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Aquatic vegetation of Nova Scotian lakes differing in acidity and trophic status

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Abstract

Aquatic macrophytes of the littoral zone were surveyed in 21 Nova Scotian lakes, and macrophyte composition was interpreted in relation to chemical and physical characteristics. The lake set included both nutrient-enriched and acidified lakes, and consequently had a wide range of water chemistry variables, notably pH (3.7–8.3) and total phosphorus (0.003–6.0 mg l^{-1}). Using canonical correspondence analysis, we related differences in vegetation among lakes to 14 water chemistry and three physical variables. Alkalinity, total phosphorus, and total nitrogen were most strongly correlated with differences in vegetation between heavily enriched, moderately enriched and non-enriched lakes. Interestingly, macrophyte composition was not strongly correlated with pH. Even in a subset of lakes consisting of moderately enriched and non-enriched lakes, alkalinity, total phosphorus and total nitrogen remained strongly correlated with vegetation differences. By contrast, vegetation differences among non-enriched lakes correlated most strongly with substrate slope, lake area, calcium, and alkalinity.

Keywords: Acidification; Nutrient enrichment; Aquatic vegetation; Water chemistry; Nova Scotia; Lakes

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1. Introduction

Human activities can affect aquatic macrophyte assemblages of lakes, notably through fertilization and acidification. Nutrient enrichment by human sources, such as sewage inputs, agricultural run-off, and abattoir waste, can cause substantial changes in the abundance and composition of aquatic vegetation (Lind and Cottam, 1969; Seddon, 1972; Jupp and Spence, 1977; Ozimek, 1978; Roelofs, 1983; Ozimek and Kowalczewski, 1984; Kerekes et al., 1984; Arts et al., 1990), with the specific effects depending on the original flora and the

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degree and nature of enrichment. Acidification of lakes by atmospheric pollutants or other causes may also change the composition of macrophyte vegetation (reviewed by Farmer, 1990). In northern Europe, lake acidification is considered to have converted numerous isoetid-dominated lakes into *Sphagnum*-dominated lakes (Grahn et al., 1974; Hultberg and Grahn, 1975; Grahn, 1977; Roelofs, 1983). Evidence for this phenomenon in North America is scant (Wile and Miller, 1983; Roberts et al., 1985; Wile et al., 1985; Stewart and Freedman, 1989), although other changes in macrophyte vegetation as a result of acidification have been documented (e.g. Gorham and Gordon, 1963).

Lakes in Nova Scotia and New England typically have little acid-neutralizing capacity (Driscoll and Newton, 1985; Kerekes et al., 1986; Underwood et al., 1986, 1987; Freedman et al., 1989), and differences in macrophyte composition amongst lakes in this region have frequently been related to pH or its correlates, such as alkalinity and calcium (Hellquist, 1980; Roberts et al., 1985; Catling et al., 1986; Jackson and Charles, 1988). The enrichment of such oligotrophic and acidic lakes may result in changes in macrophyte composition through either an increase in nutrients, or a decrease in acidity. Do nutrients or pH correlate best with vegetation differences along a gradient of enrichment? How enriched do acidic lakes need to become before differences in macrophyte composition are detectable?

The present study analyzes the above two questions using a group of 21 lakes in Nova Scotia that are either non-enriched, moderately enriched, or heavily enriched. Differences in vegetation among lakes are related to environmental variables (14 water chemistry and three physical). We have paid particular attention to water chemistry, even though sediment chemistry may also be important (Carignan and Kalff, 1980; Barko et al., 1991). Our study can thus be readily compared with a wealth of previous studies that have correlated floristic differences among lakes with water chemistry. Presumably this historical bias towards water chemistry reflects, in part, the relative ease of collecting water chemistry data that are representative of entire lakes.

2. Methods

2.1. Study lakes

The 21 freshwater lakes and ponds, hereafter referred to as 'lakes', are located in southwestern and central Nova Scotia (Table 1). Nine of the study lakes received some degree of nutrient enrichment from anthropogenic sources: five were enriched by sewage, including two pairs of constructed sewage ponds (BR and PW; each pair was considered as one lake; see Table 1 for explanation of acronyms), two natural ponds (WI and DU), and one lake (DR) which had received raw sewage until several years prior to our study. Two other ponds were enriched by cow manure and fertilizer run-off (SK and CP), and one (DC) received effluent from a chicken abattoir. A portion of one bay of Jordan Lake was isolated in 1985 by Ducks Unlimited and experimentally limed and fertilized (triple-super-phosphate, urea) between 1985 and 1987 by the Nova Scotia Department of Natural Resources. Nutrient levels remained elevated during 1989–1990 in this impoundment (JF). An adjacent non-fertilized part of Jordan Lake (JU) was also sampled. The other eleven freshwater bodies were oligotrophic (based on total phosphorus; Vollenweider and Kerekes, 1982).

