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RELATIONSHIPS BETWEEN AQUATIC PLANT COVER AND FISH POPULATIONS BASED ON MINNESOTA LAKE SURVEY DATA[1]

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Abstract **-** We compiled data on 640 Minnesota lakes to characterize relationships between aquatic plant cover and fish populations. To quantify plant cover, we combined the frequency occurrence of aquatic plants recorded in Minnesota Department of Natural Resources Fisheries Lake Surveys, total alkalinity, littoral area (surface area of lakes where aquatic plants occurred), and physical stress from wind (wind-wave power). For these same lakes, we also calculated mean trap net or gill net catch-per-effort (CPE) of 12 selected species of cool and warm water fish common throughout Minnesota. We found that differences in plant cover account for considerable differences in fish populations among lakes. Our study corroborates the findings of other studies at different scales and geographic locations showing relationships between plant community structure and fish. Lakes with high frequency occurrences of diverse plant forms had the highest CPE of phytophilic species such as northern pike and pumpkinseed; conversely, lakes with sparse monotypic plant cover had the highest CPE of benthic omnivores such as common carp and black bullhead.

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Introduction

Aquatic plant cover is viewed as an important habitat element needed to sustain fish populations, but consequences of changes in aquatic plant cover on fish populations are complex and vary with physical characteristics of Minnesota lakes (Valley et al. 2004). However, human activities, including shoreland development, agriculture and urbanization, have caused changes in lake habitats resulting in changes in fish populations. Aquatic plants in Minnesota lakes are affected by direct removal, invasive exotics (common carp *Cyprinus carpio*, rusty crayfish *Orconectes rusticus*, Eurasian milfoil *Myriophylum spicatum*), water level fluctuations, shoreline modification, and accelerated inputs of sediments and nutrients.

Many studies and anecdotal observations link fish to aquatic plant cover; however, quantitative descriptions of associations between plant cover and fish populations are inadequate. Extensive documentation in literature reviews by Janecek (1988), Dibble et al. (1996), and Valley et al. (2004) cover the use of plant cover by fish for spawning, protection from predators and harsh environments, and for food. However, the various studies done to quantify the amount of plant cover in lakes needed to optimize fish populations are relegated to mostly largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus*. The results of these studies indicate that an intermediate range of cover is often considered optimal (Valley et al. 2004). Factors that vary among lakes such as lake size, depth, and water chemistry affect these plant cover – fish relationships (Canfield and Hoyer 1992; Valley et al. 2004). Furthermore, plant type or architecture within aerial coverage is also related to fish abundance (Chick and McIvor 1994). In selected Minnesota lakes, short term (1-2 yr) experimental manipulations of plant cover were not effective in altering the abundance or size structure of bluegill and largemouth bass (Cross et al. 1992; Radomski et al. 1995; Pothoven et al. 1999). Except for a single study focusing on emergent plant cover (Radomski and Goeman 2001), the type and amount of plant cover necessary to maintain fish populations in Minnesota lakes has not been quantitatively addressed (Valley et al. 2004).

A combination of physical-chemical and biotic factors determines the type and amount of plant cover in lakes. Vestergaard and Sand-Jensen (2000) show that alkalinity and eutrophication explained much of the distribution of plant species and growth forms across Danish lakes. In Florida lakes, Canfield and Hoyer (1992) related lake fertility to higher total biomass of plants. However, except for extremely infertile lakes, adequate nutrients exist to support plant life (Barko et al. 1986), so plant cover is mostly determined by the surface area of the lake where bottom substrates are exposed to sunlight and bottom substrates (a function of water depth, transparency, and the physical force of wind-wave energy). The maximum depth to which rooted plants occur is limited by water transparency (Hudon et al. 2000). Furthermore, the physical force of wind-wave energy strongly influences plant cover directly through exposure and indirectly through its effects on substrates needed for supporting plants (Keddy 1982; Chambers 1987; and Riis and Hawes 2003). Biotic factors including fish and invertebrate grazing also affect plant growth but are generally less influential. However, fish such as common carp are known to uproot plants and disturb sediments making the water turbid and undesirable for plant growth (Parkos et al. 2003).

The Minnesota Department of Natural Resources (MNDNR) Lake Survey database (MNDNR 1993) is a valuable source of information that can be used to relate environmental factors to differences in fish populations among lakes. Schupp (1992) successfully used lake survey physio-chemical data to classify lakes to advance understanding of how these factors relate to fish community differences among lakes. Although information recorded in MNDNR Aquatic Plant surveys are a relatively rough measure of plant diversity, the addition of other variables such as cited above allow for more complete description of the type and extent of plant cover in lakes. For example, geographic information systems (GIS) have been used to successfully model the distribution of plant cover in lakes based on the predictable response of plant cover to physical-chemical factors (Vis et al. 2003; Cho and Poirrier 2005). The large number and wide geographic distribution of lakes in the lake survey data base provides a means to identify general relationships between various levels of plant cover and fish populations in Minnesota lakes. The objective of this study was to classify Minnesota lakes by type of plant cover supplemented with additional information quantifying plant habitat, and use the developed classifications to assess plant cover relationships with fish populations.

