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# Composition and spatial heterogeneity of submersed vegetation in a softwater lake in Wisconsin\*

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## Abstract

Big Muskellunge Lake, a softwater lake (pH 7.5–8.0, alkalinity 0.36 meq/L) in northern Wisconsin, harbors a diverse (25 species) submersed macrophyte vegetation. The present submersed flora combines species generally thought distinct in their ecological affinities, and is very similar to that reported in 1935. The only differences are the apparent loss of three previously infrequent *Potamogeton* species, and the addition to the flora of two infrequent *Potamogeton* species and the now abundant *Elodea canadensis*. Dramatic differences in composition and pattern of the vegetation occurred between sites of contrasting exposure and sediment type. Substantial compositional variation, at scales ranging from tens of centimeters to tens of meters, occurred along transects of contiguous quadrats at uniform depth and exposure. Analyses of species sequences along line transects detected significant segregation of species that is most plausibly explained by biotic factors such as colonization, clonal growth, and competition. Heterogeneity at small scales of a few meters or less is common in Big Muskellunge Lake. Such pattern has been neglected in macrophyte ecology, in spite of its significance for neighbor relationships which may critically influence growth and reproduction of aquatic plants.

## Introduction

Compositional change and spatial heterogeneity are fundamental and long-recognized features of plant communities (McIntosh, 1980) that have nevertheless received only limited attention in submersed aquatic plant communities. Most studies of compositional change in submersed macrophyte

communities have stressed the effects of environmental changes such as eutrophication and siltation (reviewed by Davis & Brinson, 1980) or introductions of exotic species (e.g. Nichols & Mori, 1971). However, successional sequences in relatively undisturbed lakes (Macan, 1977) and lakes acidified by precipitation (Grahn, 1977; Hendrey & Vertucci, 1980) have been reported rarely. Heterogeneity in macrophyte community structure has been studied from the standpoint of inter-lake compositional differences (e.g. Swindale & Curtis, 1957) and depth zonation (reviewed by Hutchinson, 1975; Spence, 1982). Intra-lake heterogeneity among sites of comparable depth and exposure has been considered (Swindale & Curtis, 1957; Titus, 1983), but has not been systematically studied. Such processes as competition, colonization, and clonal growth

\* For nomenclature, see Table I.

\*\* Order of authorship determined by toss of a coin.

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should be reflected in neighbor relationships which can be detected only by studying plants at relatively small (i.e. fine-textured) scales. Titus & Stephens (1983) remark on the lack of evidence for inter-plant interactions in submersed plant communities; in spite of this, competition is often assumed to determine zonation of submersed plants (e.g. Hutchinson, 1975).

This study had two major objectives. The first was to determine the macrophyte community composition of a reference lake in the context of a larger investigation of lake acidification. Our second objective was to quantify intra-lake compositional heterogeneity at several different spatial scales.

Big Muskellunge Lake is ideally suited to our objectives for several reasons. It is located in northern Wisconsin, U.S.A., a region that presently receives moderate, but not extreme, acid inputs (Loucks, 1982). The near-neutral pH and low alkalinity of the lake indicate that it is susceptible to acidification, so our work provides a benchmark for studies of possible future acidification. This study also affords the opportunity to compare present and past vegetation (Wilson, 1935) in a lake subject to limited human impact. The vegetation of Big Muskellunge Lake is unusually diverse, and therefore well suited to studies of heterogeneity and pattern in community composition.

#### Site description and field methods

Big Muskellunge Lake is a 372-ha seepage lake with a maximum depth of 21 m. It is situated in several kettles in outwash and moraine of Wisconsin age in Vilas County, Wisconsin (T31N, R7E). Soils of the largely forested watershed are sandy and gravelly, while lake sediments range from highly organic to sandy and gravelly (Wilson, 1935). Big Muskellunge is a relatively softwater lake, with midsummer (1982) pH = 7.5–8.0 and alkalinity = 0.36 meq/l. (APHA, 1975).

We selected two sampling sites in the southern part of the lake for vegetation sampling in mid-July 1982. In West Bay, where depth contours are approximately semicircular, we located the intersection of selected depth contours and stratified random compass headings from a central point in the bay. The intersections determined the starting points for three 50-m belt transects oriented along

the contours at each of two depths (2.5 and 3.5 m). SCUBA divers recorded submersed macrophytes present in 250 contiguous 20 × 20 cm quadrats. We also used a stratified random system to locate three 25-m belt transects parallel to each of three depth contours (1.0, 2.5, and 3.5 m) at the second site north and east of Brannum's Point. Sites will be indicated WB and BP respectively. We tallied macrophytes in 500 contiguous 5 × 5 cm quadrats, smaller in accordance with the generally smaller plants at that site, for each of the nine transects. Quadrat sizes were large enough to contain many individuals of any species that occurred on any transect.

For each of the 15 transects, data were summarized as relative frequencies for the species (Curtis & McIntosh, 1950). Relative frequency is the number of observations of a particular species as a percentage of the total observations of all species along the transect. In this paper, absolute frequency refers to the number of observations of a particular species as a percentage of the number of quadrats on the transect.

One line transect at each site was subjectively placed in dense vegetation, which consisted of *Potamogeton robbinsii* and *Elodea canadensis* exclusively in West Bay, and a more diverse assemblage at the Brannum's Point site. We recorded the sequence of macrophyte stems which intercepted the vertical plane defined by the transect. Transect lengths were 28 m at WB and 15 m at BP.

Most sediments at the West Bay sampling depths were unconsolidated and organic, in some areas consisting largely of partially decomposed *Potamogeton robbinsii*. In contrast, most sediments at BP were sandy at the same depths and sandy gravel at 1.0 m.