Table 1
Study lake codes, location, enrichment status (level and type) and mean pH and total phosphorus concentrations. Enrichment level of a lake was non-enriched (N), moderately enriched (M) and heavily enriched (H). Enrichment was by sewage (S), fertilizers (F), chicken abattoir wastes (C), or agricultural manure and fertilizer run-off (A)

Lake	Code	Lat., Long.	Status	pH	P ($\mathrm{mg\,l^{-1}}$)
Little Springfield	LS	44°48′, 63°44′	N	3.7	0.008
Oscar	OS	44°14′, 65°19′	N	4.5	0.010
Spruce Hill	SH	44°39′, 63°41′	N	4.8	0.005
Jacks	JA	44°44′, 63°40′	N	4.8	0.011
Tobeatic Flowage	TF	44°11′, 65°20′	N	4.8	0.017
Susies	SU	44°39′, 63°41′	N	4.9	0.003
Ragged	RA	44°37′, 63°40′	N	4.9	0.004
Power	PO	44°35′, 63°33′	N	5.1	0.010
Soldier	SO	44°47′, 63°34′	N	5.2	0.007
Lewis	LE	44°49′, 63°46′	N	5.3	0.018
Jordan unfertilized	JU	44°07′, 65°13′	N	5.6	0.013
Spectacle	SP	44°16′, 66°04′	N	6.3	0.018
Drain	DR	44°47′, 63°45′	M(S)	5.1	0.025
Jordan fertilized	JF	44°07′, 65°13′	M(F)	5.8	0.057
Duck	DU	44°48′, 63°40′	M(S)	6.8	0.320
Winder	WI	44°44′, 63°27′	H(S)	6.9	1.01
Dewey Creek	DC	45°07′, 64°27′	H(C)	7.0	0.950
Sandy Kent's	SK	45°09′, 63°19′	H(A)	7.1	1.75
Canning	CP	45°09′, 64°26′	H(A)	7.2	0.533
Bridgetown Sewage	BR	44°50′, 65°17′	H(S)	7.2	2.47
Port Williams Sewage	PW	45°05′, 64°25′	H(S)	8.3	5.95

Abundances of invertebrates and waterfowl of these lakes are described elsewhere (Staicer et al., 1994).

2.2. *Macrophyte cover*

Estimates of the cover of aquatic macrophytes (tracheophytes, charophytes, and bryophytes) were made late in the growing season of 1989 to minimize effects of seasonal variations in abundance. A stratified random design was used to locate ten sampling stations in the littoral zone of each water body, along approximately 1 km of undisturbed shoreline. Although ten samples per lake is too few to assess within-lake variation our procedure allowed a large number of lakes to be surveyed within a short time. (Note that this survey was supplemented with additional data as described later.)

At each station, cover of each species was estimated in the littoral (i.e. shallow, nearshore) zone, at a depth of 50 cm. It was necessary to control for depth, as this is an important variable affecting macrophyte distribution (Singer et al., 1983; Stewart and Freedman, 1989; Kunii, 1991), and a depth of 50 cm could be easily surveyed. It should be emphasized that the data collected therefore characterize the littoral zone, rather than the entire lake. In shallow lakes, the flora of the littoral zone may be identical with the flora of the entire lake. Using a 1 m × 1 m quadrat, percent cover was estimated in three horizons at increasing depths of the water column (surface, 25 cm, and bottom; each to a maximum cover of 100%), and summed to give total cover (to a maximum of 300%). Frequency was calculated as the proportion of stations at which a given species was observed (possible values were 0, 0.1, 0.2...1.0).

Species prominence was calculated as mean total cover × square root of frequency (Beals, 1960; Muc et al., 1989). In comparison with mean cover, such a measure downweights the importance of isolated patches of a species in analyses. Species observed in the littoral zone of lakes in 1989 and 1990 but not encountered in quadrats were arbitrarily assigned a small prominence value of 0.1, and were added to the survey data. For ordination analysis, species prominence was transformed logarithmically to prevent very prominent taxa (especially *Sphagnum* spp.) from dominating the analysis. Although it was not possible to identify *Sphagnum* individuals to species in the field, most voucher specimens were later identified as *Sphagnum torreyanum* Sull.

2.3. Water analysis

Water samples for chemical analysis were collected in August 1989, October 1989 and May–June 1990 at various positions in the lakes, including the littoral zone and outflow, for a total of four to seven samples per lake. Additional samples were available from Drain (6) and Little Springfield (5) lakes for July and August, 1990. For a given chemical variable, the mean concentration was calculated for all water samples collected on all occasions in the same lake. Water was collected at 10 cm below the surface in 1 l polyethylene bottles for major ions analysis, and in 50 ml glass vials for total phosphorus analysis.

Water samples were analyzed for chemicals indicative of nutrient status (N, P, K, Mg, Ca, Si, conductivity), acidity (pH, alkalinity, sulfate), brown-staining (dissolved organic carbon, color) and nearby marine sources (Na, Cl), all of which were potentially important influences on lake flora.

