

Effects of sediment nutrients and depth on small-scale spatial heterogeneity of submersed macrophyte communities in Lake Pleasant, Pennsylvania

R.K. Johnson and M.L. Ostrofsky

Abstract: Sediment concentrations of total and available nitrogen (N), phosphorus (P), and potassium (K) and organic matter from the littoral zone of Lake Pleasant, Pennsylvania, were highly variable. Only organic matter and total N were correlated with depth, however. This result suggests the existence of more complex environmental gradients than the prevailing paradigm of monotonic changes in sediment characteristics with increasing depth. The spatial heterogeneity of submersed aquatic plant communities was significantly correlated with depth, and available N and P. Canonical correspondence analysis demonstrated that these three factors explained 38% of the variance in community structure. Other sediment characteristics (available K, organic matter, and total N, P and K) were not significant by themselves, but all variables combined explained 63% of community-structure variance. Cluster analysis identified species or groups of species typical of endpoints on the depth versus nutrient axes. *Myriophyllum exalbescens* was typical of deep sites with relatively nutrient-rich sediments, whereas deep nutrient-poor sites were dominated by *Vallisneria americana* and *Megalodonta beckii*. Shallow nutrient-rich sites were dominated by several species of *Potamogeton* and *Elodea canadensis*, and shallow nutrient-poor sites were dominated by *Heteranthera dubia* and *Najas flexilis*. These results demonstrate the importance of sediment characteristics in determining macrophytes' community structure within lakes.

Résumé : Les concentrations de azote (N), phosphore (P) et potassium (K) totaux et disponibles et de matière organique dans les sédiments de la zone littorale du lac Pleasant en Pennsylvanie sont très variables. Cependant, seuls le N total et la matière organique sont en corrélation avec la profondeur. Cette observation indique l'existence de gradients environnementaux plus complexes que de simples changements monotones des caractéristiques des sédiments en fonction de la profondeur, comme le veut le paradigme dominant actuel. L'hétérogénéité spatiale des plantes aquatiques submergées est en corrélation significative avec la profondeur et N et P disponibles. Une analyse des correspondances canoniques montre que ces trois facteurs expliquent 38 % de la variance de la structure de communauté. Les autres caractéristiques des sédiments (K disponible, matière organique et N, P et K totaux) ne sont pas significatives par elles-mêmes, mais toutes les variables combinées expliquent 63 % de la variance de la structure de communauté. Des analyses de groupement permettent d'identifier les espèces ou les groupes d'espèces typiques des points terminaux des axes des nutriments en fonction de la profondeur. *Myriophyllum exalbescens* est caractéristique des sites profonds à sédiments relativement riches en nutriments, alors que *Vallisneria americana* et *Megalodonta beckii* prédominent dans les sites profonds pauvres en nutriments. Plusieurs espèces de *Potamogeton* et *Elodea canadensis* prédominent dans les sites peu profonds riches en nutriments et *Heteranthera dubia* et *Najas flexilis* le font dans les sites peu profonds, mais pauvres en nutriments. Ces résultats démontrent l'importance des caractéristiques des sédiments pour expliquer la structure des communautés de macrophytes dans les lacs.

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Introduction

The analysis of the density and distribution of individual organisms and of the structure of biological communities is central to ecology. The structure of submersed plant communities in lakes is of particular importance to aquatic ecologists. The nature of these communities has been shown to

affect light (Ray et al. 2001), temperature (Unmuth et al. 2000), turbulence (Petticrew and Kalff 1992), water and sediment chemistry (Wigand et al. 1997), and the abundance and composition of other biotic assemblages from epiphytes (Jackson et al. 1994) to phytoplankton (Mjelde and Faafeng 1997) to invertebrates (Dvorak and Best 1982) to fish (Chick and McIvor 1994). Plant community structure is af-

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Table 1. Overview of studies seeking relationships between environmental variables and the distribution and abundance of aquatic vascular plants among lakes.

Location	No. of lakes	Primary determinants	Reference
Denmark	82	Alkalinity, pH	Vestergaard and Sand-Jensen 2000
Wales	70	Conductivity, total dissolved solids, hardness	Seddon 1972
Cape Cod, Mass., USA	5	Pore-water nutrients	Roman et al. 2001
Ireland	574	Conductivity, alkalinity, Ca, pH	Heegaard et al. 2001
Adirondacks, N.Y., USA	31	pH, alkalinity, conductivity, Ca, Mg	Jackson and Charles 1988
Adirondacks, N.Y., USA	9	pH	Roberts et al. 1985
Nova Scotia, Canada	21	Alkalinity, total P, total N	Srivastava et al. 1995
Kejimikujik National Park, N.S., Canada	20	Ca, pH, alkalinity	Catling et al. 1986
Finland	57	Conductivity	Toivonen and Huttunen 1995
Manitoba, Canada	305 ^a	Alkalinity, filterable residue, pH	Pip 1979
New England, USA	321 ^a	Alkalinity	Hellquist 1980
Brazil	30 ^a	pH, P _{sediment} , P _{water}	Bini et al. 1999
Southeastern Ontario, Canada	16	Conductivity	Crowder et al. 1977
Japan	500	pH, alkalinity, Ca	Kadono 1982
Egypt	60 ^a	Canal width, shading, conductivity, nutrient concentrations	Khedr and El-Demerdash 1997
Egypt	3	Altitude, Ca, Mg, NO ₃ , organics	Ali et al. 1995

^aCollections from "sites" or "locations"; the actual number of lakes is not listed.

ected by history (e.g., acid rain, eutrophication, invasive species), by biotic interactions (e.g., competition, predation), and by environmental gradients (e.g., light, depth, nutrients, ice scour, turbulence). The relative importance of each to community structure, however, is often difficult to determine.