#### Statistical methods

Ordinations of transects were calculated from relative frequencies of species using the Bray-Curtis method with Sørensen distances and the original endpoint selection criteria (Beals, 1984). Its ability to use this measure, which is not sensitive to common absences (Janson & Vegelius, 1981), made Bray-Curtis ordination very attractive for our data, which had a large number of common absences. We did not consider any comparison with other methods (See e.g. Noy-Meir & Whittaker, 1977).

Computations were performed using the BCORD program (Beals, 1984).

Bray-Curtis ordinations of species were calculated from presence-absence data for quadrats using Sørensen's distance. The regression method of selecting endpoints was used because it is not sensitive to outlying samples (Beals, 1984; cf. van der Maarel, 1969).

Analyses of patterns of occurrence of individual species along the transects used variance-spacing diagrams constructed by the random pairing method (Goodall, 1974). This method of pattern analysis detects patch size with exceptional accuracy, even when patch size is variable and patches are irregularly placed (Carpenter & Chaney, 1983). Patch size was taken to be the spacing of the first variance peak larger than the variance of a random independent pattern (Carpenter & Chaney, 1983). Computations were performed by the program of Carpenter & Chaney (1983).

Multispecies patterns were analyzed by first ordinating the quadrats of each transect in species space, and then calculating a pattern analysis as described above for the spatial sequence of first axis scores. Percentage of the total sum of squares accounted for by each Bray-Curtis axis was calculated to assess the performance of the ordinations. BCORD could not accommodate the large data sets, so computations were performed using a program written in SAS matrix language. The accuracy of this program was verified in a test against BCORD using a small data set. Pattern analyses of first axis scores were computed by the random pairing method (Goodall, 1974) using the program of Carpenter & Chaney (1983).

Segregation of pairs of species was examined using the method of Pielou (1962). This analysis applies to the pattern of species with respect to each other, rather than with respect to their spatial locations. The null hypothesis that the two species are randomly intermingled was tested.

## Results

### *Site and transect composition*

We encountered 23 macrophyte species within the 6020 quadrats sampled in Big Muskellunge Lake (Table 1). *Najas flexilis*, *Myriophyllum tenel-*

Table 1. Relative frequency for submersed macrophytes at Brannum's Point and West Bay, Big Muskellunge Lake.

Species	Code	Brannum's Point	West Bay Point
<i>Najas flexilis</i> (Willd.) Rostk. & Schmidt.	NAJ	20.3	7.4
<i>Myriophyllum tenellum</i> Bigel.	MTE	15.7	8.8
<i>Eleocharis acicularis</i> (L.) R. & S.	ELE	14.3	3.7
<i>Juncus pelocarpus</i> forma <i>submersus</i> Fassett	JUN	10.9	-
<i>Potamogeton pusillus</i> L.	PPU	6.8	10.5
<i>Isoetes macrospora</i> Dur.	ISO	5.1	6.4
<i>Vallisneria americana</i> Michx.	VAL	5.0	7.5
<i>Elatine minima</i> (Nutt.) Fisch. & Meyer	ELA	4.4	-
<i>P. robbinsii</i> Oakes	PRO	3.6	27.5
<i>Ranunculus reptans</i> L.	RAN	2.5	-
<i>Elodea canadensis</i> Michx.	ELO	2.5	13.5
<i>Chara</i> sp.	CHA	2.4	0.7
<i>P. gramineus</i> L.	PGR	2.2	2.4
<i>Nitella</i> sp.	NIT	1.2	0.5
<i>Lobelia dortmanna</i> L.	LOB	1.0	-
<i>P. alpinus</i> Balbis var. <i>tenuifolius</i> (Raf.) Ogden	PAL	0.9	0.2
<i>P. richardsonii</i> (Benn.) Rydb.	PRI	0.4	0.5
<i>P. praelongus</i> Wulf.	PPR	0.3	2.1
<i>M. alterniflorum</i> DC	MAL	0.3	2.5
<i>P. amplifolius</i> Tuckerm.	PAM	0.1	5.0
<i>Eriocaulon septangulare</i> With.	ERI	0.1	-
<i>Gratiola aurea</i> forma <i>pusilla</i> Fassett	GRA	<0.1	-
<i>Megalodonta beckii</i> (Torr.) Greene	MEG	-	0.8
Total		100.0	100.0

*lum*, *Eleocharis acicularis*, and *Juncus pelocarpus* forma *submersus* comprised 61.2% of the 3871 observations at BP, and were all substantially less important in WB. *Potamogeton robbinsii*, *Elodea canadensis*, *Potamogeton pusillus*, and *M. tenellum* totaled 60.3% of the 2272 observations in WB.

Sørensen's coefficient of similarity (see Mueller-Dombois & Ellenberg, 1974; hereafter simply 'similarity coefficient') based on relative frequencies for the two sites is 0.48. This reflects the floristic similarity, but also the tendency of most species with high relative frequencies to be much better represented at one of the two sites.

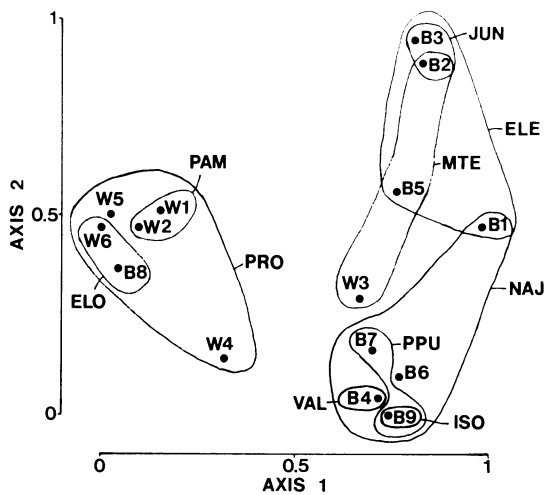


Fig. 1. Bray-Curtis ordination of 15 transects on first two axes. Transects W1–W3 and W4–W6 are at 2.5 and 3.5 m, respectively, in West Bay; transects B1–B3, B4–B6, and B7–B9 are at 1.0, 2.5, and 3.5 m, respectively, at Brannum's Point. Envelopes enclose transects in which relative frequency exceeded 20% for species shown. Species codes as in Table 1.