Methods

We compiled data on 640 lakes to characterize general relationships between aquatic plant cover and fish populations among Minnesota lakes. Only lakes in Ecological Lake Classes (ELC) 20 to 43 were analyzed, essentially eliminating lakes in Cook, Lake, and St. Louis counties (Schupp 1992). Lakes within this region are mostly located on the Canadian shield, an area of thin soils overlying igneous and metamorphic bedrock typically exhibiting very low productivity, soft water, and cold water fish communities (Schupp 1992). To quantify the suitability and extent of plant habitats in the study lakes, we characterized plant cover in lakes using the frequency of occurrence of plant types in combination with data on lake morphometry, wind power, and alkalinity. Likewise, to quantify fish populations, we used catches of fish in standardized MNDNR Fisheries lake survey netting. Empirical relationships between plant cover and fish populations in these Minnesota lakes were identified using exploratory analytical techniques.

Plant cover

To quantify plant cover in these lakes, we used the frequency occurrence of aquatic plants recorded in MNDNR fisheries lake surveys combined with information describing the effects of lake fertility (alkalinity), littoral area (plant habitat), and physical stress from wind (wind-wave power). First, we developed plant cover type based on frequency of occurrence data from the lake survey database. These data were collected from 1993 to 2001. Frequency of occurrence for a particular species was the number of plant survey transects with that species (MNDNR 1993). The number of transects in lakes ranged from 10 to 60, the number increasing with increasing lake size, generally in units of 10. Consequently, to make frequency of occurrence comparable among lakes regardless of size, we rescaled (to the nearest whole number) frequency of occurrence to the number per 10 transects for lakes where more than 10 transects were sampled. To determine consistency of identification, we examined statewide maps of species occurrences among MNDNR surveys because accurate identification of aquatic plant species requires considerable skill. Inspection of these maps revealed inconsistencies in species identification. However, identification of the most commonly occurring species appeared accurate, and we assumed these common plant species represented the most significant plant cover for fish. Next, we grouped plant species into nine cover types based on similarities in form using criteria from Duarte (1987), Janecek (1988), and Wilcox and Meeker (1992) as well as MNDNR staff input. These cover types included four types of emergent and five types of submerged plant cover (Table 1). Curlyleaf pondweed *Potamogeton crispus* was separated into a unique cover type because of its different seasonal growth pattern (rises much earlier in spring and declines earlier in summer than other plant types), and because it is a widely distributed, well-established invasive species of considerable concern to lake managers. The frequency of occurrence of all plant species within a cover type among transects was used to illustrate the magnitude of that cover type within a lake.

Second, we collected total alkalinity data for each of the study lakes from the lake survey database. Total alkalinity was used as a surrogate for lake fertility. These data were also collected from 1993 to 2001, and means were calculated if lakes were surveyed more than once.

Third, for each lake we used GIS to estimate the littoral area defined as the surface area with suitable depth for supporting rooted aquatic macrophytes. Littoral area estimates were based on calculations made using vectors from lake center to shore in 16 evenly distributed compass bearings starting at 0° N

Table 1. Aquatic plant species hierarchically classified by physical similarity.

Plant Groups			
		<u>EMERGENTS</u>	
CTL	Cattail	Narrowleaf Cattail	*Typha angustifolia*
		Hybrid Cattail	*Typha angustifolia x latifolia*
		Common Cattail	*Typha latifolia*
		Cattail group	*Typha* spp.
BR	Bulrush	Hardstem Bulrush	*Scirpus acutus*
		Leafy Bulrush	*Scirpus atrovirens*
		Water Bulrush	*Scirpus subterminalis*
		River Bulrush	*Scirpus fluviatilis*
		Threesquare	*Scirpus pungens (americanus)*
		Bulrush	*Scirpus* spp.
		Softstem Bulrush	*Scirpus validus*
RICE	Wild Rice	Wild Rice	*Zizania palustris*
LILY	Lily and Lotus	Water Shield	*Brasenia schreberi*
		Yellow Lotus	*Nelumbo lutea*
		Fragrant Waterlily	*Nymphaea odorata*
		White Waterlily	*Numphaea tuberosa*
		Little Yellow Waterlily	*Nuphar microphyllum*
		Common Yellow Waterlily	*Nuphar luteum (variegatum)*
		Little White Waterlily	*Nymphaea tetragona*
		<u>SUBMERGENTS</u>	
LG	Low Growth		
		Canada Waterweed	*Elodea canadensis*
		Water Starwort	*Callitriche verna*
		Waterwort	*Elatine* spp.
		Matted Waterwort	*Elatine minima*
		Pipewort	*Eriocaulon septangulare*
		Mud Plantain	*Heteranthera*
		Water Star-Grass	*Heteranthera dubia*
		Quillwort	*Isoetes* spp.
		Braun's Quillwort	*Isoetes echinospora*
		Lake-Quillwort	*Isoetes lacustris*
		Lobelia	*Lobelia dortmanna*
		Widgeon Grass	*Ruppia occidentalis*
		Horned Pondweed	*Zannichellia palustris*
		White Water Buttercup	*Ranunculus aquatilis*
		Yellow Water Buttercup	*Ranunculus flabellaris*
		Bladderwort group	*Utiricularia* spp.
		Humped Bladderwort	*Utricularia gibba*
		Flat-leaf Bladderwort	*Utricularia intermedia*
		Small Bladderwort	*Utricularia minor*
		Greater Bladderwort	*Utricularia vulgaris*
		Muskgrass	*Chara* spp.
		Stonewort	*Nitella* spp.
		Wild Celery	*Vallisneria americana*
FL	Fine-leaf	Bushy Pondweed	*Najas gracillima*
		Bushy Pondweed	*Najas flexilis*
		Southern Pondweed	*Najas guadalupensis*
		Spiny Naiad	*Najas marina*
		Naiad group	*Najas* spp.
		Water milfoil	*Myriophylum* spp.
		Small-leaf Water-milfoil	*Myriophylum alterniflorum*
		Farwell's Water-milfoil	*Myriophylum farwellii*
		Variable Water-milfoil	*Myriophylum heterophyllum*
		Northern Water-milfoil	*Myriophylum sibiricum*