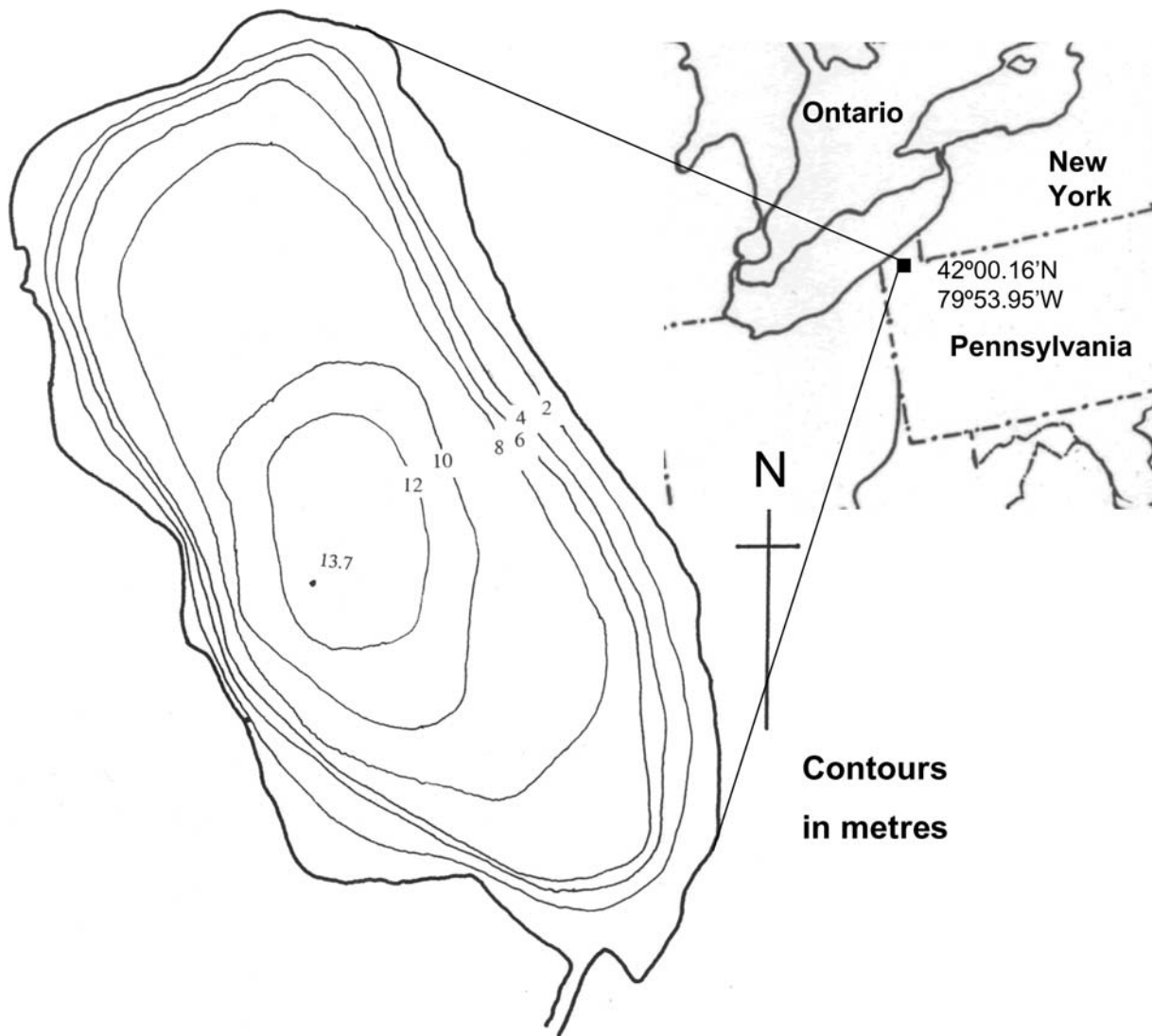
Ecologists have been successful in identifying factors controlling the structure of aquatic plant communities on a regional scale. In most of these studies, the community composition of a number of geographically proximate lakes has been found to be strongly affected by such water-quality characteristics as conductivity, alkalinity, pH, etc. (Table 1). While these studies have contributed much to our understanding of the environmental tolerances of individual species, they have not addressed the heterogeneous nature of communities within individual lakes. In fact, it has been argued that while plant communities are constrained by water chemistry on a regional scale, water chemistry cannot explain the considerable within-lake spatial heterogeneity (Duarte and Kalff 1990; Duarte and Roff 1991). Lakes with complex morphometries may, of course, have variations in water chemistries among various isolated bays and near major inflows, but for the most part, within-lake water chemistry varies little. Since it has been demonstrated that aquatic plants derive most of their nutrient requirements from the sediment (Nichols and Keeney 1976; Carignan and Kalff 1980; Barko 1982) and that plant biomass readily responds to sediment nutrient enrichment (Anderson and Kalff 1986; Duarte and Kalff 1988), an analysis of sediment chemistry, rather than water chemistry, may be a more fruitful approach in attempting to explain within-lake variations in plant community structure.

