant growth in the lakes (Figure 5). In Shoe Lake, non-rooted and floating plant biomass was significantly greater than submersed rooted plant standing crop biomass (including roots) over the year ($P < 0.05$; MANOVA and orthogonal contrast analysis), most of the time by more than two-fold. In East Graham Lake, non-rooted and floating plant biomass did not exceed rooted plant biomass; means of submersed rooted plant biomass in fact were greater than or equal to non-rooted and floating biomass on most of the sampling dates, but high sample variance prevented a statistically significant difference ($P > 0.25$). The total macrophyte biomass in East Graham Lake was significantly greater than that in Shoe Lake ($P < 0.01$), and this appears to be primarily due to greater biomass of rooted submersed plants in East Graham Lake. There were no evident differences in seasonal growth patterns of these growth habit groups between the two lakes.

Macrophyte tissue nutrient content

The N content of macrophytes tested generally ranged between 1 and 2.5% of dry mass (Table 6), while P content generally was between 0.1 to 0.5% (Table 7). In each lake the non-rooted

Table 3. Percent of all samples* from each lake containing each macrophyte species.

Taxon	Growth habit +	Shoe Lake	East Graham Lake
Ceratophyllum demersum L.	NR	91	30
Utricularia vulgaris L. var. americana Gray	NR	49	15
Myriophyllum verticillatum L.	NR	35	0
Najas flexilis (Willd.) Rostk. and Schmidt	NR	26	12
Potamogeton natans L.	FR	18	1
Potamogeton zosteriformis Fernald	FR	36	39
Potamogeton filiformis Pers.	FR	2.6	1
Nuphar variegatum Engelm.	FR	2	5
Nymphaea tuberosa Paine	FR	13	10
Pontederia cordata L.	E	1	2
Nitella flexilis (L.) Ag.	SR	0.6	14
Elodea canadensis (Michx.) Planchon	SR	6	20
Potamogeton illinoensis Morong	SR	8	24
Myriophyllum spicatum L. var. exalbescens	NR	3	54
Chara vulgaris L.	SR	25	56
Vallisneria americana Michx.	SR	0	0.3
Utricularia intermedia Hayne	NR	0	0.3
Eleocharis equisetoides (Ell.) Torr.	E	0	3
Brasenia schreberi (Gmel.	FR	0	4
Scirpus subterminalis Torr.	SR	0	4
Potamogeton amplifolius Tuckerm.	SR	0	11
Potamogeton pectinatus L.	SR	0	28

* 180 samples from Shoe Lake; 324 samples from East Graham Lake.
\+ Denotes growth habit: NR = non-rooted, SR = submerged rooted, FR = floating leaved-rooted, E = emergent.

Table 4. Maximum depth of growth of prevalent macrophyte species in Shoe and East Graham Lakes (based on plant hook samples at 1 m depth intervals).

Taxon	Shoe Lake	East Graham Lake
Chara vulgaris	2	4
Potamogeton filiformis	2	3
P. ilinoensis	2	4
P. natans	3	2
P. pectinatus	–	4
P. zosteriformis	4	4
Elodea canadensis	2	4
Najas flexilis	3	4
Ceratophyllum demersum	4	4
Myriophyllym spicatum	4	4
M. verticillatum	4	–
Utricularia vulgaris	4	4

plant group contained less N than did the rooted plant group (by 25% in Shoe Lake and 23% in East Graham Lake as of August; $P < 0.05$). This was primarily due to a 20–40% decline in N content of the non-rooted plants over the three months in both lakes ($P < 0.05$) while no significant change occurred in the rooted plants. There were some differences in N content between species, primarily again because of declines in the non-rooted ones in July and August, and because *Chara* was particularly low overall, but there were no between-lake differences within any species nor within either growth habit group. In P content, there was no difference between the rooted and non-rooted groups within either lake. In between-lake comparisons, the rooted plants of East Graham Lake contained 25% less P than those of Shoe Lake ($P < 0.01$), and the mean P content of non-rooted plants in E. Graham Lake was 29% lower than that in Shoe Lake, although

SHOE LAKE

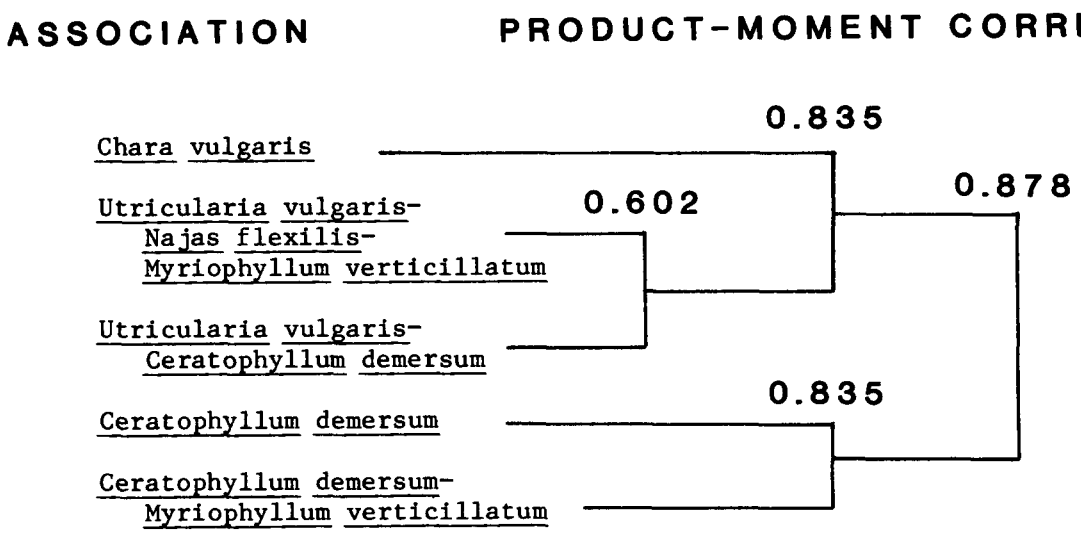

Fig. 3. Summary dendrogram from cluster analysis of prevalent submersed macrophyte species in Shoe Lake.