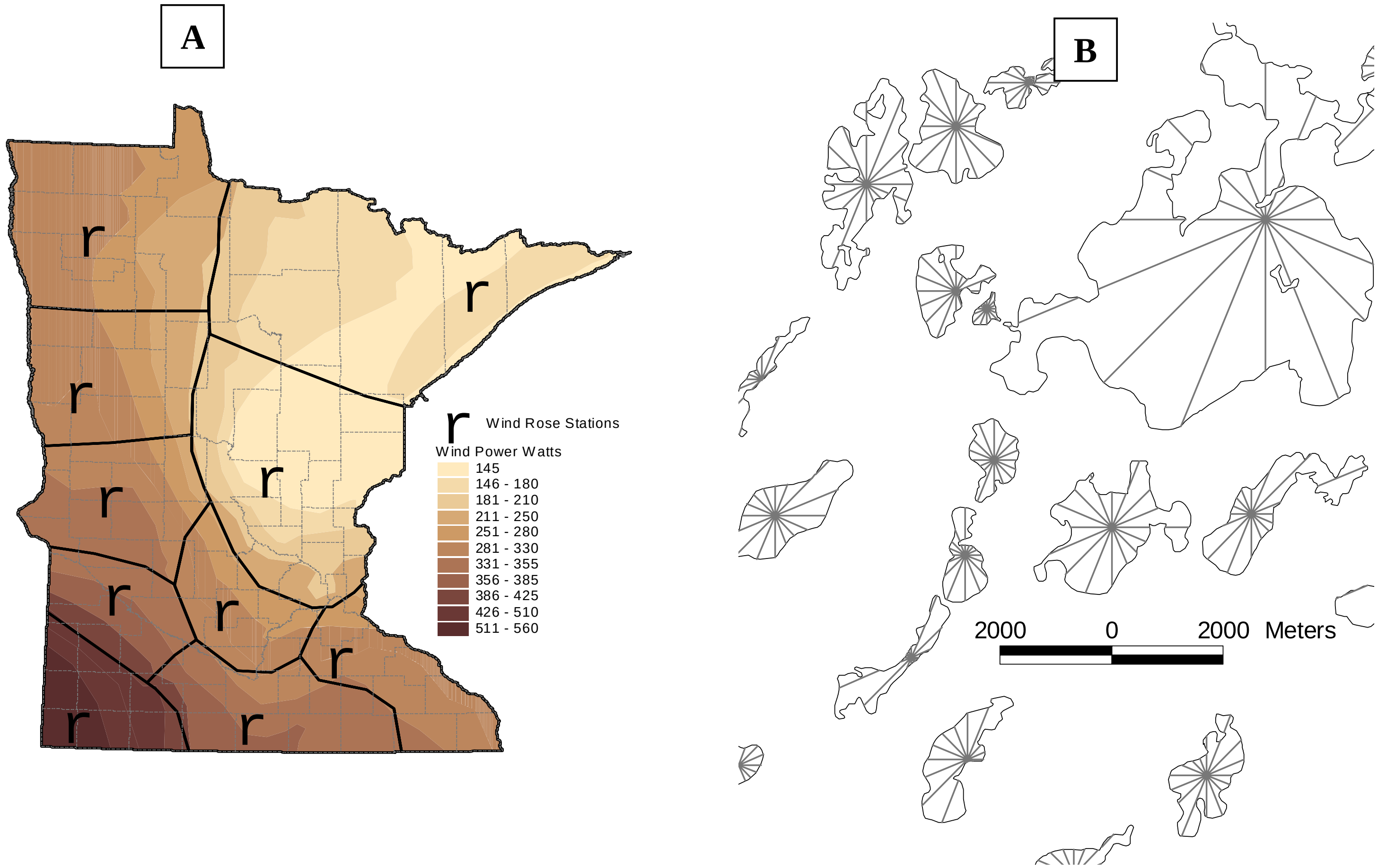
Table 1. Continued

		Whorled Water-milfoil	*Myriophylum verticillatum*
		Leafless Water-wilfoil	*Myriophylum tenellum*
		Eurasian Water-wilfoil	*Myriophylum spicatum*
		Coontail	*Ceratophyllum demersum*
NL	Narrowleaf	Berchtold's Pondweed	*Potamogeton berchtoldi*
		Nuttall's Pondweed	*Potamogeton epihydrus*
		Floatingleaf Pondweed	*Potamogeton natans*
		Bluntleaf Pondweed	*Potamogeton obtusifolius*
		Fries' Pondweed	*Potamogeton friesii*
		Small Pondweed	*Potamogeton pusillus*
		Snailseed Pondweed	*Potamogeton spirillus*
		Narrowleaf Pondweed group	*Potamogeton* spp.
		Vasey's Pondweed	*Potamogeton vaseyi*
		Robbins' Pondweed	*Potamogeton robbinsii*
		Largesheath Pondweed	*Potamogeton vaginatus*
		Flatstem Pondweed	*Potamogeton zosteriformis*
		Rafinesque's Pondweed	*Potamogeton diversifolius*
		Leafy Pondweed	*Potamogeton foliosus*
		Variable Pondweed	*Potamogeton gramineus*
		Narrowleaf Pondweed	*Potamogeton strictifolius*
		Slender Pondweed	*Potamogeton filiformis*
		Sago Pondweed	*Stuckenia pectinata*
BL	Broadleaf	Largeleaf Pondweed	*Potamogeton amplifolius*
		Illinois Pondweed	*Potamogeton illinoensis*
		Northern Pondweed	*Potamogeton alpinus*
		River Pondweed	*Potamogeton nodosus*
		Whitestem Pondweed	*Potamogeton praelongus*
		Claspingleaf Pondweed	*Potamogeton richardsonii*
		Broadleaf Pondweed Group	*Potamogeton* spp.
PC	Curled Pondweed	Curled Pondweed	*Potamogeton crispus*

and ending at 337.5° N (Figure 1). Littoral slopes for each vector were calculated using the depth contour shown on bathymetric lake maps most closely corresponding to the maximum depth of aquatic plant cover recorded in fisheries lake surveys (z_p) and the distance from shore to the intersection of that contour. The mean littoral slope of all the vectors in each lake were used to estimate lake wide littoral slope (l_s). We calculated average width of the littoral zone using the equation $l_{zp} = z_p/l_s$. Finally, we used GIS to calculate the surface area of a polygon representing the average littoral zone width around the whole lake.

Lastly, we calculated an index of wind-wave power for each lake. This index reflects the total annual amount of energy in wind driven waves directed at lakeshores. We estimated this variable using published measurements of wind power combined with lake fetch measurements. The calculations were also based on vectors from lake center to shore in 16 evenly distributed compass bearings starting at 0° N and ending at 337.5° N (Figure 1). We used GIS to extract from a statewide map total wind power (watts/m^2) at each lake (Minnesota Wind Resource Analysis Program; MNDOC 2002). The percentage of wind energy for each of the 16 standard compass bearings at each lake was based on data collected from the closest of 10 monitoring stations located around the state. We then multiplied these percentages at each bearing by the total wind power. Next, wind power along each of the 16 fetches was multiplied by the fetch length (m). Our index of lake wide wind-wave power equaled the sum of the 16 wind power-fetch products.