The variability of sediment quality in the littoral zone in lakes has been under-appreciated. In the littoral sediments (<3 m depth) of Canadohta Lake, Pennsylvania, Ostrofsky

and McGee (1991 and unpublished data) found that the coefficients of variation of the concentrations of phosphorus (P) species ranged from 63% for organic P to 133% for NH₄Cl-extractable P. Oehm et al. (1997) found that the coefficient of variation of organic matter (loss on ignition (LOI)) was 80% and that of acid-volatile sulfides 67%. In apparently uniform weed beds in Lake Memphremagog (Quebec/Vermont), Anderson and Kalff (1986) found coefficients of variation of 41%–78% for nitrogen (N), 7%–60% for P, 13%–55% for potassium (K), and 21%–100% for organic content. Even in profundal sediments, adjacent sediment samples show spatial variation that cannot be explained by analytical error or microscale variation. Downing and Rath (1988) found between-sample variance to be 2–320 times greater than within-sample variance for a variety of sediment characteristics. The causes of littoral and profundal sediment patchiness are unknown, but might include sediment shadows in the lee of macrophytes or outcrops, ice scour and rafting, groundwater-discharge discontinuities, activities of benthic invertebrates, and currents (Downing and Rath 1988).

Studies in Lake Memphremagog and adjacent Quebec lakes (Anderson and Kalff 1988) and in Lake Geneva (Lehmann et al. 1997) examined the hypothesis that aquatic plants had specific optima with respect to sediment characteristics (e.g., sediment N, P, K, grain size, water content, depth, % C, etc.). However, neither simple regressions between sediment characteristics and biomass nor analyses of variance among the sediment characteristics of monospecific stands of plants provided supporting evidence. From the results of both studies it was concluded that sediment characteristics could not explain the patchy distribution of species within a lake. One limitation of both of the above studies is that correlation and analyses of variance assume that plant biomass and composition show unidirectional changes along resource gradients,

Fig. 1. Location of Lake Pleasant, Pennsylvania, USA ($42^{\circ} 00.16'N$, $79^{\circ} 53.95'W$), and a bathymetric map showing the simplicity of the basin.



when in fact, species response is more likely to be unimodal. This curvilinear response to both simple and potentially complex combinations of site characteristics clouds the application and interpretation of simple statistical designs. Investigators seeking relationships between plant communities of many lakes and water chemistry have made frequent use of multivariate tools rather than simple correlations (see references in Table 1). Application of similar tools to within-lake data may help determine the response of macrophyte community structure to multiple nonlinear environmental gradients.

Here we test two hypotheses in a small lake of simple morphometry and uniform water chemistry. The first hypothesis is that the sediment environment is patchy, and nutrients vary in ways that are not explained by depth gradients. The second is that the heterogeneous environment that results from the interplay between sediment-quality patchiness and a more uniform depth gradient can explain a significant fraction of the observed spatial heterogeneity of aquatic plant communities on a local, within-lake scale.

Materials and methods

Description of study area

Lake Pleasant (Erie County, Pennsylvania, $42^{\circ}00.16'N$, $79^{\circ}53.95'W$) is a small (24 ha, 13.7 m z_{max}) meso-eutrophic ($35 \mu\text{g}\cdot\text{L}^{-1}$ total P in spring), moderately hard water ($100 \text{ mg}\cdot\text{L}^{-1}$ alkalinity as CaCO_3), dimictic lake of simple morphometry consisting of a single symmetric basin (Fig. 1). Land use in the watershed (3.6 km^2) is currently mixed second-growth forest and light agriculture. The high total P is an apparent legacy of intense recreational activity in the early part of the last century that included a lakeside resort hotel, picnic and dance pavilions, steam-powered water ferries, a water slide, swimming beaches, etc. Current recreational impacts, however, are very low. Approximately two-thirds of the shoreline is protected by the Western Pennsylvania Conservancy, and the Pennsylvania Fish and Boat Commission has prohibited the use of motorized boats. Perhaps as a result, Lake Pleasant is the only natural lake in western Pennsylvania that has escaped both extensive lake-

shore development and invasion by Eurasian water milfoil (*Myriophyllum spicatum*).

The western, northern, and southern shorelines of Lake Pleasant have low relief and support a rich riparian community dominated by swamp loosestrife (*Decodon verticillatus*), pickerel weed (*Pontederia cordata*), and several species of sedges (*Scirpus* spp. and *Eleocharis* spp.), out to a depth of 0.66 m (0.04 m SE). From there to a depth of 1.52 m (0.10 m SE) the plant community is a mix of *Brasenia schreberi*, *Nymphaea odorata*, and *Nuphar variegatum*. We found very little submersed plant biomass in this zone dominated by floating-leaved plants, presumably because of shading. Light measurements indicated that under these floating-leaved canopies only about 6% of surface light penetrates to a depth of 1 m. This provides a light environment equivalent to that at a depth of about 4.5 m in the absence of a canopy. A similar shading effect on submergent plants by a floating-leaved canopy has been noted in other studies (e.g., Ray et al. 2001). The eastern shore of the lake has greater topographic relief and is bounded by a road, both of which minimize the littoral transitional habitat. Only infrequently are well-developed stands of emergent or floating-leaved plants found here.

Data collection and analysis

Sampling took place in midsummer 2001. We established sampling transects at right angles to the shore at 50-m intervals. A calibrated line was swum out into the lake and anchored. Transects were sampled at 5-m intervals along this line from shore to a depth where plants were no longer present, using a metal frame with an inner sampling quadrat of 0.35 m². We avoided areas with extensive floating-leaved canopies. All "above-ground" plant material within the quadrat was picked by hand, and a sediment sample was taken from the center of the quadrat with a 3 cm diameter corer. Depth was determined using a measuring tape fixed to the quadrat frame. Collected plants were separated by species using Fassett (1980), Hellquist and Crow (1980, 1982, 1984), and Crow and Hellquist (1982, 1983). Dry biomass was determined following oven-drying (60 °C) to constant weight.