The polar ordination of all 15 transects (Fig. 1), based on relative frequency data presented in Appendix 1, further illustrates the compositional dichotomy between the two sites. Five of the six WB transects are clustered toward the left end of the first axis, and eight of the nine BP transects appear toward the right end of the first axis. The poles on the first axis are separated by a Sørensen's distance (hereafter simply 'distance') of 0.98.

Considerable compositional variation not strictly due to site differences is also evident in Figure 1. The poles of the second axis are at the same site yet have little in common, as reflected in their distance of 0.95. Furthermore, in no case are all three transects sampled at the same site and depth tightly clustered in the ordination, although two of the three are always close neighbors. The clustered pair always had a similarity  $> 0.63$ , while each member of the pair was at least 0.49, and as much as 0.92 units, distant from the third transect. An additional indication of variation within the five site/depth combinations is that in all cases, each of the three most frequent species shows highly significant non-homogeneous distributions ( $\chi^2$  test;  $p < 0.01$ ) among the three transects.

The envelopes indicating the transects in which species attained a relative frequency of at least 20%

(Fig. 1) elucidate the compositional basis of the ordination pattern, and permit a rough categorization of transects. Transects on the left side of the first axis were dominated by *P. robbinsii*, *E. canadensis*, and *P. amplifolius*, while *N. flexilis*, *P. pusillus*, *V. americana*, and *Isoetes macrospora* were most frequent in transects with high values on the first axis but low values on the second. A third cluster of transects occurs in the upper right portion of the ordination, with important species being *E. acicularis*, *M. tenellum*, and *J. pelocarpus* forma *submersus*. There is no clearcut boundary between the two transect clusters on the right, either on the basis of position in the ordination or location of relative frequency isolines.

### Species relationships

The ordination of species based on their relative frequencies in the 15 transects explained 40% of the total sum of squares in the 345-cell data matrix (Fig. 2). *Isoetes macrospora* and *Juncus pelocarpus* forma *submersus* are the poles of the first axis with a distance of 0.98, while *Eleocharis acicularis* and *Potamogeton amplifolius* are the second axis poles with a distance near 1.0, reflecting the presence of several contrasting species distribution patterns.

Five clusters are outlined (Fig. 2), four of which correspond to interpretable distribution patterns. Species in group 1 (*Potamogeton amplifolius*, *P. robbinsii*, *Elodea canadensis*, and *P. praelongus*)

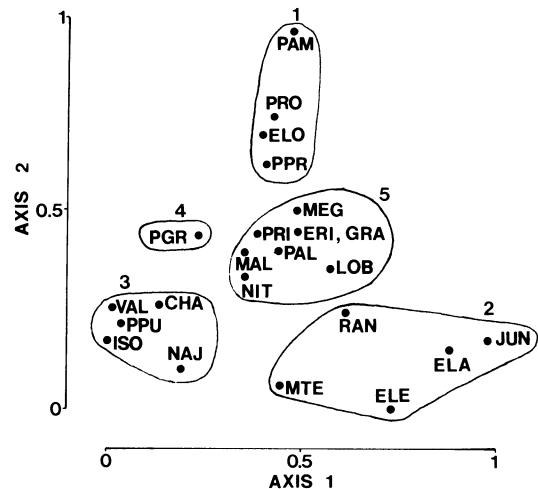


Fig. 2. Bray-Curtis ordination of 23 submersed macrophyte species on the first two axes. Species codes as in Table 1.

are relatively robust, flexuous-stemmed plants most common in WB transects and poorly developed at BP. Species in group 2 (*Juncus pelocarpus* forma *submersus*, *Elatine minima*, *Eleocharis acicularis*, *Ranunculus reptans*, and *Myriophyllum tenellum*) are short-statured plants well represented at BP, generally at the shallower depths, and absent or poorly represented in WB. Group 3 (*Isoetes macrospora*, *Potamogeton pusillus*, *Vallisneria americana*, *Chara*, and *Najas flexilis*) is morphologically diverse, but consists largely of species of intermediate stature with highest relative frequencies at 2.5 or 3.5 m at BP. In most cases these species also have moderately high relative frequencies in WB. They are relatively widespread, each occurring in at least 10 of the 15 transects (for all species, median number of transects of occurrence is only 6). The only other species which matches this broad occurrence among our transects is *Potamogeton gramineus*, which alone forms group 4 left of the center of the ordination.

The final cluster, group 5 in the center of the ordination, includes eight species with the lowest mean relative frequencies for the 15 transects. They exhibit diverse, generally sporadic, distributions which are difficult to interpret because of the limited number of occurrences for each species. Endpoint selection by regression dictates a limited influence for these relatively rare species in shaping the ordination.

#### Compositional variation within transects

Compositional variation within each transect fit one of three general types: (1) gradual compositional change along the transect; (2) abrupt shifts between common and rare species; and (3) abrupt shifts among common species. An example of each type is presented here.