EAST GRAHAM LAKE

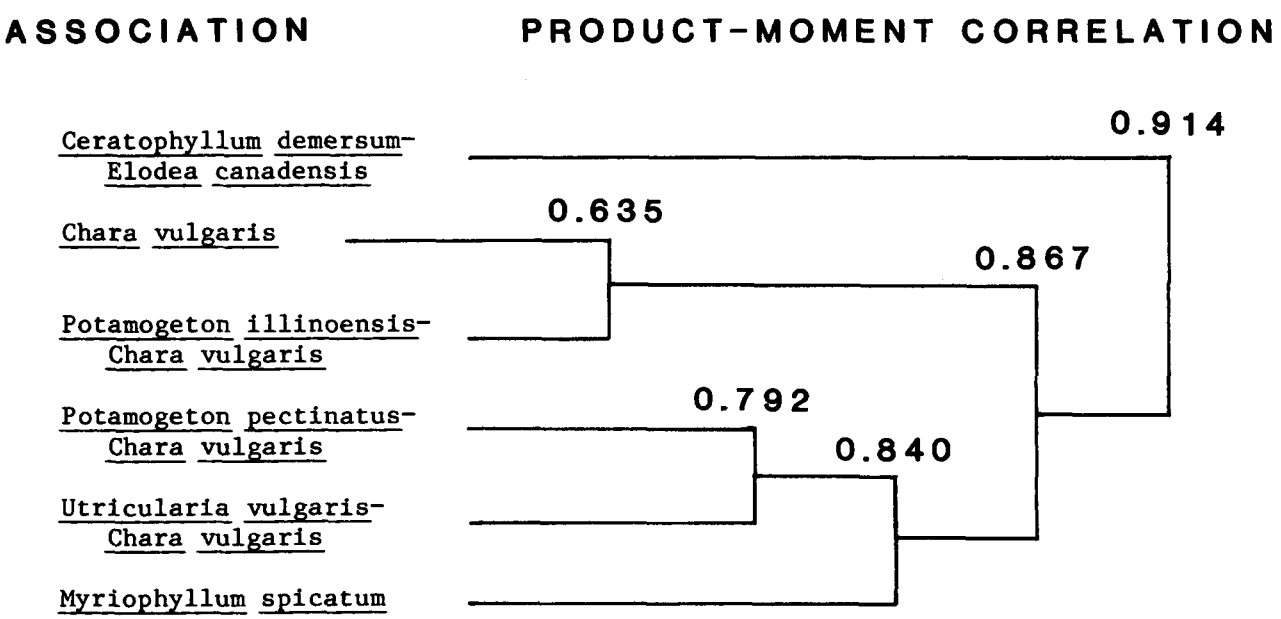

Fig. 4. Summary dendrogram from cluster analysis of prevalent submersed macrophyte species in East Graham Lake.

Table 5. Percent of samples collected from each macrophyte association at each sample depth in Shoe Lake and East Graham Lake.

Association	Depth (metres)				
	1/2	1	2	3	4
SHOE LAKE					
Chara vulgaris	33	54	13		
Utricularia vulgaris-Najas flexilis-Myriophyllum verticillatum	64	36			
Utricularia vulgaris-Ceratophyllum demersum	22	30	35	13	
Ceratophyllum demersum	5	32	36	27	
Ceratophyllum demersum-Myriophyllum verticillatum	15	45	15	20	5
EAST GRAHAM LAKE					
Ceratophyllum demersum-Elodea canadensis	7	18	29	29	18
Chara vulgaris	67	23	10		
Potamogeton illinoensis-Chara vulgaris	23	54	18	5	
Potamogeton pectinatus-Chara vulgaris	31	58	8	4	
Utricularia vulgaris-Chara vulgaris	29	42	8	17	4
Myriophyllum spicatum		14	34	34	18

the significance in this case was marginal ($P \approx 0.053$). Individually, *Chara, Elodea* and *Najas* showed differences in P content between lakes (all lower in E. Graham Lake) significant at the 0.05 level; all other individual differences were not significant. On a seasonal basis, some individual species were relatively stable in P content over the three months; however, several showed significant declines, and the pooled growth habit groups and pooled plants overall declined in P content in both lakes.