All chemical analyses were carried out by the Water Quality Branch, Inland Waters Directorate, Moncton, N.B., using their standard procedures as summarized below (Water Quality Branch, 1984). Dissolved organic carbon was measured with an automated system, involving the conversion of organic carbon compounds to CO_2 gas in an acid-persulfate-UV digester, and then colorimetric determination of the CO_2 concentration using loss of color in a borate buffered alkaline phenolphthalein solution. Dissolved nitrogen (NO_3 and NO_2) was determined colorimetrically on an autoanalyzer, after reaction with a solution of sulfanilamide, *N*-1-napthylethylenediamine and H_3PO_4 to form an azo dye. Total nitrogen was measured, after UV digestion, colorimetrically on an autoanalyzer by reaction with the same solution as for dissolved nitrogen which formed the same azo dye. After mixing an aliquot of the sample with a $LiNO_3$, 1% H_2SO_4 solution, dissolved potassium and sodium were measured by flame photometry at 768 nm and 589 nm, respectively, and compared to an internal lithium standard. Dissolved calcium and magnesium were determined by automated atomic absorption. Dissolved sulfate and chloride were measured using ion chromatography. Reactive silica was determined colorimetrically at 660 nm using the heteropoly blue method. Specific conductance was measured with a Pt electrode conductivity meter, and then corrected to 25°C. Apparent color, measured in Hazen units, was obtained by visual comparison of a shaken sample with standard brown color solutions. A pH meter with glass and calomel electrodes and calibrated with standard buffer solutions was used to measure pH. Alkalinity was determined by gran titration, using a radiometer pH meter, autoburette, and printer. Specifically, this procedure involved the mixing of a 100 ml aliquot of sample with 0.25 ml 1 N KCl and titration to pH 3.7 with 0.001 N HCl. Turbid samples were filtered first before measurements of dissolved organic carbon, nitrogen, sodium and potassium were made. More detailed descriptions of the chemistry of these lakes are in preparation (C. Staicer and B. Freedman, unpublished data, 1989, 1990).

2.4. *Physical characteristics*

Bottom type was noted for each station, and was scored on a scale representing the different particle sizes (1, boulders; 2, rocks; 3, gravel; 4, sand; 5, silt; 6, coarse organic detritus; 7, fine organic mud; 8, clay); median values were used in the analyses. Slope was recorded at each station as depth over distance to shore; mean values were used. Lake area was determined from topographic maps or aerial photographs. An isolated bay of each of JU, SO, and SU was examined in this study, so only the appropriate partial lake areas were estimated for these lakes. Exposure was not recorded, but is related to average slope and lake area.

2.5. *Multivariate analysis*

Canonical correspondence analysis (CCA) was used to relate environmental variables to differences in the macrophytic associations among lakes. The CCA was performed using the program CANOCO (Ter Braak, 1988). As in standard correspondence analysis (Gauch, 1982), CCA uses an iterative, two-way, weighted-averaging algorithm to ordinate sample and species scores. In CCA, however, after new sets of sample scores are produced, they are regressed on the environmental variables, so that the resultant orientation of ordination axes reflects linear combinations of statistically important environmental variables. The important variables can be deduced by comparing inter-set correlations (i.e. correlations of environmental variables with the species axes, the latter consisting of sample scores). Inter-set correlations are reported here rather than canonical coefficients, because strong correlations among environmental variables can destabilize the latter (Ter Braak, 1988).

To determine whether linear or logarithmic forms of each of the 17 environmental variables were more useful in explaining vegetation differences, correlation coefficients were calculated between both forms of a variable and the first two ordination axes generated by detrended correspondence analysis (DCA, using DECORANA; Hill, 1979). The form with the strongest correlation coefficient with either DCA axis was used in the CCA. Both the DCA and CCA generated similar ordination diagrams and results, but for simplicity only the CCA results are presented here.

The number of environmental variables included in a CCA is limited by sample size ($n-2$ or less). For the full data set of 21 lakes, the maximum number of environmental variables allowed was 19, so all 17 variables were included in the analysis. For the subset of 12 non-enriched lakes, only 10 environmental variables could be used in the CCA. These were selected on the basis of their ranked-strength of correlation with DCA axes for the same set of 12 lakes.

3. Results

The lakewaters encompassed a wide range of acidity, from pH 3.7 to 8.3 (Table 1). The values of total phosphorus concentration in the lake waters (0.003–6.0 mg l^{-1}; Table 1) corresponded to a broad range of trophic status, from ultra-oligotrophic to hyper-eutrophic according to the phosphorus–trophic relationship proposed by Vollenweider and Kerekes (1982).

Fifty-six macrophyte species were encountered in the lakes (Fig. 1). Certain species occurred over a wide range of pH and phosphorus concentrations, notably *Eriocaulon septangulare*, *Nuphar variegatum*, *Nymphaea odorata*, *Pontederia cordata*, *Typha latifolia*, and to a lesser degree, *Sparganium americanum* and *Eleocharis robbinsii*. Species found exclusively in high-pH/high-phosphorus lakes included *Lemna minor*, *Carex pseudocyperus*, *Bidens cernua*, *Potamogeton natans*, and *Sparganium eurycarpum*. Species occurring exclusively in low-pH/low-phosphorus lakes included *Sphagnum* spp., *Fontinalis novae-angliae*, *Potamogeton confervoides*, *Juncus militaris*, *Chamaedaphne calyculata*, and *Myrica gale*.

3.1. Macrophyte composition and lake enrichment status

Relationships of macrophyte composition and water chemistry were explored using canonical correspondence analysis. When all 17 chemical and physical variables were included in the CCA, lakes separated according to their nutrient enrichment status (Fig. 2). The first ordination axis (eigenvalue 0.886, accounting for 16.2% of total variance) separated the heavily enriched lakes from other lakes, while the second axis (eigenvalue 0.635, 11.6% of total variance) separated moderately enriched lakes from non-enriched lakes.