Cored sediments were held under refrigeration (less than 5 days) until analyzed. Available N and P were extracted from fresh sediment using 1 mol·L⁻¹ LiCl and 24 h of end-to-end agitation on a shaker table (Boatman and Murray 1982). Samples were centrifuged and the supernatant was split. One aliquot was used for K analysis using a Perkin-Elmer atomic absorption spectrophotometer and the remainder was analyzed for NH₃-N using the phenate method (American Public Health Association 1995). Available P was extracted using 0.1 mol·L⁻¹ NaOH – 0.1 mol·L⁻¹ NaCl (Anderson and Kalff 1986) and analyzed using the molybdenum blue technique (Strickland and Parsons 1968).

Following the determination of available N, P, and K, the remaining sediment was oven-dried (60 °C) and wet/dry conversions were calculated so that the above parameters could be expressed as mass per gram sediment dry weight. Total N and total carbon (C) were determined on dry sediment with a Perkin-Elmer CHN elemental analyzer. A known weight of dried sediment (0.01–0.04 g) was digested with nitric and perchloric acids, and the resulting solution diluted to

Table 2. Summary of water depths and chemical characteristics of sediments of sampled quadrats from Lake Pleasant, Pennsylvania.

Variable	Mean	Range
Depth (cm)	198	35–438
Available N (mg·g ⁻¹)	0.055	0.001–0.361
Total N (%)	0.86	nd–3.09
Available K (mg·g ⁻¹)	0.326	0.026–1.097
Total K (mg·g ⁻¹)	3.43	0.52–8.09
Available P (µg·g ⁻¹)	57.1	1.2–263.3
Total P (µg·g ⁻¹)	567.9	107.1–1309.9
Organic C (%)	13.35	1.39–37.65

Note: nd, not detectable.

100 mL with distilled water. Total K was determined on an aliquot with an atomic absorption spectrophotometer, and total P was analyzed on the remainder of the sample using the molybdenum blue technique (Strickland and Parsons 1968).

From these data we constructed two matrices: site × plant species and site × site characteristics. We eliminated those quadrats without plants present (the deepest along each transect) and those species with a relative frequency less than 5%. To identify frequently occurring groupings of species we performed cluster analysis on Bray–Curtis doubly standardized (Poole 1974) plant-biomass data. The double standardization gives each species a relative importance value at each site when all species and all sites have been given equal weight. The site attributes of emergent natural groupings were compared using analysis of variance. To identify environmental factors influencing community composition, we used canonical correspondence analysis (CCA; ter Braak and Smilauer 1998; CANOCO 4, Microcomputer Power, Ithaca, New York), using both the unstandardized plant-species matrix and the site-characteristic matrix. Tests for normality led us to natural-log transform available N, P, and K. The remaining variables (depth, % C, total N, total K, and total P) were approximately normally distributed. All parameters were then normalized to a mean of zero with unit variance. A Monte Carlo test using 199 permutations was included in the CCA to test significance of the canonical axes.

Results

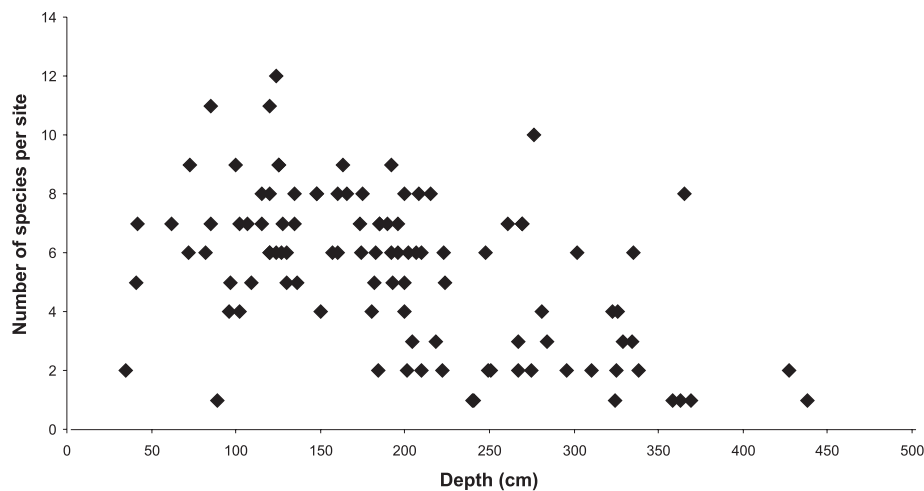
Overall we characterized the sediments and identified and quantified submersed aquatic plants from 103 quadrats along 18 transects. We provide a summary of the sediment characteristics of the quadrats (Table 2). Ranges of values overlapped those observed in similar studies (e.g., Lake Memphremagog; Anderson and Kalff 1986). Quadrats ranged from 35 to 438 cm in depth. Within this littoral zone, however, there was considerable variability in sediment characteristics. The most variable parameter measured was N, both available and total, with coefficients of variation of 104% and 78%, respectively. However, even the least variable parameter, P, had coefficients of variation of 67% and 36% for available P and total P, respectively. Most of the chemical characteristics were significantly correlated with each other (Table 3). The abundance of significant correlations is typical in a suite of lake-sediment characteristics

Table 3. Correlations among depths and chemical characteristics of sampled quadrats.

	% C	Total N	Total P	Total K	ln(available K) ^a	ln(available N) ^a	ln(available P) ^a
Depth	0.396	0.281	-0.051	-0.08	-0.077	-0.06	-0.123
% C	—	0.689	0.358	0.066	0.516	0.522	0.433
Total N		—	0.563	0.379	0.654	0.516	0.588
Total P			—	0.606	0.673	0.443	0.692
Total K				—	0.604	0.395	0.528
ln(available K) ^a					—	0.681	0.686
ln(available N) ^a						—	0.606

Note: At 100 df, critical $r = 0.200$.

^aAvailable K, N, and P were natural log transformed to stabilize variance.

Fig. 2. Number of taxa of submersed aquatic plants versus depth from 103 quadrats in Lake Pleasant, Pennsylvania.