Figure 1. (A). Estimated wind power across Minnesota from the Minnesota Wind Resource Analysis Program (MNDOC 2002) and the locations of the eight monitoring stations used to extract wind rose data. (B). Fetch lines for 16 standard compass directions for a selected group of Minnesota lakes used to estimate wind-wave power.



Fish Abundance

Trap nets and gill nets were also set in the same 640 lakes during the same years when aquatic plant sampling occurred. Nets were set according to guidelines by MNDNR (1993). We gathered from the lake survey database trap net and gill net catch per effort (CPE) data for 12 fish species common to most of the study lakes. Mean CPE were calculated when more than one survey was done between 1993 and 2001, and we chose the gear that most likely provided the best measurement of relative abundance. We used trap net CPE to describe relative abundance of pumpkinseed *Lepomis gibbosus*, bluegill, rock bass *Ambloplites rupestris*, bowfin *Amia calva*, white sucker *Catastomus commersoni*, black crappie *Pomoxis nigromaculatus*, and common carp. We used gill net CPE to describe relative abundance of northern pike *Esox lucius*, black bullhead *Ameirus melas*, yellow bullhead *A. natalis*, yellow perch *Perca flavescens*, and walleye *Sander vitreus*. All CPE data were transformed ($\log_{10}$ CPE + 1) to improve the distribution of the data. Subsequently, we used principal components analysis (PCA) to reduce redundancy, whereby the 12 CPE variables were reduced to three. A correlation matrix was used as input to PCA, and the first three principal components were selected without rotation. Lastly, correlations between factor loadings for each variable and all three principal components were calculated.

Analysis

One hundred lakes (verification lakes) were randomly selected from the complete set of 640 to serve as a reference set for verification of relationships modeled with the remaining 540 lakes (model lakes). We used K-means cluster analysis to classify the model lakes into plant cover groups (PCG) based on the 9 plant cover types (Table 1). Before this analysis, frequency of occurrence data were transformed into square roots or square root arcsines to improve the distribution of the data by spreading the ends (McCune and Grace 2002). K-means cluster analysis procedure in JMP 5.1 (SAS 2002) was used to obtain the best 4-, 5-, 6-, 7-, 8-, 9-, and 10-group clusters to characterize PCG. For selecting the optimal number of clusters for further analysis, we sought to minimize the number of clusters while still accounting for a significant amount of variation in the data set (observed as the amount of group separation with the first two principal components of the data in a biplot). The results of K-means cluster analysis with different numbers of clusters were tested with discriminate analysis describing differences among clusters (group means), misclassification rates, and examination of group separation on canonical plots. Misclassification rates were calculated as the rate of disagreement between assignments from discriminate analysis and K-means cluster analysis. Only group assignments with a probability of 90% or higher for the same group classified by K-means cluster analysis were considered correctly classified. Discriminate analysis formulas were also used to calculate group assignments and misclassification rates for the 100 verification lakes.