Heavily enriched lakes were characterized by a high abundance of *Lemna minor*, *Sparganium eurycarpum*, *Carex pseudocyperus*, *Elodea canadensis*, *Typha latifolia* and *Potamogeton foliosus* (see Fig. 1 for other associated species). These lakes were non-acidic (pH at least 6.9) and hyper-eutrophic (total phosphorus concentration at least 0.5 mg l^{-1}).

Moderately enriched lakes were characterized by species such as *Potamogeton oakesianus*, *Utricularia intermedia*, *Utricularia purpurea*, and *Scirpus cyperinus*. Notably, species characteristic of acidic/oligotrophic waters, such as *Dulichium arundinaceum* and *Sparganium americanum*, and those characteristic of more alkaline/eutrophic waters, such as *Elodea canadensis*, *Typha latifolia*, and *Potamogeton gramineus* often coexisted in this intermediate group of lakes. The three lakes comprising this group (DR, DU and JU) were the only lakes with phosphorus concentrations between 0.025 and 0.32 mg l^{-1}. The pH range (5.1–6.8) that these lakes encompassed also included five other non-enriched lakes (PO, SO, LE, JU, SP).

The non-enriched lakes ($P < 0.018$ mg l^{-1}, pH range 3.7–6.3) were characterized by species such as *Eleocharis robbinsii*, *Utricularia vulgaris*, and *Potamogeton confervoides*. The first axis of a CCA that included only the non-enriched lakes separated isoetid-dominated lakes (Fig. 3, lower right corner: RA, SH, SP, and SO) from *Sphagnum*-dominated lakes (Fig. 3, lower left corner: LS, JU, TF, and OS). Isoetid-dominated lakes are all large (bay or whole lake area of 24–60 ha), clearwater, with gravel–rock bottoms and are dominated by the isoetids *Lobelia dortmanna*, *Eriocaulon septangulare*, and *Isoetes tuck-*

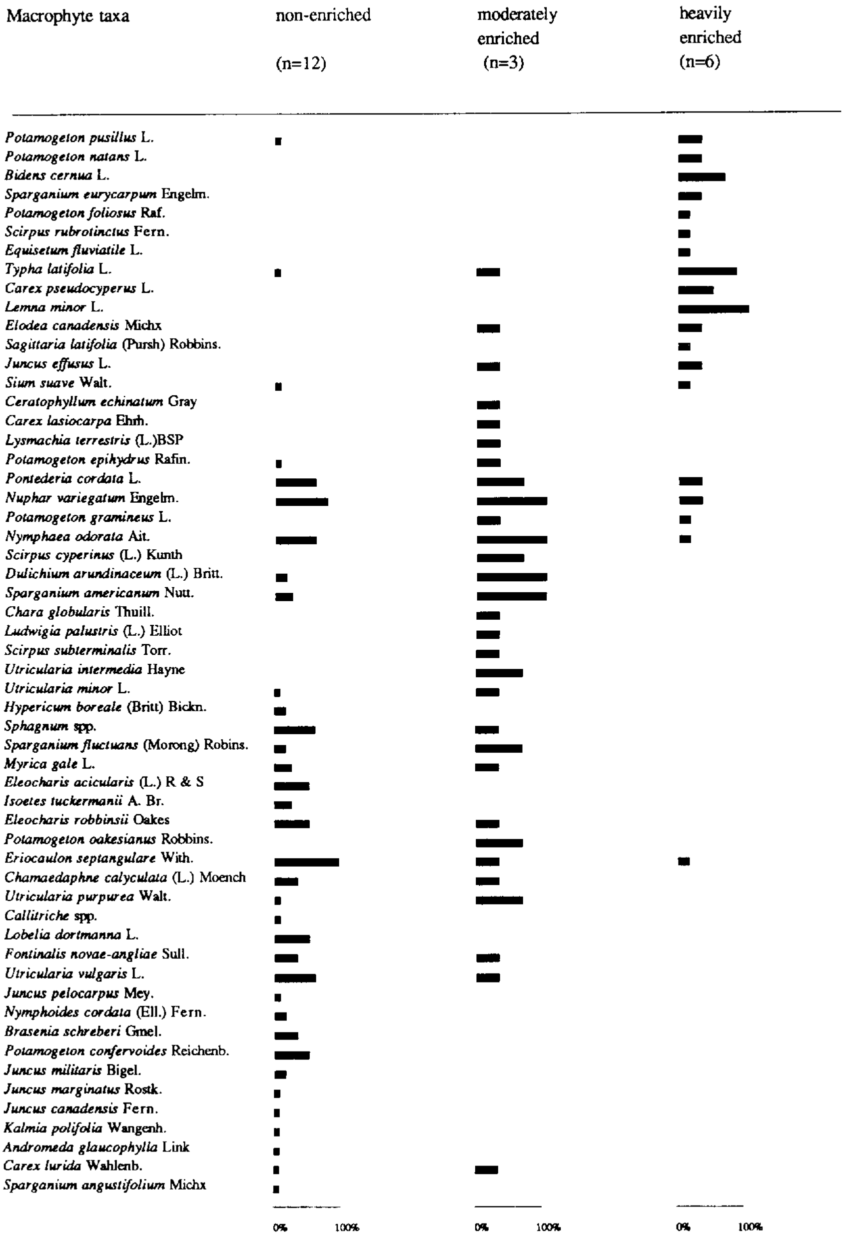

Fig. 1. Occurrence of macrophyte species, expressed as a percentage of lakes in each lake group (non-enriched, moderately enriched, heavily enriched lakes) which contained a given species. Species are arranged as ordered by the first axis of the full CCA of all lakes.