Enrichment experiments

For the non-rooted plants *Ceratophyllum demersum* and *Utricularia vulgaris* (Fig. 6), those growing in East Graham Lake were stimulated photosynthetically by nitrogen enrichments at Shoe Lake levels ($P < 0.05$) and in *C. demersum* by exposure to Shoe Lake water ($P < 0.05$), but neither was stimulated by phosphorus enrichments ($P > 0.76$). For these species growing in Shoe Lake, there was no stimulation of photosynthesis by enrichments of either N or P ($P > 0.73$). Photosynthetic rates of *C. demersum* from Shoe Lake were not different from the enriched samples

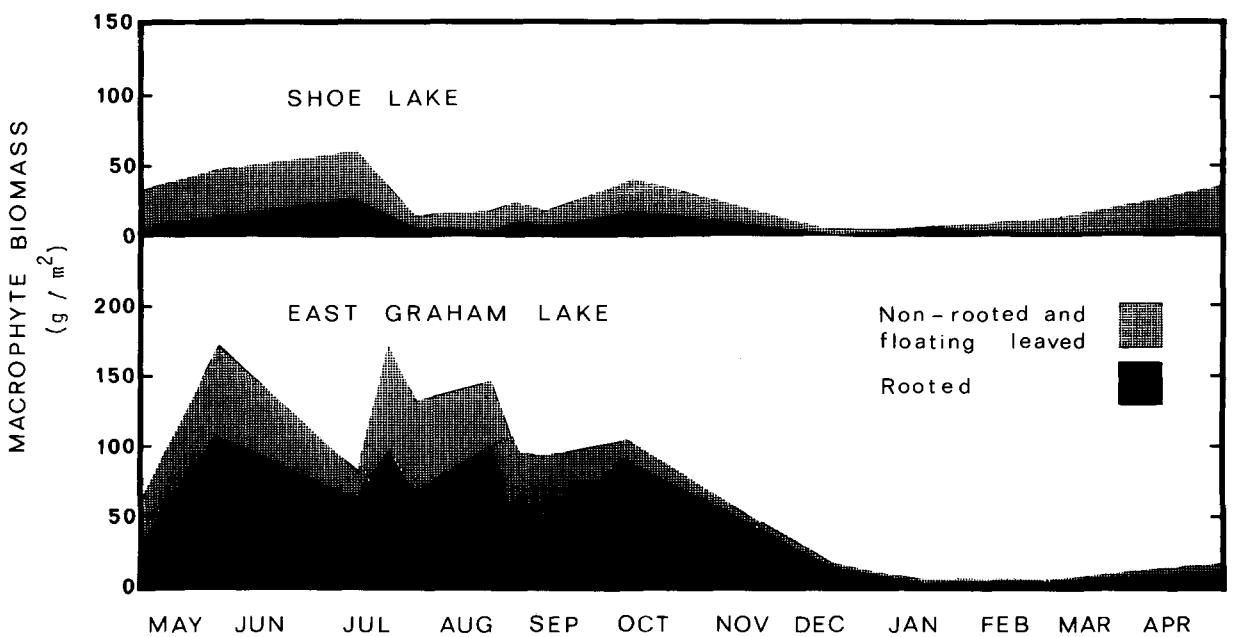

Fig. 5. Variations in macrophyte standing biomass in Shoe and East Graham Lakes during 1980 and 1981.

Table 6. Total nitrogen content of tissue of macrophytes (whole plant homogenates) in Shoe Lake and East Graham Lake during a summer growth season.

Taxon	Lake	Total Nitrogen Percent of dry mass SD; n = 3		
		June	July	August
Ceratophyllum demersum	Shoe	2.27 (0.51)	1.70 (0.07)	1.44 (0.13)
	E. Graham	2.37 (0.62)	1.91 (0.01)	1.61 (0.19)
Utricularia vulgaris	Shoe	2.12 (0.23)	1.86 (0.13)	1.71 (0.20)
	E. Graham	2.29 (0.37)	2.06 (0.32)	1.50 (0.13)
Myriophyllum verticillatum	Shoe	2.44 (0.66)	2.05 (0.62)	2.03 (0.47)
M. spicatum	E. Graham	2.06 (0.47)	2.24 (0.41)	1.78 (0.20)
Najas flexilis	Shoe			1.99 (0.85)
	E. Graham		2.18 (0.67)	1.51 (0.45)
Potamogeton natans	Shoe		2.05 (0.12)	1.98 (0.29)
	E. Graham		2.21 (0.24)	1.82 (0.34)
Potamogeton zosteriformis	Shoe	2.44 (0.18)	2.32 (0.46)	2.29 (0.09)
	E. Graham	2.38 (0.36)	2.24 (0.32)	2.52 (0.10)
Elodea canadensis	Shoe	2.16	2.04 (0.38)	2.21 (0.32)
	E. Graham	2.49 (0.22)	2.08 (0.06)	2.12 (0.39)
Chara vulgaris	Shoe	0.78 (0.21)	1.17 (0.71)	1.07 (0.14)
	E. Graham	0.98 (0.19)	0.97 (0.03)	0.94 (0.26)

from East Graham Lake ($P = 0.61$), while both of the former were about 30% greater than the rates in the non-enriched East Graham Lake control plants. In *U. vulgaris*, rates in the Shoe Lake plants were similar to those in the East Graham Lake plants enriched with Shoe Lake water ($P = 0.73$), but in this case there was no significant difference between these and the non-enriched East Graham control plants ($P = 0.40$); only the N enrichment of the East Graham Lake plants produced an effect in this case.

For the rooted plant *Najas flexilis* (Fig. 7), there was no effect of N and P enrichment of East Graham Lake plants ($P = 0.69$). Photosynthesis of the samples enriched with Shoe Lake water was about half that in the controls ($P = 0.02$).

In East Graham Lake phytoplankton (Fig. 8), chlorophyll biomass was unaffected by enrichments of P or C at levels found in Shoe Lake. Biomass increases of 160–290% occurred when Shoe Lake levels of N were present in the enrichments.

Epiphytic growth (primarily *Oscillatoria* sp., with some diatoms and green algae) on East Graham Lake macrophytes was over 300% greater in presence of Shoe Lake water than in controls with East Graham Lake water (Fig. 9).