To further describe PCG, we looked at their spatial distribution and association with other Minnesota lake classifications. The geographical distribution of plant groups was done using GIS to map and overlay with Minnesota ecological land classification subsections that divides the Minnesota landscape into sections described by key ecological factors including topography, climate, soils, and vegetation (IIC 2006). We also used simple cross tabulation to compare PCG's with two other lake classifications, the Ecological Lake Classification (Schupp 1992) and Plant Community Classification (PCC; Reschke 2006).

We used linear statistical models fitted with least squares to identify relationships between fish populations (principle components 1 and 2; $\log_{10}$ +1 catch per effort of northern pike, pumpkinseed, bluegill, yellow bullhead, rock bass, bowfin, whiter sucker, yellow perch, walleye, black crappie, black bullhead, and common carp) and plant cover factors (Plant Cover Group, wind-wave energy, percent littoral area, and alkalinity) in MNDNR lake surveys. Interactions terms between PCG (a nominal variable) and the three other continuous variables were included in the models. Cross-validation of models was done by using the verification set of 100 lakes. We used the models parameterized with the model set data to estimate CPE of the 12 species and principal components of verification lakes. R-square values (R^2) to judge the model fit to the verification lakes were then calculated between the predicted values from the models and the observed values. Comparisons were made to R^2 values of models on the original data to check for inconsistencies.

Finally, we compared the predictive fit of our PCG classification to fish population response variables with plant community classification (PCC) and the MNDNR ecological lake type classification (ELC) predictors in one-way and two-way ANOVA models. For these comparisons, we intentionally restricted our analysis to 251 lakes in five distinctly different ELC (24, 25, 27, 34, 43), which also kept the number of categories similar in comparison to PCG and PCC. One-way ANOVA models were constructed for PCG, PCC, and ELC to describe variation in each fish population response variable (principle components 1 and 2; log10 +1 catch per effort of northern pike, pumpkinseed, bluegill, yellow bullhead, rock bass, bowfin, white sucker, yellow perch, walleye, black crappie, black bullhead, and common carp). We combined PCG with each of the other two lake classifications in two-way ANOVA models of the fish population response variables. Adjusted R^2 values of these models were calculated and used to evaluate the relative explanatory power of these ANOVA models.

Results

Plant cover

Lakes in the model and verification data sets were physically similar. A few soft-water lakes were still represented in both data sets despite removing Ecological Lake Classes 1-19 (Schupp 1992). Most lakes were relatively small (median surface area = 113 ha) with an average of 47% of lake area shallower than the maximum depth of rooted aquatic vegetation (Table 2). Overall, submergent plant cover type (fine-leaf, low growth, narrow-leaf, broad-leaf, and *Potamogetan crispus*; Figure 2) occurred more frequently than emergent types (cattail, bulrush, rice, and lily; Figure 2).

Based on group separation and subsequent fit by discriminate analysis, which described group means, variances, and misclassification rates, we determined that variation in plant cover types among lakes was best summarized with K-means cluster analysis using six groups of lakes. A principal component analysis of the six cover type groups showed a distinct group on the first axis characterized by low plant cover frequencies (Group 1; Figure 3). The opposite end of the first axis reflected a high overall frequency of occurrence of all cover types except cattail, and was best represented by Group 4 and to a lesser extent Group 2. Group 3 describes lakes with frequent occurrences of *Potamogetan crispus.* Finally, Groups

Table 2. Mean, median, range, and coefficient of variation of total lake surface area, average slope of lake bottom in littoral area (littoral slope), littoral area, wind-wave power index, total alkalinity, and maximum plant depth among 540 model lakes and 100 verification lakes.

	Model lakes				Verification lakes			
	Mean	Median	Range	C.V.	Mean	Median	Range	C.V.
Area (ha)	258	113	6 - 3,961	162.1	314	121	10 - 3,374	189.4
Average littoral slope (%)	4.8	4.1	0.1 - 19.8	63.6	4.6	4.3	0.5 - 11.2	58.1
Littoral area (%)	46.9	44.3	5 - 100	45.8	45.3	38.8	4.3 - 100	52.4
Wind-wave power index	18.6	13.0	1.8 - 169.4	94.8	19.4	13.1	2.4 -112.7	102.5
Total alkalinity (mg/L)	126	128	1 - 335	43.1	121	117	8 - 374	53.0
Maximum plant depth (m)	4.3	4.3	0 - 10.7	44.6	4	4	0.6 - 8.5	45.7

Figure 2. Mean ± 95% confidence intervals, median, 25th and 75th quantiles, and range of nine plant cover types (cattail, CTL; bulrush, BR; rice; lily; *Potamogetan crispus*, PC; fine-leaf, FL; low growth, LG; narrow-leaf, NL; and broad-leaf, BL) among model lakes (n = 540). The mean is the horizontal axis inside the diamond; the 95% confidence intervals are the vertical axis inside the diamond; the horizontal line across the middle of the box is the median; the lower and upper horizontal ends of the box are the 25th and 75th quantiles, respectively; and the range is the length of the vertical dotted line including the upper or lower most quantile.