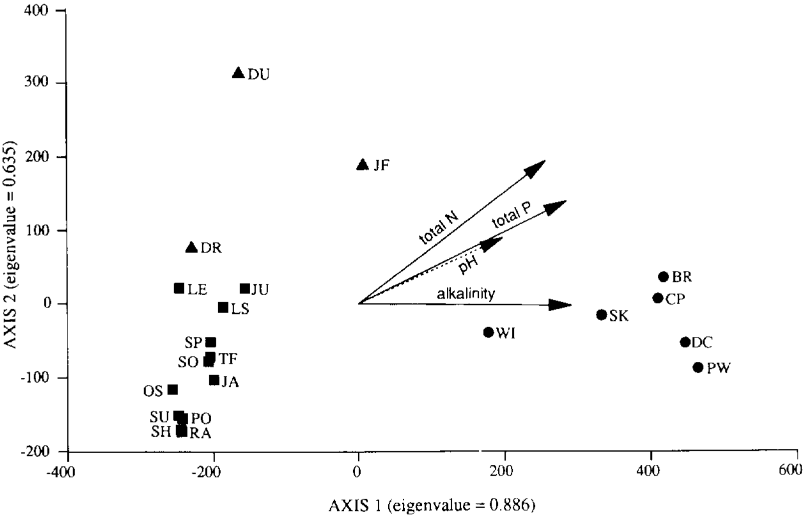

Fig. 2. Lake ordination by the first two CCA axes. Arrows represent correlations of the three most important chemical variables (solid line) and pH (dashed line) with the axes. The length of the arrow represents the magnitude of influence of a variable in the CCA ordination, and its direction the axes most influenced. Thus alkalinity is most influential in separation along the first axis, total phosphorus (total P) and total nitrogen (total N) are influential on both axes, and pH is of relatively minor importance. Symbols indicate lake enrichment status: ■, non-enriched; ▲, moderately enriched; ●, heavily enriched; refer to Table 1 for explanation of lake codes.

ermanii, the small spike-rush *Eleocharis acicularis* and the small rush *Juncus pelocarpus*. The *Sphagnum*-dominated lakes are small (bay or whole lake area of 11–39 ha) and have brown-stained water (except for LS). These lakes are dominated by *Sphagnum* spp. and by species tolerating a peat substrate, such as *Sparganium americanum*, *Brasenia schreberi*, *Pontederia cordata*, and *Chamaedaphne calyculata*. Other non-enriched lakes tended to have a flora intermediate to that of these two groups.

3.2. Environmental variables and the full lake set

As suggested above, the CCA ordination of vegetation and lakes can be interpreted on the basis of gradients in environmental variables. For simplicity, the scales of the environmental variables are not given in the following discussion (please refer to Table 2 to determine if the linear or logarithmic form of a given variable was used).

Environmental variables strongly correlated with the first CCA axis (i.e. species axis based on sample scores; Table 2) included alkalinity ($r = 0.91$), total phosphorus ($r = 0.89$), magnesium ($r = 0.87$), calcium ($r = 0.84$), and total nitrogen ($r = 0.81$). Correlations with the second ordination axis (Table 2) were weaker; total nitrogen ($r = 0.40$) and color ($r = 0.33$) were most prominent. Interestingly, pH did not rank amongst the strongest correlations with either axis ($r = 0.62$ and $r = 0.19$, respectively).

It is possible that strong correlations of environmental variables with ordination axes could be due, in part, to covariance among variables. For example, total phosphorus was strongly correlated with the first axis, but this could reflect its strong correlation with

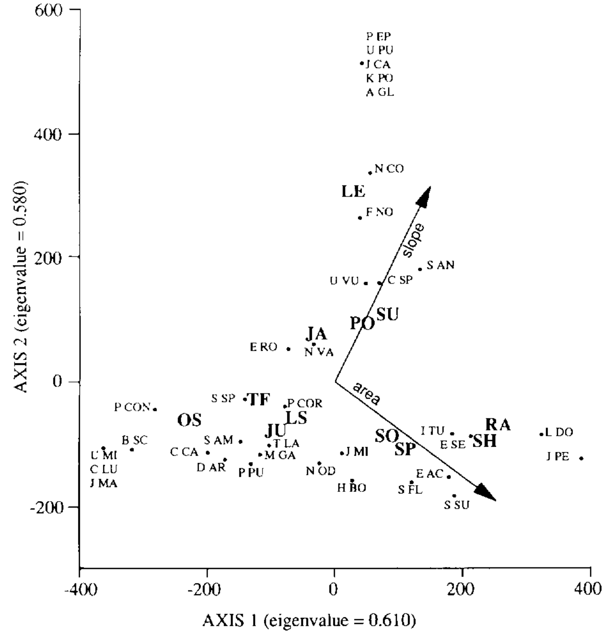

Fig. 3. First two CCA axes for the non-enriched lakes, with taxa (small font), lakes (large font), and arrows representing correlations of the two environmental variables most strongly correlated with the species axes. Lake codes are explained in Table 1; taxa names are abbreviated by the first three letters of both the specific and generic name (see Fig. 1 for full names).

alkalinity ($r = 0.88$). To explore this possibility, partial CCA analyses were performed, in each of which a selected chemical variable was a covariate (Table 2). Partial CCA analyses were run with three prominent environmental variables, namely total phosphorus, alkalinity, and total nitrogen.