Shading experiments

Potamogeton pectinatus plants transplanted within East Graham Lake as controls grew well, while those taken from East Graham Lake to Shoe Lake suffered increasingly poorer growth with increasing presence of shade factors (Table 8). Epiphyte-free plants in the open littoral zone of Shoe Lake produced fewer new shoots (relative to East Graham Lake controls) and no flowers; plants with intact epiphytes produced still fewer new shoots and were in poorer visual condition, and those under *C. demersum* mats did not survive at all.

Estimates of rooted macrophyte growth as percent bottom cover in presence and absence of artificially constructed *C. demersum* mats in 1980 (Table 9) indicated that growth outside of the mats was similar to or exceeded that initially present in the early summer, while under the mats growth was much less extensive with bare sedi-

Table 7. Total phosphorus content of tissue of macrophytes in Shoe Lake and East Graham Lake during a summer growth season.

Taxon	Lake	Total Phosphorus Percent of dry mass SD; n = 3		
		June	July	August
Ceratophyllum demersum	Shoe	0.47 (0.28)	0.28 (0.02)	0.13 (0.08)
	E. Graham	0.23 (0.05)	0.24 (0.01)	0.12 (0.02)
Utricularia vulgaris	Shoe	0.20 (0.02)	0.24 (0.06)	0.16 (0.01)
	E. Graham	0.17 (0.02)	0.19 (0.08)	0.14 (0.02)
Myriophyllum verticillatum	Shoe	0.41 (0.06)	0.28 (0.12)	0.21 (0.03)
M. spicatum	E. Graham	0.19 (0.12)	0.20 (0.05)	0.17 (0.07)
Najas flexilis	Shoe			0.32 (0.04)
	E. Graham		0.19 (0.14)	0.13 (0.05)
Potamogeton natans	Shoe		0.24 (0.08)	0.19 (0.06)
	E. Graham		0.27 (0.11)	0.15 (0.05)
Potamogeton zosteriformis	Shoe	0.34 (0.19)	0.22 (0.07)	0.24 (0.04)
	E. Graham	0.25 (0.08)	0.20 (0.08)	0.22 (0.06)
Elodea canadensis	Shoe	0.43	0.27 (0.09)	0.29 (0.06)
	E. Graham	0.23 (0.01)	0.24 (0.08)	0.20 (0.01)
Chara vulgaris	Shoe	0.11 (0.01)	0.09 (0.01)	0.10 (0.01)
	E. Graham	0.09 (0.01)	0.05 (0.02)	0.07 (0.03)

ment occurring at the very center of the shaded areas. The same results occurred the following summer, in this case quantified with biomass data (Table 10).

Discussion

The moderately high eutrophy of this entire aquatic system likely is a result of the abundant phosphorus, significant inputs of which we assume originate from local and regional human habitation and activities. While there is some fluctuation of P through the system reflecting biogeochemical dynamics, concentrations sufficient to sustain high aquatic productivity (above 20–30 μgL^{-1}) are present throughout, both in the water and in the sediments. The observed differences in levels of eutrophy within this system appear to reflect differences in levels of available nitrogen. Even at their highest at the Shoe Lake inflow, the aqueous N concentrations are relatively low among the ranges known for productive systems (Wetzel 1983), and N-fixation within the system probably contributes significantly to the productivity inasmuch as cyanophytes are abundant here (Thompson 1988). Thus, inputs of N along the stream leading to Shoe Lake, the origins of which we currently are studying, have a major impact on the subsequent productivity patterns as shown both by the correlative and experimental data in this study. While sediment content of N in both lakes is above levels considered minimally sufficient to support abundant macrophyte growth (0.04–0.17 mgL^{-1}; Mulligan and Baranowski 1969; Peltier and Welch 1969; Nichols and Keeney 1976), the removal of N from epilimnetic water even within Shoe Lake, as well as in subsequent lakes, produces severe reduction in availability of this nutrient in East Graham Lake water, and this is the likely reason that all parameters indicate a less eutrophic condition there relative to Shoe Lake. While the wetlands surrounding the lakes may be influencing the watershed inputs, the lakes clearly are acting as major nutrient sinks here via growth and sedimentation of planktonic and suspended biota.

The difference in macrophyte community struc-

Table 8. Visual condition and reproductive response of *Potamogeton pectinatus* transplanted from East Graham Lake to Shoe Lake, in comparison with transplant controls within East Graham Lake (plants transplanted in June 1980, observed in August 1980).

	Visual condition* (No. of plants observed)			New shoots (mean no. per plant)	No. of plants producing flowers	Total no. plants observed
	Good	Fair	Poor			
Control (East Graham Lake)	6	0	0	2.3	6	6
Periphyton-free	6	0	0	0.8	0	6
Periphyton intact	1	4	1	0.2	0	6
Periphyton intact, under mat	0	0	3	0	0	3

* Visual Condition
Good: plants robust, green color similar to untreated plants
Fair: plants intermediate in appearance
Poor: plants flaccid, black

Table 9. Percent cover of rooted macrophyte species in Shoe Lake littoral zone areas after a growth season in presence and absence of constructed floating mats of *Ceratophyllum demersum*, in comparison with initial conditions.

Taxon	Initial conditions June 1980	Outside mat August 1980	Under mat August 1980
Area 1			
Chara vulgaris	95	95	30
Potamogeton natans	0	6	5
Potamogeton zosteriformis	5	10	5
Nymphaea odorata	0	20	0
Utricularia vulgaris	0	5	0
Area 2			
Chara vulgaris	65	60	25
Potamogeton natans	5	5	5
Myriophyllum spicatum	5	20	5
Vallisneria americana	0	10	0

Table 10. Biomass of rooted macrophyte species in Shoe Lake littoral zone areas after a growth season in presence and absence of constructed floating mats of *Ceratophyllum demersum* in comparison with initial conditions (biomass expressed as $g\,m^{-2}$ ash-free dry mass, mean $\pm$ SD, n = 3).