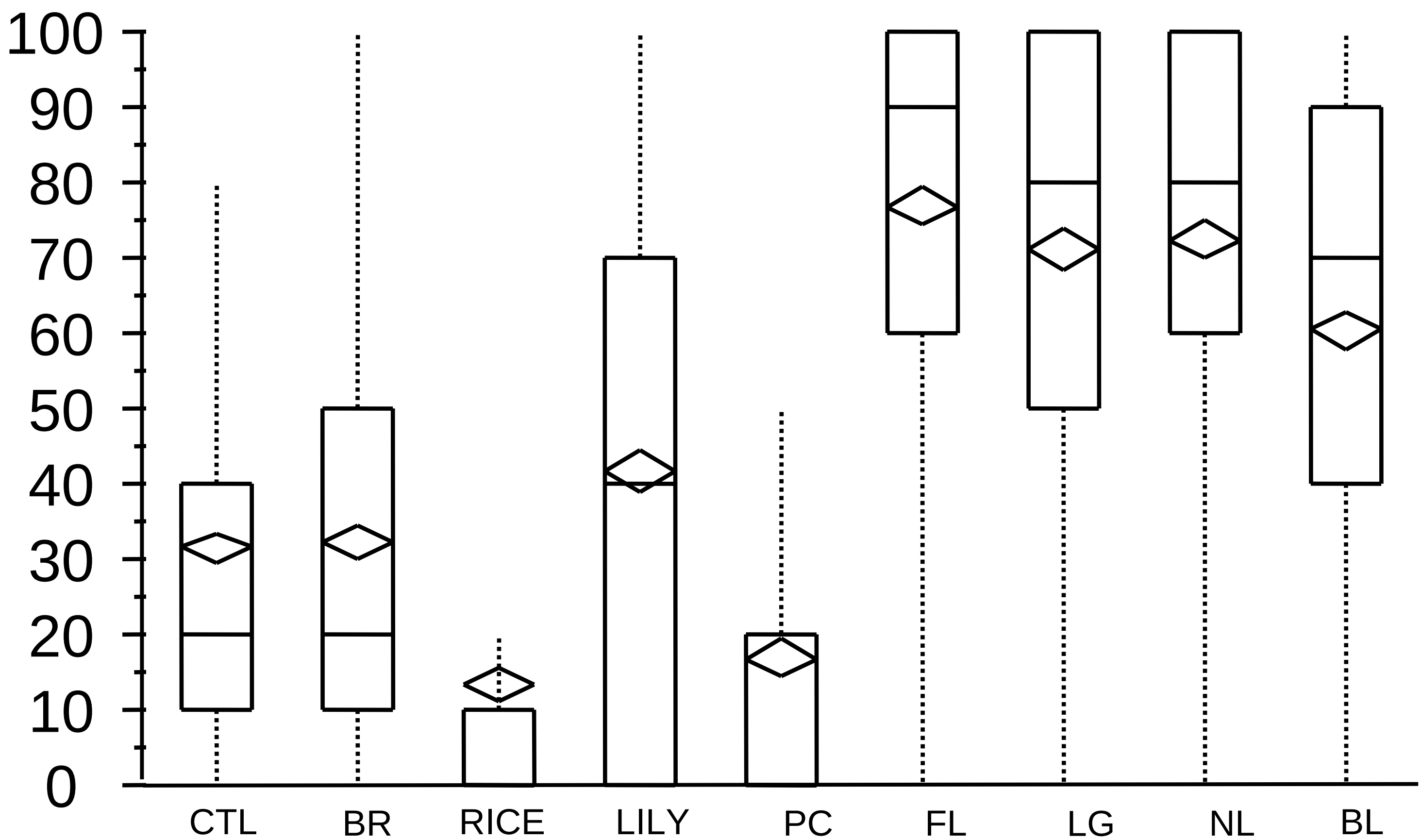
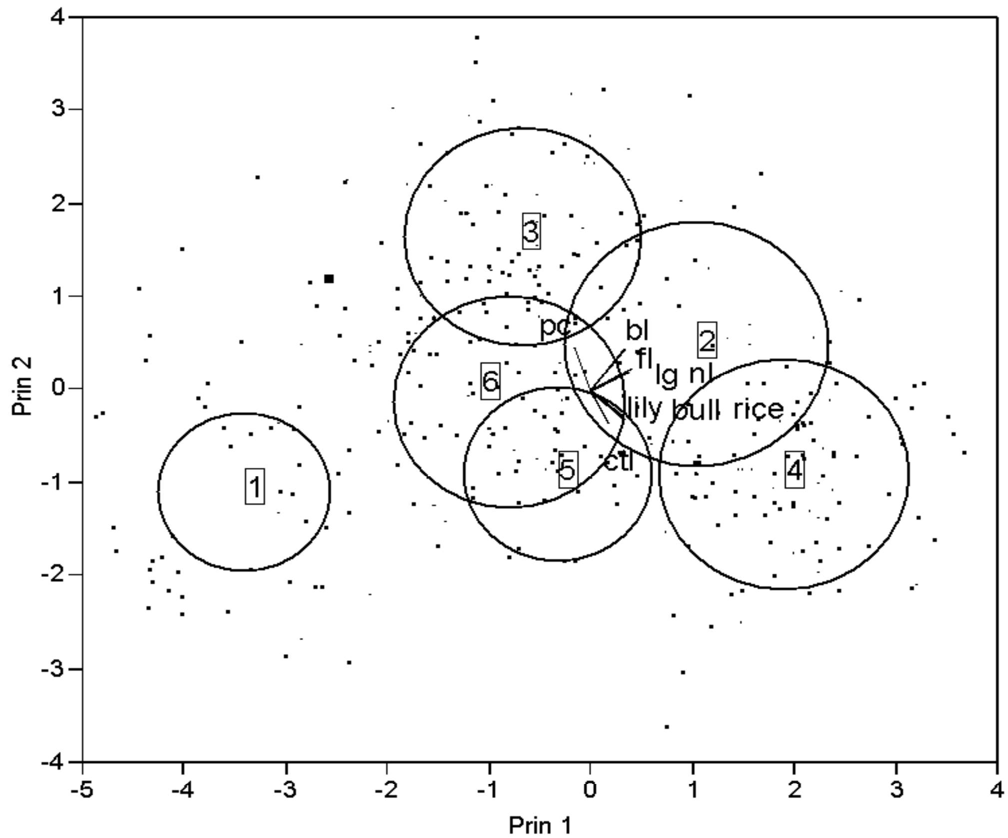