The partial CCA with alkalinity as a covariate indicated that total phosphorus and total nitrogen were still important when the effect of alkalinity was removed; that is, they were still the variables with the strongest correlation with the first axis ($r = 0.62$ and $r = 0.72$, respectively). In contrast, calcium and magnesium were not as strongly correlated with the first or second axes of the partial CCA as in the full CCA This indicates that their importance in the full CCA occurred via their correlation with alkalinity. (Calcium and magnesium are therefore not considered in the following two partial correlations.)

The second partial CCA, with total phosphorus as a covariate, indicated that alkalinity and total nitrogen were still important (variables with strongest correlations with first axis; $r = -0.57$ and $r = 0.51$, respectively). In the third partial CCA, with total nitrogen as a covariate, alkalinity and total phosphorus were still among the variables most strongly correlated with the first CCA axis ($r = -0.72$ and $r = -0.60$, respectively).

Therefore, alkalinity, total phosphorus, and total nitrogen were the most important variables in separating macrophyte assemblages among the 21 lakes.

3.3. Environmental variables and partial lake sets

To determine whether the above conclusions were robust across a smaller range of variation of environmental variables, the six heavily enriched lakes were removed from the

Table 2
Inter-set correlations (correlations between species axes and environmental variables) for the first two axes of full and partial CCAs. Dashed lines indicate variables excluded from the analysis either because they were covariables or, in the not-heavily enriched lake set, to allow adequate degrees of freedom

	Lake set									
	All ($n=21$)								Not-heavily enriched ($n=15$)	
	None[a]		Alkalinity		ln P		ln N		None	
	1[b]	2	1	2	1	2	1	2	1	2
Alkalinity	0.91	−0.00	–	–	−0.57	−0.27	−0.72	−0.23	0.52	0.72
ln total P	0.89	0.29	0.62	0.15	–	–	−0.60	0.09	−0.78	0.51
Mg	0.87	0.04	0.11	0.03	−0.48	−0.26	−0.71	−0.26	–	–
ln Ca	0.84	0.20	0.44	−0.21	−0.12	−0.44	−0.41	−0.38	0.35	0.64
ln total N	0.81	0.40	0.72	−0.00	0.51	−0.10	–	–	0.63	0.63
ln K	0.80	0.07	0.13	−0.11	−0.28	−0.36	−0.48	−0.35	–	–
ln NO_2+NO_3	0.79	0.28	0.50	−0.22	0.15	−0.46	−0.17	−0.49	0.37	0.75
ln Si	0.76	−0.12	−0.20	0.13	−0.50	−0.09	−0.58	−0.11	–	–
ln area	−0.70	−0.18	−0.23	−0.46	0.15	−0.41	0.34	−0.39	−0.56	0.13
Bottom	0.69	0.20	0.27	0.28	−0.06	0.26	−0.25	0.26	0.39	0.15
pH	0.62	0.19	0.25	−0.09	0.01	−0.20	−0.13	−0.19	0.27	0.19
ln conductivity	0.61	0.10	0.14	−0.28	−0.05	−0.45	−0.16	−0.50	0.02	0.47
Na	0.46	0.19	0.23	−0.10	0.09	−0.11	−0.02	−0.07	0.21	0.61
Slope	−0.45	0.01	0.01	−0.55	0.27	−0.49	0.36	−0.46	−0.27	0.42
ln DOC	0.41	0.06	0.07	0.25	−0.10	0.22	−0.17	0.20	0.20	−0.03
ln S	0.35	0.08	0.09	−0.34	0.06	−0.36	−0.01	−0.32	–	–
ln color	0.21	0.33	0.34	0.21	0.23	0.29	0.19	0.32	0.37	0.10

[a] Covariable.
[b] Axis.

analysis. The CCA of the remaining 15 lakes was still strongly correlated with total phosphorus, alkalinity, and total nitrogen (Table 2).

However, in a CCA of the 12 non-enriched lakes, slope, area, and bottom score were most strongly correlated with one of the two CCA axes (Fig. 3, Table 3). Three partial CCAs with each of bottom score, slope, and area as covariates indicated that the importance of bottom score was due to covariance with slope, but the importance of area and slope was robust. The influence of physical factors in the non-enriched lakes contrasts with the results obtained when enriched lakes were included (i.e. certain chemical variables were most prominent).