Gradual compositional change occurred along transect W3 (2.5 m, WB, Fig. 3). Six of the seven species with absolute frequency  $> 10\%$  for the entire transect showed distinct peaks along the first axis: *Najas flexilis* and *Potamogeton pusillus* peaked at low axis scores, *Eleocharis acicularis* and *Vallisneria americana* peaked near the center of the axis, and *Myriophyllum tenellum* and *Isoetes macrospora* dominated at high axis scores (Fig. 3A). Axis score tended to increase with distance along the transect, indicating monotonic shift in vegeta-

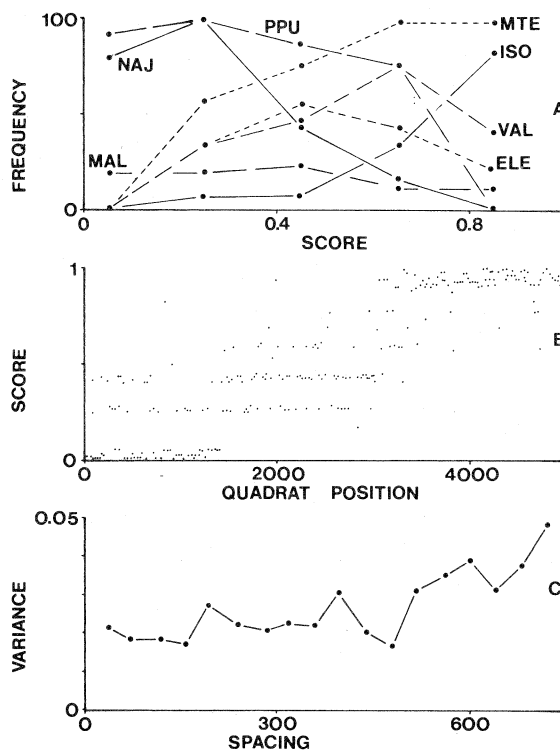


Fig. 3. Ordination and pattern analysis of transect W3 (West Bay, 2.5 m).

A: absolute frequency versus first axis score for species with overall absolute frequency  $> 10\%$ . The coordinate of each point on the abscissa is the center of the ordination axis interval that contains the quadrats from which frequencies were calculated. Ordination axis intervals did not overlap. Frequency values for each interval are based on 28 or more quadrats. The axis explains 82% of the total sum of squares. Species codes as in Table 1.

B: ordination score versus quadrat position along transect (cm); C: variance (pooled from eight independent analyses) versus spacing (cm).

tion along the transect (Fig. 3B). Random pairing analysis showed that variance among axis scores tended to increase with spacing (Fig. 3C). The grain of pattern at this site is larger than the transect (50 m).

Abrupt compositional change involving common (absolute frequency  $> 10\%$  for the transect) and rare (absolute frequency  $< 10\%$  for the transect) species occurred on transect W5 (3.5 m, WB; Fig. 4). *Elodea canadensis* and *Potamogeton Robbinsii* dominated quadrats with low axis scores, which tended to occur on the right of the transect (Fig. 4A). Rare species, which tended to occur with

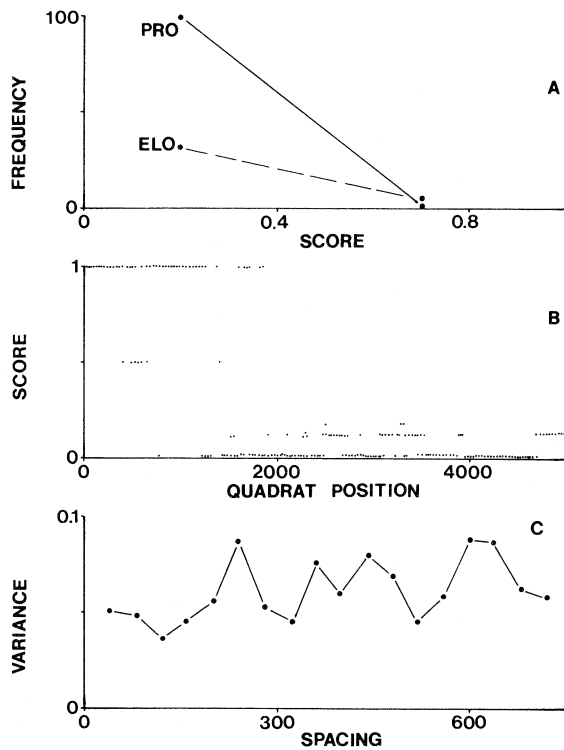


Fig. 4. Ordination and pattern analysis of transect W5 (West Bay, 3.5 m).

A: absolute frequency versus first axis score for species with overall absolute frequency  $> 10\%$ . Smoothing was done as for Figure 4A, except that frequency values for each interval were based on 70 or more quadrats. The axis explains 56% of the total sum of squares. Species codes as in Table 1. B: ordination score versus quadrat position along transect (cm). C: variance (pooled from eight independent analyses) versus spacing (cm).

low frequencies on the left of the transect, included *Potamogeton amplifolius*, *P. pusillus*, and *P. praelongus*. A sharp transition between these two assemblages occurred between 1 500 and 2 000 cm (Fig. 4B). Random pairing analysis of axis scores indicated a pattern scale of about 240 cm, which reflects patches of rare species (Fig. 4C). The pattern analysis did not examine scales larger than 800 cm and therefore was not affected by the large-scale (ca 2 000 cm) transition between common and rare species.

Abrupt compositional change on a much smaller scale, and involving pairs of common species (absolute frequency  $> 10\%$  for the transect) occurred on transect B1 (1.0 m BP; Fig. 5). A gradual transition between two species pairs occurred along the ordination axis, with *Eleocharis acicularis* and *Najas*

*flexilis* dominant at low scores, and *Juncus pelocarpus* forma *submersus* and *Ranunculus reptans* dominant at high scores (Fig. 5A). However, scores of 0.5, which indicate a 4-species mixture, occur throughout the transect (Fig. 5B). Brief, abrupt shifts to scores near 0 or 1, indicating dominance by one or the other species pair, were scattered along the transect. Random pairing analysis of axis scores indicated that the full cycle length of compositional change was about 120 cm (Fig. 5C).