Figure 3. Results of K-means cluster analysis showing the arrangement of six plant cluster groups (1-6) ordinated along principal components (Prin 1 and Prin 2). The strength and direction of influence of plant types (fl, bl, lg, nl, pc, lily, bull, rice, ctl) along this ordination is shown with vectors.



5 and 6 depicted moderate frequency occurrence of plants with Group 5 being better represented by cattail and lily.

Discriminate analysis assigned lakes to groups with reasonable accuracy and precision. Only 7 % of the model lakes were assigned to the wrong K-means cluster. A total of 64% of model lakes and 69% of the verification lakes were correctly classified at a probability exceeding 90%. Discriminate analysis means for the plant cover groups (PCG; Figure 4) were consistent with K-means cluster analysis (Figure 3) showing separation of groups from low to high plant cover frequency, and secondarily the occurrence of *Potamogetan crispus* and rice. The occurrence of rice largely separates Group 4 from the other groups (Figure 4). The geographical distribution also differs among PCG groups (Figure 5). PCG 2 and 4, groups with the highest frequency of occurrences and most diverse plant cover, are predominately located in north central Minnesota (ECS subsections: St. Louis Moraines, Pine Moraines, and the Hardwood Hills; IIC 2006). At the other extreme, PCG 1 and 3 are mostly relegated to southern Minnesota (ECS subsections: Anoka Sand Plain, Minnesota River Prairie, Big Woods, St. Paul-Baldwin Plains and Moraines, and Coteau Moraines; IIC 2006). All lakes in the southwestern Minnesota Coteau Moraines ECS were classified in Lake Group 1 (sparse plant cover).

Figure 4. Mean frequency of occurrence of nine cover types (cattail, CTL; bulrush, BL ; rice; lily; *Potamogetan crispus*, PC; fine-leaf, FL; low growth, LG; narrow-leaf, NL; and broad-leaf, BL) in the six plant cover groups determined with K-means cluster analysis.