Taxon	Initial conditions June 1981	Outside mat August 1981	Under mat August 1981
Area 1			
Chara vulgaris	5.7 (8.3)	47.2	3.4 (9.7)
Myriophyllum spicatum	0.04 (0.1)	0	0
Ceratophyllum demersum	0	0.5 (0.9)	0
Area 2			
Chara vulgaris	11.8 (10.6)	5.0 (8.7)	0
Myriophyllum spicatum	2.2 (2.8)	6.1 (7.1)	0
Ceratophyllum demersum	0	0.3 (0.6)	1.2 (1.9)
Nuphar variegatum	0	32.7 (55.9)	0
Najas flexilis	0.2 (0.3)	0.5 (0.4)	0.03 (0.1)
Potamogeton confervoides	0.3	0	0

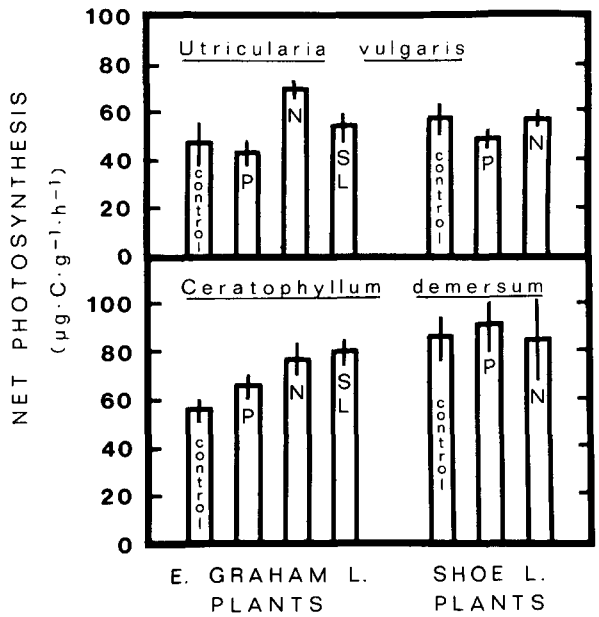

Fig. 6. Photosynthetic rates of *Ceratophyllum demersum* and *Utricularia vulgaris* from Shoe and East Graham Lakes in presence of enrichments of phosphorus, nitrogen (nitrate and ammonia), and filtered Shoe Lake water (SL). P and N enrichments in East Graham Lake water to final concentrations similar to those in Shoe Lake.

ture in Shoe and East Graham Lakes is striking, considering that differences in the levels of eutrophy and of pH-alkalinity are not great. This illustrates the magnitude of the influence of, and sensitivity of plants to, those factors which do

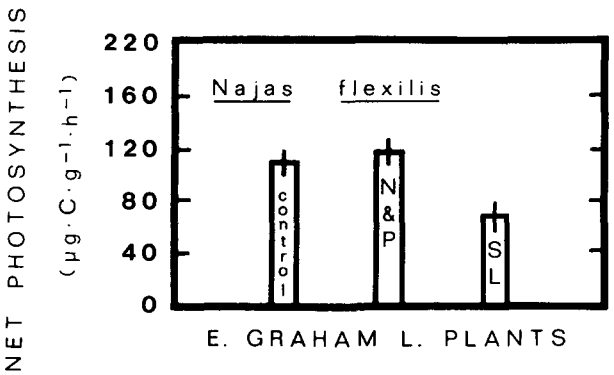

Fig. 7. Photosynthetic rates of *Najas flexilis* from East Graham Lake in presence of phosphorus and nitrogen (nitrate and ammonia) enrichments approximating Shoe Lake levels, and in presence of filtered Shoe Lake water.

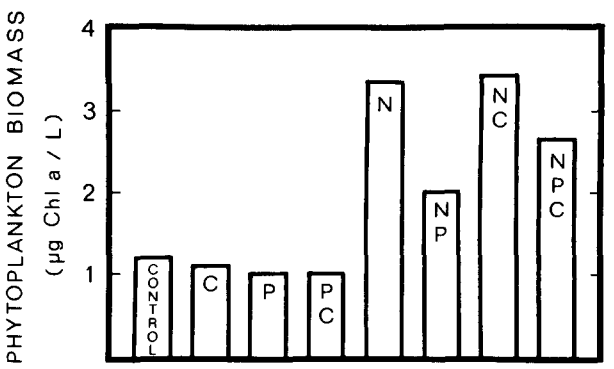

Fig. 8. Chlorophyll biomass of East Graham Lake phytoplankton after three-week exposures to enrichments of phosphorus, nitrogen (nitrate and ammonia), and carbon (sodium bicarbonate) approximating levels in Shoe Lake.

control distributions and growth rates of macrophyte species. The macrophytes in these two lakes differ in species composition, growth habit groups, and depth distribution, as well as total standing crop biomass.