#### Patterns of individual species

Pooled variance-spacing curves based on eight independent random pairing analyses were calculated for the species using each transect on which a species' absolute frequency exceeded 10%. The po-

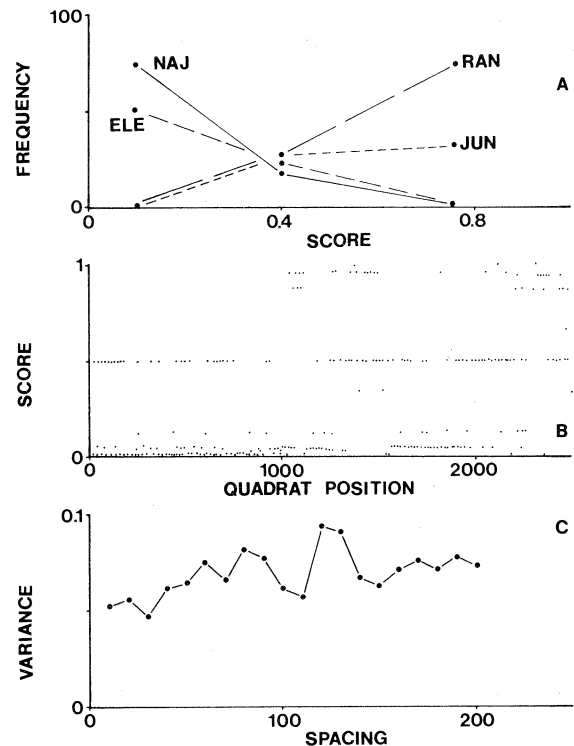


Fig. 5. Ordination and pattern analysis of transect B1 (Brannum's Point, 1.0 m). A: absolute frequency versus first axis score for species with overall absolute frequency  $> 10\%$ . Smoothing was done as for Figure 4A, except that frequency values for each interval were based on 66 or more quadrats. The axis explains 69% of the total sum of squares. Species codes as in Table 1. B: ordination score versus quadrat position along transect (cm). C: variance (pooled from eight independent analyses) versus spacing (cm).

Table 2. Scale of pattern (cm) for 14 species determined by random pairing analysis of transects for which the species had absolute frequency > 10%. Multiple entries occur where more than one transect met this criterion.

Species	Brannum's Point			West Bay	
	1.0 m	2.5 m	3.5 m	2.5 m	3.5 m
<i>Elatine minima</i>	80	-	-	-	-
	>200				
<i>Eleocharis acicularis</i>	50	80	-	600	-
	70				
	>200				
<i>Elodea canadensis</i>	-	-	80	-	440
					440
					480
<i>Isoetes macrospora</i>	-	-	160	>800	320
<i>Juncus pelocarpus</i>	100	-	-	-	-
f. <i>submersus</i>	150				
	>200				
<i>Myriophyllum alterniflorum</i>	-	-	-	80	-
<i>Myriophyllum tenellum</i>	40	180	160	>800	-
<i>Najas flexilis</i>	70	10	120	>800	>800
		10	120		
		20			
<i>Potamogeton amplifolius</i>	-	-	-	40	-
				40	
<i>Potamogeton praelongus</i>	-	-	-	-	80
<i>Potamogeton pusillus</i>	-	-	>800	>800	240
			100		440
<i>Potamogeton robbinsii</i>	-	-	200	120	>800
				160	>800
					>800
<i>Ranunculus reptans</i>	>200	-	-	-	-
<i>Vallisneria americana</i>	-	30	-	120	80
					240

sitions of the first peaks that exceeded the variance of a random independent pattern are presented as a measure of patch size (Carpenter & Chaney, 1983). Patch size ranged from 10 cm to more than 800 cm (Table 2). Consistent differences in patch size between sites were more apparent than differences among species or differences among depths. For example, all species analyzed at 2.5 m at both sites (*Eleocharis acicularis*, *Myriophyllum tenellum*, *Najas flexilis*, and *Vallisneria americana*) had smaller patch sizes at BP than at WB. Smaller patch sizes at BP also occurred for all species analyzed at 3.5 m at both sites (*Elodea canadensis*, *Isoetes macrospora*, *Najas flexilis*, *Potamogeton pusillus*, and *P. robbinsii*).

*Najas flexilis* was the only species that was sufficiently abundant to be analyzed at all depths at each

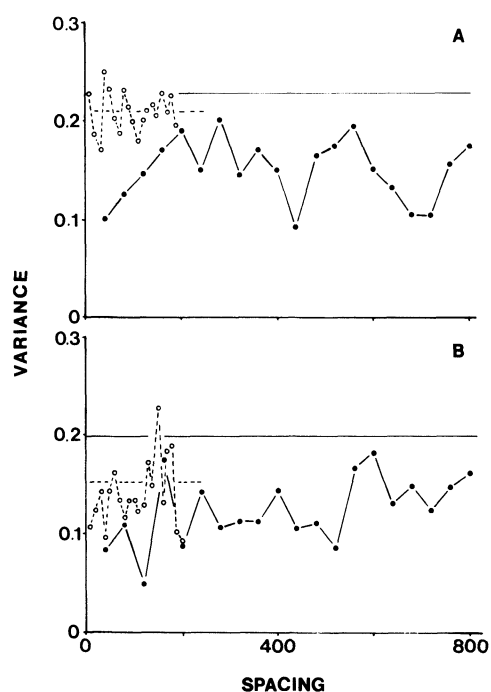


Fig. 6. Variance versus spacing (cm) for *Najas flexilis* at Brannum's Point (dashed lines, open circles) and West Bay (solid lines, closed circles). Each curve is the mean of eight independent analyses.