(Williams et al. 1976; Ostrofsky 1987). Total C and total N were significantly correlated with depth ($p < 0.005$), but total P, total K, and available N, P, and K were not.

From the same 103 quadrats we also identified 17 species of submersed aquatic plants. The assemblage was typical of moderately hard-water lakes (Moyle 1945). Quadrats contained from 1 to 12 species (average richness = 5.4). Species richness was correlated with depth ($r = -0.56$, $p < 0.001$), although scatter in the data precluded the construction of a predictive relationship (Fig. 2). Six of the plant species (*Potamogeton amplifolius*, *Potamogeton pusillus*, *Ceratophyllum demersum*, *Megalodonta beckii*, *Heteranthera dubia*, and *Najas flexilis*) had relative frequencies greater than 50% (Table 4). Plant dry biomass in quadrats varied from 0.09 to 144.62 $\text{g}\cdot\text{m}^{-2}$ (average = 33.7 $\text{g}\cdot\text{m}^{-2}$). Maximum biomass was found between depths of 0.75 and 1.5 m (Fig. 3). *Potamogeton robbinsii*, *Potamogeton* sp., *Ceratophyllum echinatum*, and *Ranunculus longirostris* were eliminated from further analysis on the basis of low relative frequencies. The final plant-species matrix contained 99 sites and 13 species.

At a similarity of 62.5%, cluster analysis identified seven distinct groups of sites based on relative-importance values (Bray-Curtis doubly standardized) of species identified from those sites. Five of these groups were quite homogeneous; the remaining two were more mixed. Eight sites (group D; Fig. 4) were dominated by *Chara* sp. (relative importance > 65%), 17 sites (group E) by *P. amplifolius* (relative importance > 72%), 10 sites (group B) by *N. flexilis* (29% < relative importance < 99%), 6 sites (group C') by *Myriophyllum*

Table 4. Submersed aquatic plants identified from Lake Pleasant, Pennsylvania.

	Frequency ^a	Max. biomass ($\text{g}\cdot\text{m}^{-2}$)	Avg. biomass ($\text{g}\cdot\text{m}^{-2}$)
<i>Ceratophyllum demersum</i>	67	26.2	3.26
<i>Megalodonta beckii</i> ^b	62	139.0	7.82
<i>Potamogeton pusillus</i>	60	75.5	4.60
<i>Potamogeton amplifolius</i>	60	79.6	23.37
<i>Heteranthera dubia</i>	56	17.1	3.74
<i>Najas flexilis</i>	56	12.5	1.69
<i>Vallisneria americana</i>	46	13.2	1.90
<i>Potamogeton richardsonii</i> ^b	43	27.5	4.16
<i>Chara</i> sp.	39	70.4	8.65
<i>Myriophyllum exalbescens</i> ^b	19	17.2	4.27
<i>Potamogeton crispus</i>	14	3.6	0.64
<i>Elodea canadensis</i>	14	26.2	3.22
<i>Potamogeton zosteriformis</i> ^b	12	3.8	1.48
<i>Ranunculus longirostris</i> ^b	3	1.0	0.44
<i>Potamogeton</i> sp.	3	1.1	0.46
<i>Potamogeton robbinsii</i>	2	22.4	13.14
<i>Ceratophyllum echinatum</i>	1	0.04	0.04

^aThe number of quadrats, out of 103 surveyed, in which a species occurred. Maximum (Max.) and average (Avg.) biomass are given in oven-dry weight.

^bPennsylvania Species of Special Concern (Bissel et al. 1989).

Fig. 3. Dry-weight biomass of submersed aquatic plants versus depth from 103 quadrats in Lake Pleasant, Pennsylvania.