One of the most visually obvious comparative features is the prevalence of the non-rooted macrophytes *Ceratophyllum demersum* and *Utricularia vulgaris*, along with the euplanktonic alga *Cladophora fracta* (Cheney and Hough 1983) in

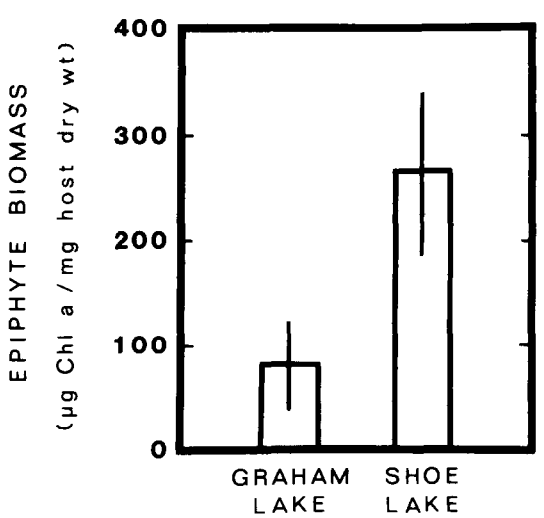

Fig. 9. Chlorophyll biomass of epiphytic algal communities on macrophytes from East Graham Lake exposed to filtered water from East Graham Lake or Shoe Lake.

Shoe Lake, which was confirmed in the macrophyte sampling. These are responding as do the phytoplankton to inflowing nutrient availability, consistent with observations of Goulder and Boatman (1971). *C. demersum* is particularly known for its nitrophily (Goulder and Boatman 1971; Toetz 1971; Best 1980). Its ability to grow rapidly in the upper water column enables it to maximize light availability for which it competes with phytoplankton (Chapman *et al.*, 1974; Phillips *et al.*, 1978), thus simultaneously adapting to and contributing to the light attenuation factor in the lake.

The depth distribution of the other species is another visually obvious difference between the two lakes, also confirmed by the data. A major variable along the depth gradient is light penetration: at 2 m East Graham Lake has 22–25% of surface PAR, while Shoe Lake has 8–16%. At 4 m East Graham Lake still has 5–6% of surface PAR while at that depth Shoe Lake has less than 3%; the former exceeds, and the latter is below, minimum light requirements reported for some *Potamogeton* species (Pearsall 1920; Bourne 1932). We found that in Shoe Lake the plants exist in three distinct depth zones similar to ones suggested by Rickett (1922; 1924) for lakes Mendota and Green. In East Graham Lake, with a less severe light gradient, zonation is much less clearly defined. Moreover, the few plants which were collected in 4 m samples in Shoe Lake were primarily non-rooted species (some of which may have sunk to that level or were taken by the sampler on its way down to that depth), while in East Graham Lake at that depth several rooted species were found, including *P. pectinatus* which requires relatively high light intensities (Wilson, 1941). Overall, East Graham lake clearly supports plant growth at greater depth than does Shoe Lake, which strongly suggests that plankton-induced turbidity is a major factor (discussed further below).

While sediment nutrient content does not appear to be significant variable in the lakes (Fornwall, 1986), sediment particle size and organic content do vary between lakes, and the increased prevalence of fine organic sediment with depth in Shoe Lake may influence rooted plant growth negatively because of its potential instability and/or accumulation of toxic decomposition products (Barko, 1983). However, Spence (1982) suggests that where turbulence is minimal, which is true of Shoe Lake, fine nutrient-rich sediments can be highly supportive of rooted plants, consistent with observations of Pearsall (1920), Wilson (1935), Barko and Smart (1979), and Grace and Wetzel (1981). Some rooted species do grow well in the organic Shoe lake sediments, notably *Myriophyllum* and *Elodea*, which is normal for these species (Misra, 1938; Chapman *et al.*, 1974; Reed, 1977; Nichols and Shaw, 1986). Furthermore, in the transplant experiments the sediment was a constant, i.e. inhibition of rooted plant growth occurred in Shoe Lake even though the plants were rooted in their original sediments from Graham Lake.

The tissue nutrient contents of the macrophytes tested were consistent with general ranges for both P and N previously published for these or similar species by many workers (Misra, 1938; Gerloff and Krombholz, 1966; Hutchinson, 1975; Nichols and Keeney, 1976; Smart, 1980; Barko and Smart, 1981). With the exception of *Chara vulgaris*, all plants in both lakes contained P at percentages above the generally critical limiting level (0.13% dry weight) established by Gerloff and Krombholz (1966) and were mostly at the upper end of the normal range (0.1–0.28). In the case of the *Chara* plants the values may be underestimates due to presence of nonviable tissue sampled from the dense perrennial beds and the generally high ash content of this genus (Westlake, 1975), and thus not directly comparable to those of the other species. The N levels also were above (again with the exception of *Chara*) the general critical figure (1.3%) given by Gerloff and Krombholz (1966), although they were in the lower part of the normal range (0.8–5.4), and the decline of N content in the non-rooted plants began to approach the critical level in late summer. Similar declines in N content were observed in *Myriophyllum spicatum* and *Ceratophyllum sp.* by Nichols and Keeney (1976). In general, the plant tissues appear to be under-

stocked in N relative to their P content, and as such probably are limited to lower growth rates than can be supported by the P availability. The nutrient enrichment experiments provided more definitive results, confirming the prediction that the non-rooted plants in East Graham Lake could be stimulated by Shoe Lake-level N enrichments, in the case of *C. demersum* to the same level of photosynthesis stimulated by Shoe Lake water itself and to the same level exhibited by Shoe Lake plants in the same experiment. Thus the difference in N concentration in the lakes can account fully for the difference in abundance of these plants in the two lakes. The non-rooted plants in Shoe Lake did not respond to nutrient enrichment, as predicted, nor did the rooted plant *Najas flexilis* in East Graham Lake, as predicted. It appears that the low N availability in East Graham Lake relative to Shoe Lake results primarily in fewer numbers and smaller sizes of individual non-rooted plants, rather than plants with lower N content.