Horizontal line associated with each variance-spacing curve denotes the expected variance of a random, independent pattern. A: 2.5 m depth (transects B6 and W3). B: 3.5 m depth (transects B7 and W4).

site. Variance-spacing graphs show that *N. flexilis* at WB had a lower variance than a random, independent pattern at all spacings examined (Fig. 6). In contrast, *N. flexilis* at BP had several variance peaks at spacings < 200 cm that exceeded the variance of a random, independent pattern.

#### Species segregation

Pairwise tests for segregation using species' sequences along transects revealed strong segregation of all pairs examined. In WB Pielou's segregation statistic of *Elodea canadensis* and *Potamogeton robbinsii* was highly significant ( $p < 10^{-4}$ ; Table 3). Thus, the distributions of these co-dominant species are distinctly non-random with respect to each other. The variance peak for *E. canadensis* at 200 cm was very strong, suggesting rather consistent clumps at this scale and reinforcing our visual impression of loosely rooted clumps of *E. canadensis*

Table 3. Analysis of sequence data for *Elodea canadensis* and *Potamogeton robbinsii* in West Bay. Absolute frequencies, scale of pattern (cm) determined by random pairing, mean run length (number of stems), and Pielou's segregation statistic are tabulated.

Species	Fre- quency	Scale	Mean run length	Segregation statistic
<i>Elodea canadensis</i>	0.507	200	3.21	0.484
<i>Potamogeton robbinsii</i>	0.879	120	4.90	

scattered in a matrix of *P. robbinsii*.

Similar evidence for segregation was found in pairwise comparisons of four species at BP (Table 4). *Lobelia dortmanna*, which is distinctive among these plants for its lack of horizontal stems, tended to occur in groups of a few plants, reflected in relatively short run lengths and small scale of pattern. Even *L. dortmanna* was not randomly distributed with respect to the three rhizomatous or stoloniferous species. All three clonal species were non-randomly distributed with respect to each other. The strongest segregation occurred between *Myriophyllum tenellum* and *Ranunculus reptans*.

## Discussion

### Overall composition

Fassett (1930) was among the first to note the correlation between submersed macrophyte growth form and distribution among lakes varying in water chemistry. In a survey of 9 lakes in northern Wisconsin, Fassett found that small, rosulate species characterized the vegetation of softwater lakes, while larger, flexuous-stemmed species dominated more alkaline lakes. A similar dichotomy between elodeid and isoetid vegetation occurs in Swedish Lakes (Jensén, 1979; Jensén & van der Maarel, 1980). This appears to be an accepted pattern, although Wilson (1935), in reference to medium hardwater lakes of Vilas County, Wisconsin, asserted that one may frequently encounter luxuriant vegetation 'of the flexuous type' in sheltered bays, and a distinctly different vegetation of rosulate or softwater species on sandy sediments within the same lake. His data on Silver Lake and the Big Muskellunge Lake vegetation support this observa-

Table 4. Pairwise analysis of sequence data for 4 species at Brannum's Point. Above diagonal: Pielou's segregation statistics (all are significant,  $p < 10^{-4}$  except *Juncus* vs. *Lobelia*,  $p = 0.017$ ). Below diagonal: mean run lengths. Lower part of table presents absolute frequencies and scale of pattern (cm) determined by random pairing.

	<i>Juncus pelocarpus f. submersus</i>	<i>Lobelia dortmanna</i>	<i>Myrio- phyllum tenellum</i>	<i>Ranunculus reptans</i>
J.p.	-	0.139	0.531	0.449
L.d.	3.78 (J) 1.68 (L)	-	0.410	0.499
M.t.	3.43 (J) 5.65 (M)	2.15 (L) 7.98 (M)	-	0.743
R.r.	5.57 (J) 2.69 (R)	3.81 (L) 4.20 (R)	17.48 (M) 5.00 (R)	-
Frequen- cy	0.477	0.260	0.507	0.173
Scale	160	15	100	280

tion, as do some of the vegetation surveys of the English Lake District (Pearsall, 1920) and of New York (Muenscher, 1934). However, it appears that only a small minority of lakes harbors both rosulate and flexuous-stemmed species in abundance, perhaps because few lakes have the requisite water chemistry and diversity of sediment types.

A comparison of our intensive 1982 sampling with the extensive, lake-wide biomass sampling of Wilson (1935) reveals a rather remarkable floristic similarity between Big Muskellunge Lake in 1982 and in the early 1930s. Wilson recorded 25 submersed species, two more than we found in our transects. These included *Littorella americana* and *Nostoc* sp., both of which we collected elsewhere in the lake but not in our transects, and three pondweeds we did not see: *Potamogeton spirillus*, *P. epihydrus*, and *P. natans*. These pondweeds were not of major importance in Wilson's study, and may exist today in areas of the lake we did not visit. We report *Elodea canadensis*, *Potamogeton alpinus*, and *P. richardsonii*, none of which Wilson listed. The latter two are presently infrequent enough that they could have been missed in an extensive biomass sampling exercise such as Wilson's, and thus are not necessarily new additions to the lake. One vegetation change is obvious - *Elodea canadensis*, reported by Wilson for nearby Little John Lake but not for Big Muskellunge, was one of the two most frequent species in three of our 15

transects in 1982. It has plainly secured an important place in the lake.

Convincing evidence for vegetational or even floristic change, except in the case of *Elodea*, does not exist for Big Muskellunge Lake. This contrasts with most successional studies of submersed macrophyte communities, which have been demonstrated to change dramatically in the presence (see Davis & Brinson, 1980) or absence (e.g., Macan, 1977) of human impact, or with the advent of introduced species (e.g. Lind & Cottam, 1969). Spence (1964) documented photographically the generally limited expansion of floating-leaved and emergent vegetation in 50+ years in Scottish lochs, except in areas of active sedimentation. Low rates of sedimentation in Big Muskellunge, a seepage lake, may explain the stability of its submersed vegetation.