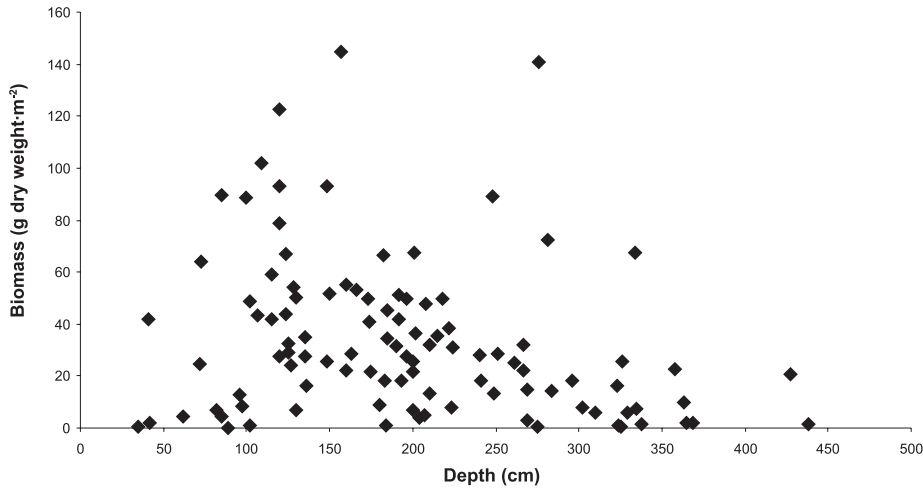
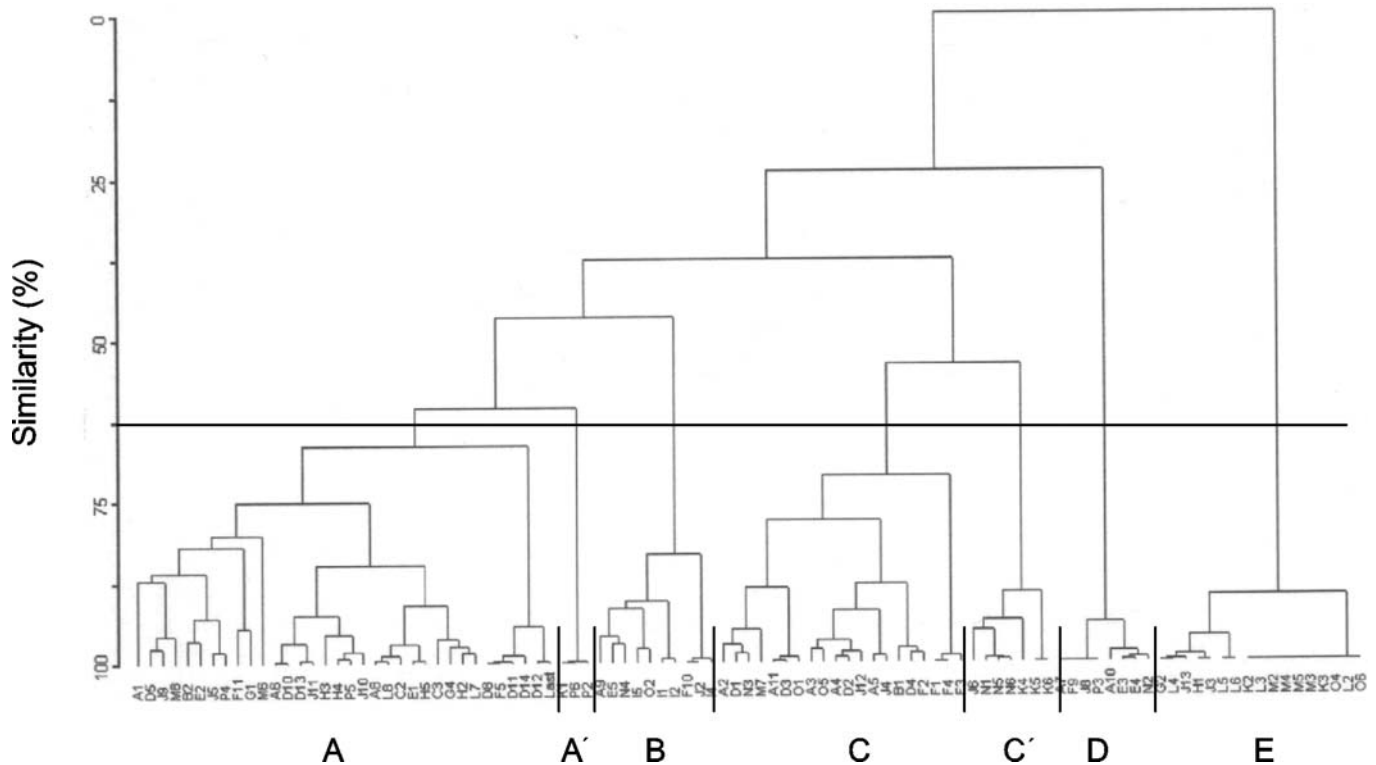


Fig. 4. Bray–Curtis similarity in the species composition of 99 quadrats in Lake Pleasant, Pennsylvania. Biomass values for the 13 most frequent species were doubly standardized. The horizontal line indicates 62.5% similarity and separates quadrats into seven groupings.



exalbescens (relative importance > 51%), and 3 sites (group A') by *C. demersum* (relative importance > 90%). The remaining two groups (A and C) were more heterogeneous: sites in group C were dominated by one to three species of *Potamogeton* (other than *amplifolius*) and those in group A by *Vallisneria americana* or *H. dubia*.

Analyses of variance among these seven groups showed that sites from groups E, C', and A' had significantly ($p < 0.0001$) higher levels of organic matter than those from groups A, B, C, and D, which did not differ from each other. Sites from groups C' and A' were significantly ($p = 0.0018$) deeper than those from groups A, B, C, and D, and as a con-

sequence also had lower average plant biomass. Groups A' and C' had significantly ($p = 0.0008$) more total N than groups A, B, C, and D. Groups C, E, C' and A' had significantly ($p = 0.0110$) higher available N than did groups A and B. Groups A', E, and C' had significantly ($p = 0.0002$) higher available P than groups D and A. There were no significant differences among the groups with respect to total P, total K, or available K. Groups D, E and A', for which single-species relative importance exceeded 65%, had significantly lower species richness than the other groups.

We used CCA to identify important environmental gradients affecting the distribution of macrophytes. In the first ap-

Fig. 5. Canonical correspondence analysis (CCA) biplot of (a) environmental factors versus sites and (b) environmental factors versus species. The species matrix is composed of percent stand composition by weight. Environmental factors are normalized to zero mean and unit variance. TC, total C; TK, total K; TN, total N; TP, total P; availK, available K; availN, available N; availP, available P; Cd, *Ceratophyllum demersum*; Ch, *Chara* sp.; Ec, *Elodea canadensis*; Hd, *Heteranthera dubia*; Mb, *Megalodonta beckii*; Me, *Myriophyllum exalbescentis*; Nf, *Najas flexilis*; Pa, Pc, Pp, Pr, and Pz, *Potamogeton amplifolius*, *P. crispus*, *P. pusillus*, *P. richardsonii*, and *P. zosteriformis*, respectively; Va, *Vallisneria americana*.