Lastly, in a CCA of the same 12 non-enriched lakes, but with all physical variables omitted from the analysis, calcium, magnesium and alkalinity were most strongly correlated with the axes (Table 3). Partial CCAs with each of calcium, magnesium, and alkalinity as covariables indicated that covariance with calcium accounted for the importance of magnesium, but that calcium and alkalinity were robust correlates of the macrophyte CCA

Table 3
Inter-set correlations (correlations between species axes and environmental variables) for the first two axes of full and partial CCAs of the non-enriched lake set ($n = 12$). Dashed lines indicate variables excluded from the analysis, either because they were covariables or to allow adequate degrees of freedom, or in one case to limit the analysis to chemical variables. Slope, color, bottom, and area are physical (phys) variables; others are chemical (chem) variables

	Variable type									
	phys + chem								chem	
	None[a]		ln area		Slope		Bottom		None	
	1[b]	2	1	2	1	2	1	2	1	2
Alkalinity	0.37	−0.18	0.10	0.07	0.44	0.19	0.41	0.13	0.37	−0.18
ln total P	−0.35	0.11	−0.17	0.52	−0.43	0.18	−0.39	0.11	−0.35	0.12
Mg	–	–	–	–	–	–	–	–	0.43	0.09
ln Ca	–	–	–	–	–	–	–	–	0.44	0.46
ln total N	−0.25	0.05	−0.22	0.56	−0.26	0.47	−0.22	−0.21	−0.25	0.01
ln K	–	–	–	–	–	–	–	–	0.12	−0.27
ln $NO_2 + NO_3$	–	–	–	–	–	–	–	–	0.30	0.11
ln Si	–	–	–	–	–	–	–	–	–	–
ln area	0.52	−0.38	–	–	0.62	0.40	0.65	0.03	–	–
Bottom	−0.33	−0.42	−0.54	−0.04	−0.13	0.38	–	–	–	–
pH	0.30	0.12	0.30	0.00	0.23	0.07	0.26	−0.67	0.30	0.11
ln conductivity	0.32	0.32	0.46	−0.03	0.17	−0.06	0.13	−0.75	0.33	0.31
Na	–	–	–	–	–	–	–	–	–	–
Slope	0.31	0.63	0.66	0.36	–	–	−0.09	−0.58	–	–
ln DOC	−0.28	0.14	−0.10	0.46	−0.32	0.47	−0.34	−0.56	−0.28	0.14
ln S	–	–	–	–	–	–	–	–	−0.10	0.09
ln color	−0.27	0.19	−0.06	0.50	−0.34	0.31	−0.36	−0.47	–	–

[a] Covariable.
[b] Axis.

(results not shown). Notably, these factors were statistically much more important than pH per se in determining macrophyte associations (Table 3).

4. Discussion

Aquatic vegetation of the littoral zone differed substantially between non-enriched, moderately enriched and heavily enriched lakes. Ordination techniques separated lakes of these three enrichment levels on the basis of macrophyte composition (Fig. 2). In terms of water chemistry, this translated into strong correlations between the ordination axes and each of alkalinity, total phosphorus and total nitrogen (Fig. 2, Table 2).

Differences in vegetation between heavily enriched lakes and non-enriched lakes are hardly unexpected. Changes in vegetation caused by eutrophication have been well documented (Lind and Cottam, 1969; Seddon, 1972; Jupp and Spence, 1977; Ozimek, 1978; Roelofs, 1983; Ozimek and Kowalczewski, 1984; Kerekes et al., 1984; Arts et al., 1990).

The question of interest, however, is how eutrophic need lakes become before such differences are detectable? In non-enriched lakes (total phosphorus less than 0.018 mg l^{-1}, total nitrogen less than 0.35 mg l^{-1}), neither total phosphorus nor total nitrogen were strongly correlated with among-lake differences in vegetation (Table 3). Instead, physical variables (slope and area) and pH-related factors (calcium and alkalinity) were the best correlates. Inclusion of moderately enriched lakes (total phosphorus 0.025–0.32 mg l^{-1}, total nitrogen 0.29–4.52 mg l^{-1}) in the analysis, however, was sufficient to allow this enrichment gradient to reappear; again, total phosphorus, alkalinity, and total nitrogen were strongly correlated with the lake ordination axes (Table 2).

Nutrient enrichment results in increases not only in total phosphorus and nitrogen, but also in pH. When this covariance between nutrient enrichment and pH was taken into account, however, pH per se was not strongly correlated with vegetation differences between heavily enriched and non-enriched lakes or between moderately enriched and non-enriched lakes. Other studies have similarly indicated that enrichment can have large effects on vegetation even when pH change is negligible (e.g., Kerekes et al., 1984). Jackson and Charles (1988) suggested that vegetation in acidic lakes will reflect pH, not nutrient differences among lakes. Vegetation of our acidic ($3.7 > pH > 6.8$) lake set, comprised of the moderate and non-enriched lakes, however, was clearly correlated with nutrient (total phosphorus and nitrogen) levels in the water. Thus, in at least some situations, this simple and univariate rule of thumb based on pH does not hold. Notably, the Adirondack lake set of Jackson and Charles (1988, upon which their hypothesis was based) and the full lake set of the present study have roughly similar pH ranges (4.5–7.8, and 3.7–8.3, respectively), but very different ranges of total phosphorus (0.003–0.063 mg l^{-1}, and 0.003–6.0 mg l^{-1} respectively). Not unexpectedly, vegetation differences among lakes correlated best with pH and related factors in the former study, and with nutrient concentrations in the present study. Although water pH is undoubtedly important in determining the available form of N, P, and C, which may be of critical importance in competitive interactions (e.g. Roelofs et al., 1984), the effect of pH is statistically overshadowed in the present study by the large gradient of total nutrients.