#### *Species relationships*

Several authors have classified submersed macrophytes either by growth form (e.g., Fassett, 1930; Hutchinson, 1975) or patterns of distribution among lakes (e.g., Iversen, 1929; Olsen, 1950; Seddon, 1972; Pip, 1979). We have determined species groups based on intensive sampling within a lake, rather than the more common approach of discerning associations from large scale surveys of many lakes. The groups of species depicted in our ordination (Fig. 2) thus may each contain species that do not share responses to a wide range of water chemistry regimes.

Fassett (1930), Moyle (1945), and Swindale & Curtis (1957) all completed surveys of lakes in Wisconsin or Minnesota, and delimited groups of associated species with similar distributions. Although at least two thirds of the species we list for Big Muskellunge Lake were found in all three studies, one might not expect close correspondence between groups determined on the basis of extensive and intensive sampling. This serves to emphasize the good correspondence we did find between Fassett's (1930) growth form categories and two of our species clusters. All four members of our group 1 are in Fassett's class of macrophytes with 'long lax stems and compound or flexuous leaves', and all five members of our group 2 belong to Fassett's class of 'plants with stiff leaves in a close rosette or on short, rigid unbranched stems'. In contrast, the relatively rare species in our group 5 and the widespread

species of group 3 do not share a common growth form. The correspondence of our group 1 and 2 with Fassett's growth forms reinforces the contention that simple growth form categories, such as those of Jensen (1979), can be ecologically meaningful groups.

#### *Spatial pattern of the vegetation*

Our analyses reveal essentially four scales of pattern prominent in the submersed vegetation of Big Muskellunge Lake: (i) site-to-site and transect-to-transect variation on a scale of up to hundreds of meters; (ii) within-transect heterogeneity on a scale of 10–50 m; (iii) variation between nearby quadrats on a scale of 100–200 cm; and (iv) variation in neighbor relationships of individual stems, on a scale no larger than a few centimeters. Most previous work has emphasized only the longest of these scales of pattern.

Studies of compositional variation independent of variations in depth and exposure are not common in the literature. Swindale & Curtis (1957) used a homogeneity criterion in selecting stands, but noted that 'the vegetation along particular contours was, in the great majority of communities, uniform'. Titus (1983) found homogeneous distributions of frequent species along depth contours in Chenango Lake, New York. In contrast, macrophytes in Big Muskellunge Lake are heterogeneous along depth contours of substantially uniform exposure.

The causes for spatial heterogeneity are far less clear than its existence. However, a process of elimination allows us to delimit the processes that are probably responsible for generating pattern at each scale. The complex environmental gradients most likely to cause intra-lake patterns are substrate, exposure and water depth. Of these, only substrate is variable within our transects. Potentially important biotic factors include autotoxicity, bioturbation, clonal growth, colonization, competition and allelopathy, herbivory, pathogens, and phenology. We eliminated phenological effects by restricting sampling to a short segment of the growing season.

Not all of the processes that can generate pattern in the submersed vegetation are likely to operate at all scales. Below, we discuss the probable causes of heterogeneity among and within transects, and segregation of species.

### *Compositional variation among transects*

Depth-dependent environmental gradients, coupled with differences in exposure and the attendant variations in water turbulence and sediment features, are widely regarded as the most important abiotic influences on macrophyte distribution (Hutchinson, 1975; Spence, 1982). Both depth and exposure are correlated with compositional differences among some, but not all, of our transects. As previously noted, vegetation at all three 1.0-m transects is distinct from that at greater depths, as marked by the isolation of these transects in the ordination (Fig. 1). Greater turbulence and coarser sediments at 1.0 m may cause this distinction. The 2.5- and 3.5-m transects, however, are intermingled on the ordination, which may reflect more subtle environmental changes between 2.5 and 3.5 m than between 1.0 and 2.5 m.

Contrasting sediments may be responsible for the dichotomy between the positions of WB and BP transects in the ordination (Fig. 1). WB transects were generally located on loosely consolidated sediments which consisted largely of partially decomposed detritus from *Potamogeton robbinsii*. For the most part, BP sediments were sandy and firm, even at 3.5 m. The two exceptions to these generalizations are notable: In transect W3, in WB, grouped with BP transects, *P. robbinsii* was infrequent and the sediment was sandy, perhaps the consequence of a steeper slope at that transect or its greater exposure to turbulence. Transect B8 at BP was grouped with WB transects. This grouping reflects the high relative frequencies of *P. robbinsii* and *Elodea* (Appendix 1). We noted no obvious exposure or slope differences from the other 3.5 m BP transects, but the sediment was loosely consolidated.

The distinctness of transect B8 among the 3.5-m transects, coupled with that of B5 at 2.5 m and B1 at 1.0 m, shows that compositional variation may be appreciable even among transects at the same depth within a site (BP) chosen for uniform exposure. The ordination of transects (Fig. 1), the distance measure themselves, and the  $\chi^2$  homogeneity tests mentioned above all support this point.

*P. robbinsii*, which apparently consists of tissues particularly refractory to decay, may play an important role in sedimentation, which was held critical by Pearsall (1920) and Misra (1938). Partially

decomposed stems of *P. robbinsii* form a matrix which may influence subsequent colonization and success of other species. Aside from forming an influential matrix, the very presence of a large clone of *P. robbinsii* (or any other species) can easily lead to compositional heterogeneity. Clonal growth cannot provide the sole explanation for variation at a particular depth within a site, however, as the annual *Najas flexilis* is quite irregularly distributed over the three transects at each of the three depths at Brannum's Point.