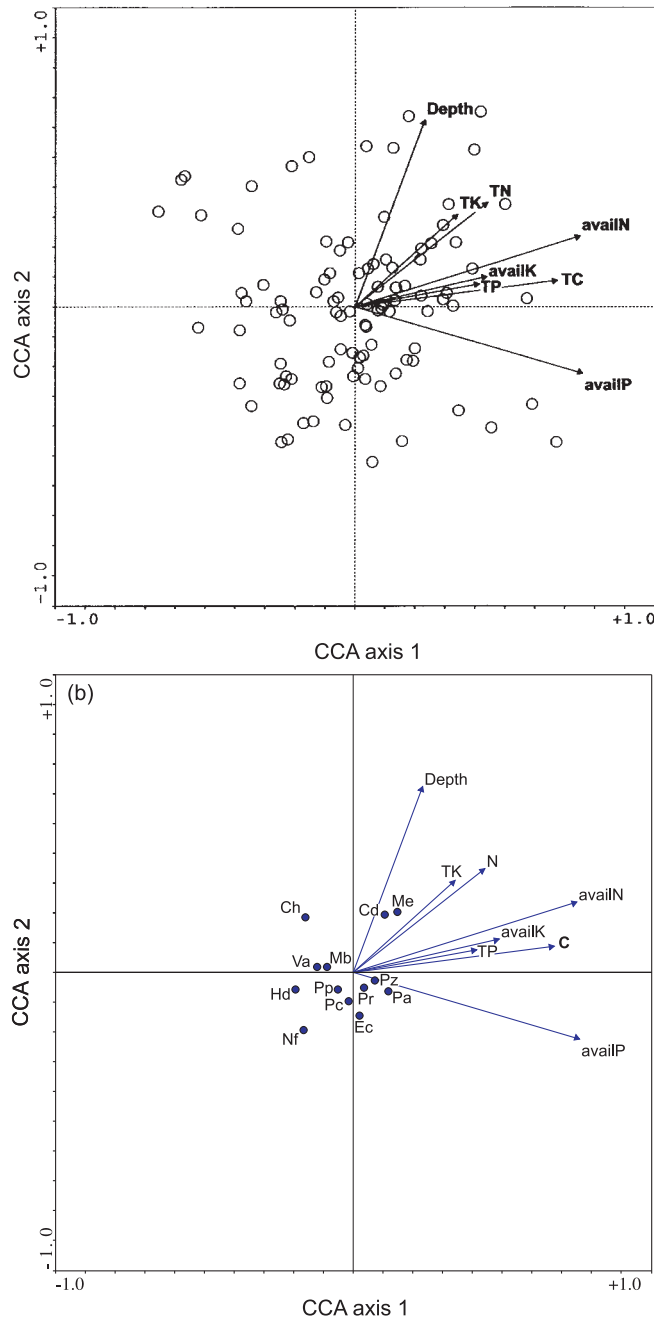


Table 5. Contribution of site characteristics to explaining the variance in species composition using stepwise forward selection.

Environmental variable	<i>p</i>	Variance explained	Cumulative variance explained
Available N	0.0100	0.16	0.16
Depth	0.0050	0.11	0.27
Available P	0.0050	0.11	0.38
Total N	0.0550	0.07	0.45
Total K	0.1300	0.06	0.51
Organic matter	0.2100	0.05	0.56
Total P	0.2900	0.04	0.60
Available K	0.9100	0.02	0.63

plication of CCA we used plant biomass in the site \times species matrix. The first two CCA axes explained 69.4% of the variance in the species–environment relationship. The most important environmental factors as revealed by significant correlations with CCA axis 1 were available P ($p < 0.01$) and depth ($p < 0.01$). The most important variables correlated with CCA axis 2 were available N ($p < 0.001$) and organic content ($p < 0.001$). The variance-inflation factors of all variables were low (<4), suggesting that the high correlations among site characteristics noted above did not confound the interpretation of CCA (ter Braak and Smilauer 1998). We did, however, suspect that since depth influences community biomass quite independently of community composition, using biomass in the plant \times site matrix might have given undue importance to depth in the CCA analysis. Consequently, we repeated CCA using each species' relative contribution to total site biomass rather than to biomass itself. Here the first two CCA axes explained 63.6% of the variance in the species–environment relationship ($p = 0.0100$). Sampling sites showed good separation on both CCA axes 1 and 2 (Fig. 5a). All measured site characteristics were significantly correlated with CCA axis 1 ($p < 0.001$ for organic matter, available N, and available P; $p < 0.01$ for total N and available K; $p < 0.05$ for total N and total K) except depth. Depth was, however, significantly correlated with CCA axis 2 ($p < 0.001$), as was total N ($p < 0.05$). We used stepwise forward selection to determine the relative contribution of each variable to the total species variance explained (Table 5). The centers of species distributions along these environmental gradients are plotted (Fig. 5b). *Ceratophyllum demersum* and *M. exalbescentis* lie farthest along both the depth and the available-N axes, while *N. flexilis* and *H. dubia* lie in the opposite directions. Similarly, *P. amplifolius* and *Chara* sp. are at opposite ends of the available-P axis.

Discussion

There is a rich literature describing the effects of water chemistry on the composition of aquatic plant communities among lakes, and much of the variation seen in aquatic plant communities between lakes has been explained by water-quality characteristics like alkalinity, pH, conductivity, etc. However, there has been no corresponding effort to determine the cause of heterogeneous distribution of plant species within a single lake of uniform water chemistry.

Examination of biotic interactions among species has produced no explanation for patchy distributions. Chambers and Prepas (1990) did a series of removal experiments in in-situ weed beds in Long Lake, Alberta, and asked whether plants grew better in the absence of neighbors than otherwise. They concluded that interspecific competition was slight or played only a minor role in structuring plant communities. However, they did find that dominant plant biomass was significantly correlated with abiotic factors (distance from shore, % C, exchangeable P, depth). These conclusions are supported by other similar studies. McCreary et al. (1983) used deWitt diagrams to show that interspecific effects were less important than environmental factors, and Titus and Stephens (1983) used removal experiments but were unable to show significant differences in biomass or winter bud production between plants with and without neighbors.