Regulation of growth rates by N availability also was very clear in the East Graham Lake phytoplankton enrichment experiment. These results do not support the prediction of the Phillips *et al.* (1978) model that the phytoplankton in East Graham Lake would be unresponsive to nutrient enrichment because of allelopathic suppression by the macrophytes. Thus phytoplankton are more abundant in Shoe Lake because N availability is higher there, as is true of the non-rooted macrophytes and periphyton. The nutrient-driven eminence of phytoplankton, periphyton and non-rooted macrophytes in Shoe Lake provides the basis for the light-limitation of rooted macrophytes there. Periphyton shading probably is more inhibitory than phytoplankton shading here, which was found also by Sand-Jensen and Søndergaard (1981) in eutrophic lakes. Phytoplankton do play a significant role, however, as described also by Peltier and Welch (1969), Morgan (1970), Jupp and Spence (1977), Manny *et al.* (1978), Sand-Jensen and Søndergaard (1981), Best *et al.* (1984), and Lachavanne (1985). Also,

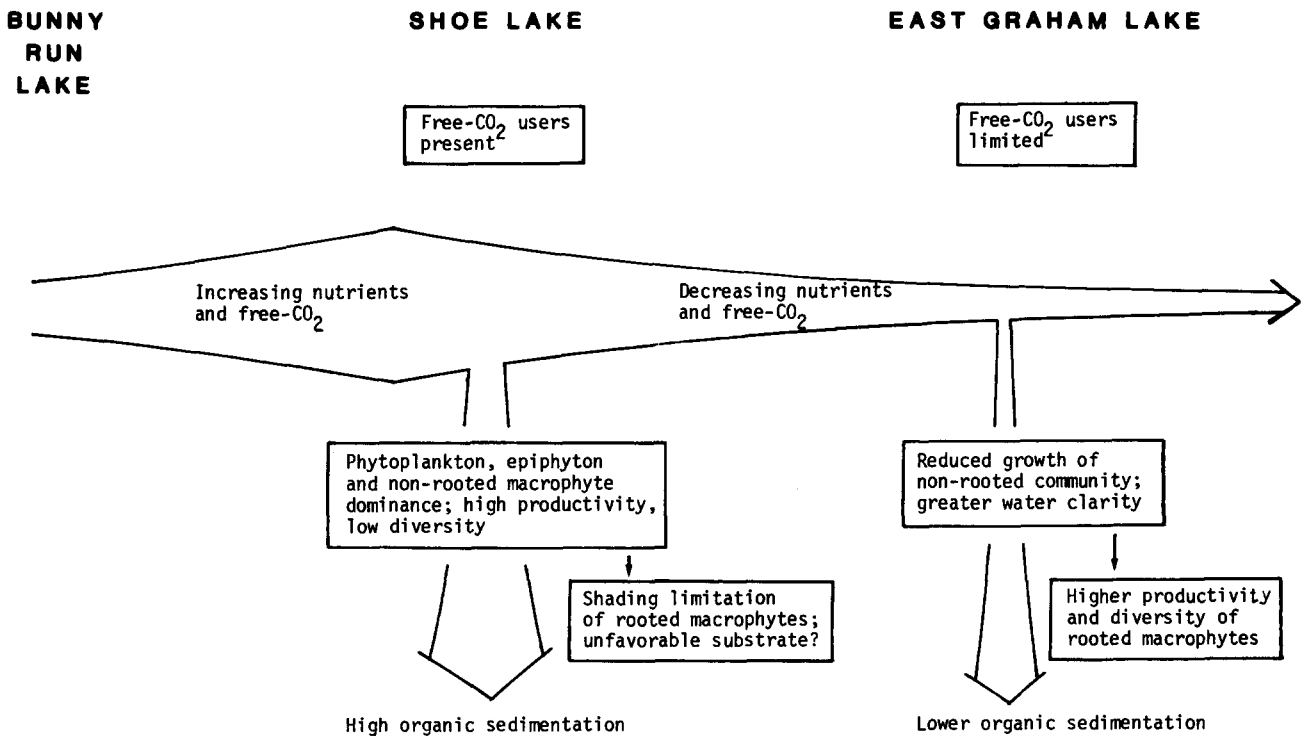

Fig. 10. Summary of community dynamics in the Stoney Creek (West Branch) chain of lakes represented by Shoe and East Graham Lakes.

phytoplankton growth was found to precede or accompany macrophyte decline in experimentally enriched ponds (Moss, 1976; Mulligan *et al.*, 1976).

The shading experiments indicated that the non-rooted macrophyte populations (*C. demersum*) were the primary contributors to light attenuation and inhibition of rooted plant growth. As mentioned above, the role of non-rooted macrophytes has not been emphasized in formal models of rooted macrophyte decline, but several workers in fact have reported their prevalence in eutrophic situations. Best (1980) has done much to characterize *Ceratophyllum demersum*, which is a major component of eutrophic lake plant communities here and elsewhere. Peltier and Welch (1969), Chapman *et al.* (1974), and Adams and Prentki (1982) remark on the early dominance of this and similar plants with nutrient loading, and Filbin and Barko (1985) found that *C. demersum* dominates a eutrophic reservoir, both by overwintering well and by rapid growth rates, and combines with phytoplankton and periphyton to restrict rooted macrophyte growth.