### *Compositional variation within transects*

Both gradual and abrupt shifts in composition occurred along transects in Big Muskellunge Lake. Where compositional change was gradual, species' distribution followed overlapping individualistic curves (Fig. 3A) similar to the distribution patterns of macrophytes along depth gradients (Pearsall, 1921) or synthetic compositional gradients based on data from many lakes (Swindale & Curtis, 1957). While gradual compositional change was monotonic along some entire transects, abrupt compositional change along other transects occurred on two spatial scales. Over spaces of tens of meters, abrupt shifts between common and rare species were determined largely by the patterns of the dominants (Fig. 4). Over shorter spaces of ca 1 m, abrupt shifts in occurrence among common species produced a more fine-grained pattern (Fig. 5).

Within a given transect, compositional trends may reflect substrate variation or biotic factors (Figs. 3, 4). Variation in community composition (Fig. 5) or abundance of individual species (Table 2 on short scales of 10–200 cm) is most likely due to biotic factors.

When species are considered individually, the most consistent differences in scale of pattern occur between sites, rather than among depths or species. Smaller patch sizes occurred at BP for all species that occurred at a given depth at both sites (Table 2).

Inter-site variation in biotic factors can account for the intriguing difference in scale of pattern between BP and WB. Within a range of scales where biotic factors should be most important (10–200 cm), BP vegetation is fine-grained while WB vegetation is either coarse-grained or homogeneous (Table 2, Fig. 6). If colonization pattern were involved, then annuals and diaspore-producing spe-

cies would show stronger inter-site differences than clonal perennials. However, inter-size differences were similar for an annual (*Najas flexilis*), perennials that frequently produce spores or seeds (*Isoetes macrospora*, *Potamogeton pusillus*, *Vallisneria americana*), and clonal perennials that only rarely produce seeds (*Eleocharis acicularis*, *Myriophyllum tenellum*, *Potamogeton robbinsii*). Differences in clonal growth rates may explain differences in pattern of clonal species. Competitive interactions may also differ between sites.

### *Segregation of species*

Conclusions about species' interrelations based on quadrat samples are inevitably influenced by the size and spacing of quadrats (Pielou, 1977). We have attempted to minimize potential artifacts by (1) selecting quadrat size appropriate to the stature of the plants, and (2) comparing quadrats over a range of spacings. To supplement our quadrat data, we examined sequences of shoots along transects. Such data are independent of, and not confounded by, spatial scales (Pielou, 1977). Results for several selected species pairs showed strong segregation in every case (Tables 3 and 4). Therefore, these species are not randomly distributed with respect to each other. This conclusion corroborates the inferences of non-randomness and heterogeneity that emerged from quadrat data.

Evidence for non-random shoot sequences along transects accompanies patchy distributions at small scales of 15–280 cm (Tables 3 and 4). At such small scales, variation in physical/chemical factors is probably scant. However, effects of clonal growth and competition cannot be ruled out. Competition is the most plausible explanation for the non-random interactions of *Lobelia dortmanna*, which does not produce horizontal stems.

### *Significance of heterogeneity in macrophyte ecology*

Collectively, our data demonstrate substantial heterogeneity in structure of submersed macrophyte communities. Coarse-grained heterogeneity (up to hundreds of meters) is long recognized and most commonly attributed to substrate or depth differences among sites. Fine-grained heterogeneity (a few centimeters to a few meters) has not been

carefully examined by macrophyte ecologists. These high-frequency patterns are most plausibly explained by biotic factors, especially clonal growth, colonization, and competition.

In this study, some inferences about the processes that control pattern are possible because (i) features of the sampling design (e.g. transects along depth contours) eliminate effects of particular environmental variables, and (ii) contiguous quadrat techniques were combined with analyses of plant-by-plant transect sequences that directly assess the pattern of neighbor relationships. More detailed discrimination of the relative importance of colonization, growth, and competition would require removal and transplant experiments (Antonovics & Levin, 1980). The few such experiments performed in lakes have detected significant interactions among neighboring macrophytes (Titus & Stephens, 1983; McCreary *et al.*, 1983).

The existence of biotically-mediated patchiness is less surprising than the neglect of small-scale heterogeneity and neighbor interactions in the literature that deals with submersed macrophytes. Much more research on submersed plant interactions must underlie any comprehensive attempt to explain variations in macrophyte distribution and abundance.

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## Appendix 1

*Relative frequency for submersed macrophytes in 15 transects. Transect codes as in Figure 1, Species codes as in Table 1.*

	B1	B2	B3	B4	B5	B6	B7	B8	B9	W1	W2	W3	W4	W5	W6
PAM								1		48	29	1		4	1
PRO								45	+	28	40	1	28	71	47
ELO	+		+					30		18	8	1	15	19	32
PPR				4				1			6		+	2	7
JUN	8	36	44												
ELA	1	19	16												
ELE	27	21	21		21	1						10	+		
RAN	15	1													
MTE	3	8	12		48		22					23			
ISO	1	1		12	3	14	11	+	24			13	9		
PPU	1	2	+	11	5	6	22	7	22			17	16	2	5
VAL				23	3	2	11	9	14		5	12	9		5
CHA	1	1	1	7	2	13	4		1			1	1		
NAJ	36	6	3	34	11	61	23	2	34	2		11	18		
PGR	2	1	2	4	2	2	5	1	2	2	10	3	3		1
MEG														1	3
ERI	+														
GRA		+													
LOB	3	3	1		+										
PAL	1	3	1	3	1		1				2	+			
NIT					4		1	+	2			1			
MAL	1				+			1		3		6	1		
PRI				3			1	3				1			