Investigations into the relationship between sediment characteristics and plant community structure have generally led to the conclusion that sediment characteristics could not explain community structure (Anderson and Kalff 1988; Lehmann et al. 1997), in part because of the lack of correlations between species distribution and sediment nutrient concentrations, and in part because of the prevailing paradigm that nutrients, organic matter content, particle size, light intensity, and depth vary in concert across the littoral zone. However, a few studies (e.g., Anderson and Kalff 1986; Duarte and Kalff 1988) have demonstrated that aquatic plant community biomass has responded to sediment nutrient enrichment, and the data we report here support the hypothesis that aquatic plant community structure also responds to variations in sediment nutrient concentrations and depth.

The littoral zone in Lake Pleasant extended to about 4 m in depth, with maximum plant biomass found between 0.75 and 1.5 m, likely being constrained by wave energy and available light. Within this littoral zone the ranges of all measured sediment characteristics spanned one or more orders of magnitude. Such broad ranges allow for considerable spatial discrimination of plants based on competitive interactions within particular niche optima. More significant, however, is the observation that while all nutrient concentrations were strongly intercorrelated, only C and total N were significantly correlated with depth. This result suggests that the littoral zone is better represented by a patchwork of relatively nutrient-rich and nutrient-poor sites distributed across all depths rather than a simple monotonic change with increasing depth. This increased complexity allows for a finer partitioning of the littoral zone based on both light (depth) and nutrient requirements.

Lake Pleasant has perhaps the richest submersed aquatic flora of the region, with large populations of species of special concern (Bissel et al. 1989). Here almost 64% of the variation in community structure could be explained by depth and sediment nutrient characteristics. Available N and available P were the most important of these characteristics. In the CCA biplot the distribution of the species' centroids indicates that while no species shows a preference for the extremes of any environmental gradient, *C. demersum* and *M. exalbescens* lie farthest along both the depth and the available-N axes, while *N. flexilis* and *H. dubia* lie in the opposite directions. These observations are supported by the

cluster analysis, where the site groupings dominated by the former two species (groups A' and C') are from significantly greater depths and significantly greater available-N concentrations than are sites dominated by the latter two species (groups B and A). Similarly, *P. amplifolius* and *Chara* sp. are at opposite ends of the available-P axis, and the cluster analysis showed significant differences with respect to available P between group D (*Chara* sp.-dominated) and group E (*P. amplifolius*-dominated).

Neither *C. demersum*, an unrooted macrophyte, nor *Chara* sp., a nonvascular macroalga, can use nutrients from sediments directly. We decided not to exclude them from our analysis, however. *Ceratophyllum demersum* was the most frequently encountered species at all sites – across all depths, but with highest relative importance in the deeper sites. While it does not draw upon sediment nutrients, one of our variables was depth, and our hypothesis predicted that plant community composition would be a function of the interplay between depth and sediment nutrients. *Ceratophyllum demersum*, then, is an example of a species for which depth is far more important than sediment nutrients. Our rationale for retaining *Chara* sp. in the analysis was based on our assumption that there must be some aspect of sediment quality that discouraged the presence of rooted plants that would otherwise competitively displace *Chara* sp. In fact, sites in group D (dominated by *Chara* sp.) had significantly less organic matter, less available N, and less available P.

In general, the CCA biplot suggests that sites that are deep with nutrient-rich sediments will be dominated by *C. demersum* and *M. exalbescens*, whereas deep sites with nutrient-poor sediments will be dominated by *Chara* sp., *V. americana* and *M. beckii*. A mix of *Potamogeton* species and *Elodea canadensis* will dominate shallow nutrient-rich sites. Shallow nutrient-poor sites will be dominated by *H. dubia* and *N. flexilis*. These projections are consistent with the site differences found with cluster analysis, and largely consistent with the speculations of Chambers and Kalff (1987) and Chambers (1987), who argue that canopy/erect species (e.g., *C. demersum*, *M. exalbescens*, *P. amplifolius*) are dominant where nutrients are abundant, and bottom-dwelling species (e.g., *H. dubia*, *N. flexilis*, *Chara* sp.) are dominant where sediments are infertile. The observation that depth and sediment nutrient concentrations are not significantly correlated suggests that at any particular depth, both nutrient-rich and nutrient-poor patches will exist, supporting different communities of plants across a spatial scale determined by nutrient patch size.

Large-scale heterogeneity in the distribution of nutrients in profundal sediments and its causes are well known (Hilton et al. 1986). The causes of fine-scale heterogeneity are less well understood, even as such heterogeneity is becoming more widely appreciated. There have been, as yet, no studies to estimate resource patch size, although work in the profundal zone (Downing and Rath 1988) suggests that patches are small rather than large, on the order of metres. Littoral patches may be even smaller because they are influenced by such localized phenomena as minor topographical irregularities causing sediment shadows, ice action, upwelling groundwater, and activities of biota. Patchiness in nutrients across the littoral zone independent of depth can thus promote conditions favorable to a diverse assemblage of

submersed plant species. Given the biotic assemblages and environmental factors that submersed aquatic plants have been shown to influence (e.g., Jackson et al. 1994; Unmuth et al. 2000; Ray et al. 2001), their local spatial heterogeneity has the potential to influence ecosystem structure and function on a variety of scales within a lake. Knowledge of factors affecting macrophyte community structure from a combination of both past regional-scale multi-lake studies and smaller scale, within-lake studies can provide a valuable set of data for predicting and interpreting macrophyte influence on other lake biotic communities of economic or conservation concern. In the future a more intimate knowledge of the major factors affecting habitat heterogeneity at different scales will enable scientists and managers to better understand the temporal changes in species composition and richness in both disturbed and undisturbed aquatic systems.

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