A summary description of the system studied here is shown in Figure 10. Following the eutro-

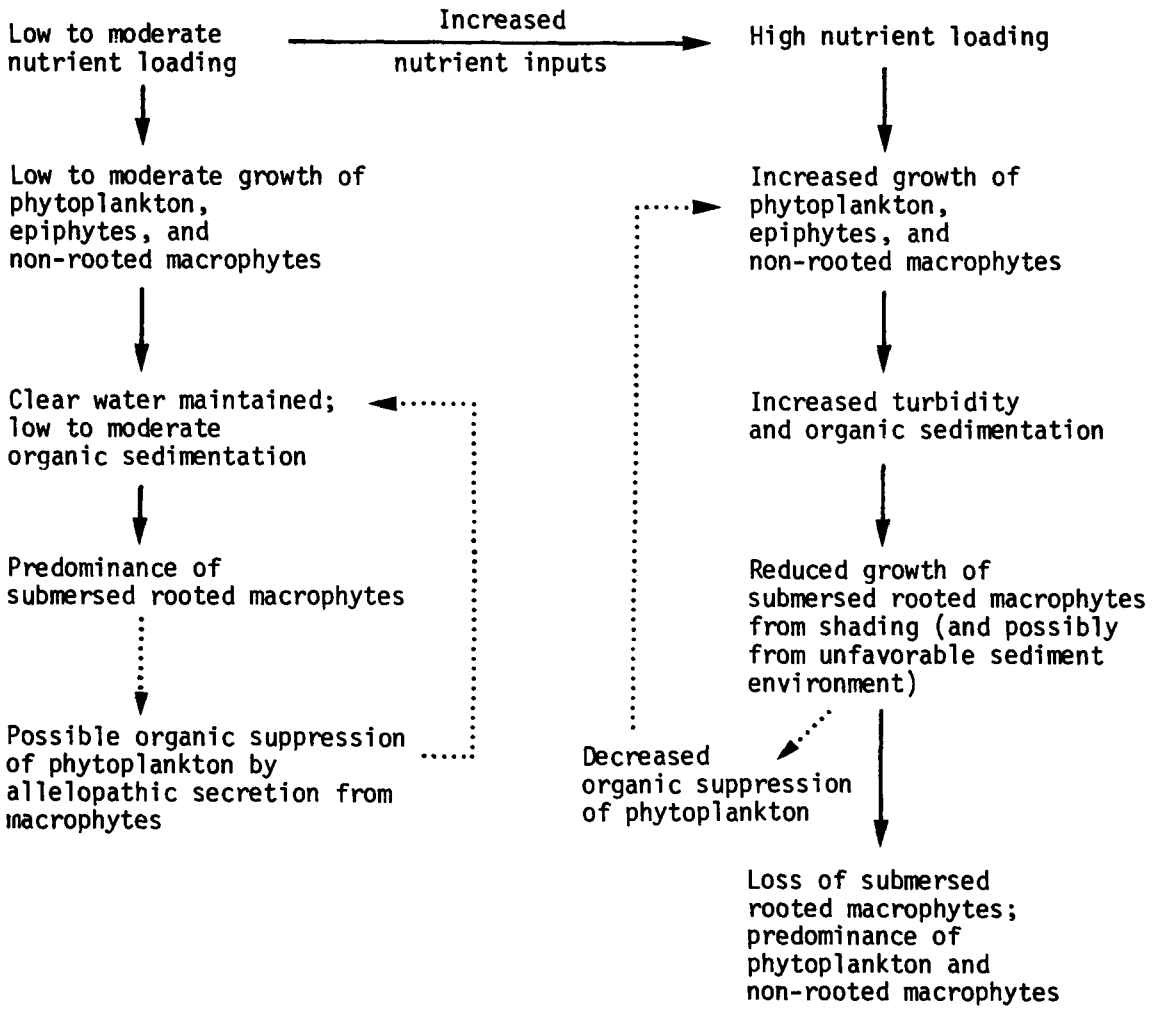

Fig. 11. A general descriptive model of aquatic plant relationships to eutrophication. Modified from Phillips *et al.* (1978) and Wetzel and Grace (1983).

phication of Shoe Lake, there is a de-eutrophication (or oligotrophication) of subsequent lakes by sedimentation of biomass having absorbed the nutrients flowing through (West Graham Lake, not studied and not shown in Figure 9, is in the chain between Shoe and East Graham Lakes and undoubtedly contributes to this process). We believe that nutrient removal is accomplished primarily by the non-rooted macrophytes and phytoplankton, although a comprehensive nutrient budget remains to be done. The decreasing nutrient availability (especially N) removes the dominance of the suspended and planktonic biomass, and the productivity and diversity of rooted macroflora increases. Changes in species composition with respect to changing availabilities of light and free-CO_2 in this system are described in Fornwall (1986). A similar chain-of-lakes progression, although of lesser magnitude, was described by Wetzel (1973) in which the lake with maximal phytoplankton productivity and minimal macrophyte diversity was followed by two lakes of decreasing phytoplankton productivity and increasing macrophyte diversity.

Our results generally are consistent with the Wetzel and Hough (1973) model, as we believe are those of most other workers. The Phillips *et al.* (1978) model does not seem to correctly account for the dynamics of our system, and as these are typical temperate zone, moderately calcareous lakes, we feel that it does not have sufficiently general applicability. Thus while quantitatively significant allelopathic suppression of phytoplankton by macrophytes may occur in some situations, we do not believe that it is universally the primary factor in the macrophyte-eutrophy relationship. Finally, we would like to give greater emphasis to the non-rooted macrophyte functional group in a model of macrophyte-eutrophication dynamics, as suggested in Figure 11.

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