Why do the three variables of total phosphorus, total nitrogen, and alkalinity correlate so strongly with vegetation differences along an enrichment gradient? Perhaps these chemical parameters are simply the best indicators of other, unmeasured, enrichment-linked parameters, and are not in themselves causally linked to vegetation change (Farmer and Adams, 1991). Total phosphorus and nitrogen concentrations in lake water, for example, may be closely correlated with available phosphorus and nitrogen in the sediments, presumably the main source of nutrients for many macrophytes (Carignan and Kalff, 1980; Barko et al., 1991). Other studies of lakeshore vegetation have indicated that diffuse competitive pressure increases with sediment nutrient concentration (Wilson and Keddy, 1986a), resulting in the replacement of small stress-tolerant species with larger competitively superior species (Wilson and Keddy, 1986b; Gaudet and Keddy, 1988; Keddy, 1989).

When effects of the enrichment of sediment and water with phosphate can be separated, water enrichment has been shown to have direct effects on macrophyte growth and community structure as well (Roelofs, 1983; Roelofs et al., 1984). In particular, high phosphorus concentrations in lake water can result in high densities of phytoplankton and epiphytes, which reduce light available to submerged macrophytes (Schindler and Fee, 1974; Jupp

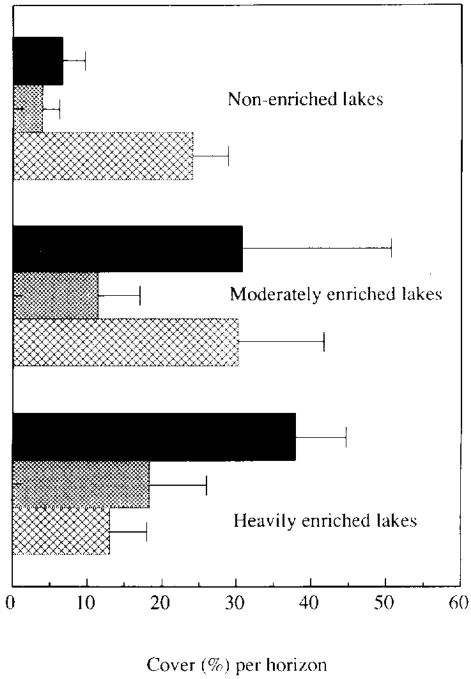

Fig. 4. Mean (±SE) cover of macrophytes in non-enriched ($n=12$), moderately enriched ($n=3$), and heavily enriched ($n=6$) lakes, in each of three horizons of the water column: surface (solid lines), 25 cm deep (narrow crosshatching), and lake bottom (wide crosshatching). Cover was measured in each horizon in each lake to a maximum of 100%.

and Spence, 1977; Phillips et al., 1978; Sand-Jensen and Søndergaard, 1981; Ozimek and Kowalczewski, 1984; Roelofs et al., 1984). In the present study, most plant cover was located closer to the surface in heavily enriched lakes and closer to the bottom in non-enriched lakes (Fig. 4), suggesting light limitation in the former. This trend was reflected in a change in dominant growth forms from isoetids and bryophytes in non-enriched lakes to emergents and free-floating plants in heavily enriched lakes (Fig. 1). Presumably, differences between lakes in water clarity are even more important for vegetation at depths deeper than the 50 cm depth examined in this study. Lastly, high concentrations of phosphorus and other sewage components may be toxic to certain plants (Forsberg, 1964; Ozimek, 1978).

Observations of strong correlations between macrophyte composition and either total phosphorus or total nitrogen in lakewater are surprisingly uncommon among studies that have used statistical procedures to relate macrophyte composition to water chemistry. By contrast, numerous other water chemistry variables have been reported to be strongly correlated with among-lake differences in vegetation, including alkalinity (e.g. Pip, 1979; Kadono, 1982; Fraser and Morton, 1983; Jackson and Charles, 1988; Kunii, 1991), pH (Kadono, 1982; Catling et al., 1986; Jackson and Charles, 1988; Kunii, 1991), calcium (Jensen, 1979; Catling et al., 1986; Jackson and Charles, 1988; Kunii, 1991), magnesium (Jackson and Charles, 1988; Kunii, 1991), conductivity (Swindale and Curtis, 1957; Seddon, 1972; Jensen, 1979; Jackson and Charles, 1988; Kunii, 1991), organic color (Catling et al., 1986; Stewart and Freedman, 1989), and nickel and manganese (Wile and Miller, 1983). These studies, however, have tended to involve sets of lakes which encompass a narrower range of trophic status or data sets that have not included phosphorus and nitrogen concentrations.

We hope this study suggests further avenues of research on enriched lakes, specifically surveys involving considerations of sediment chemistry and the chemical forms of nitrogen and phosphorus, variables we were not able to include in this study, and experimentation to establish mechanisms of change.

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