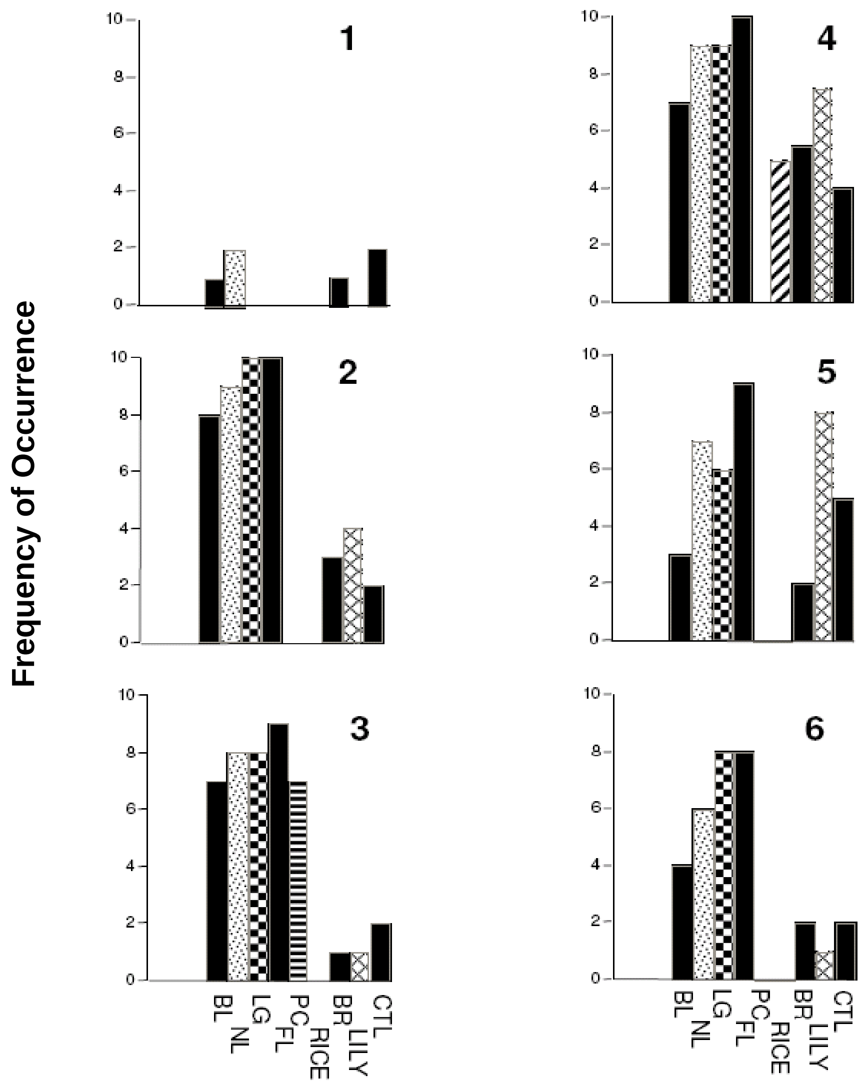


Figure 5 A. Geographical distribution of lakes (black dots) in Plant Cover Groups 1 through 6. Maps include boundaries of Ecological Land Class Subsections defined in B (IIC 2006).

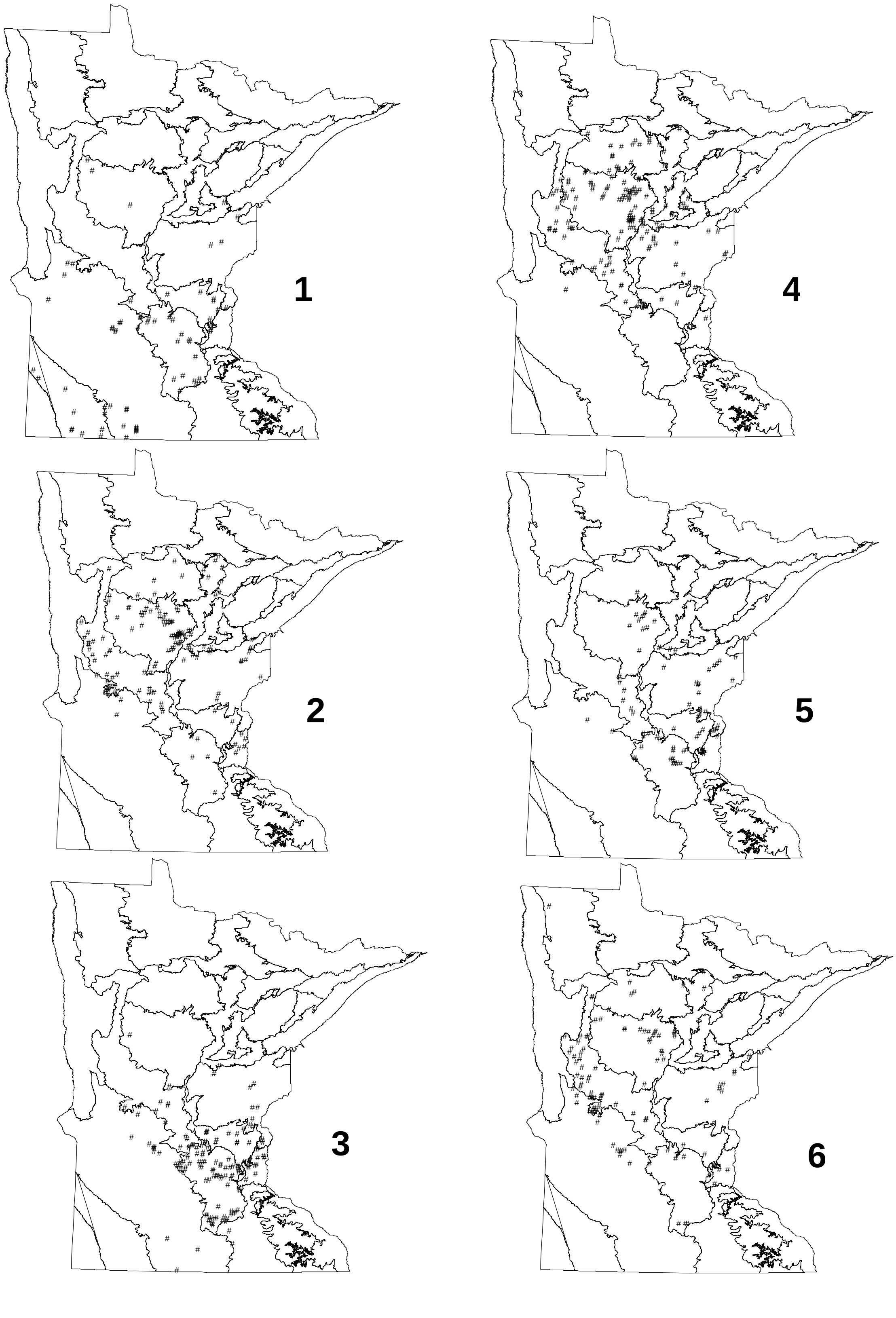
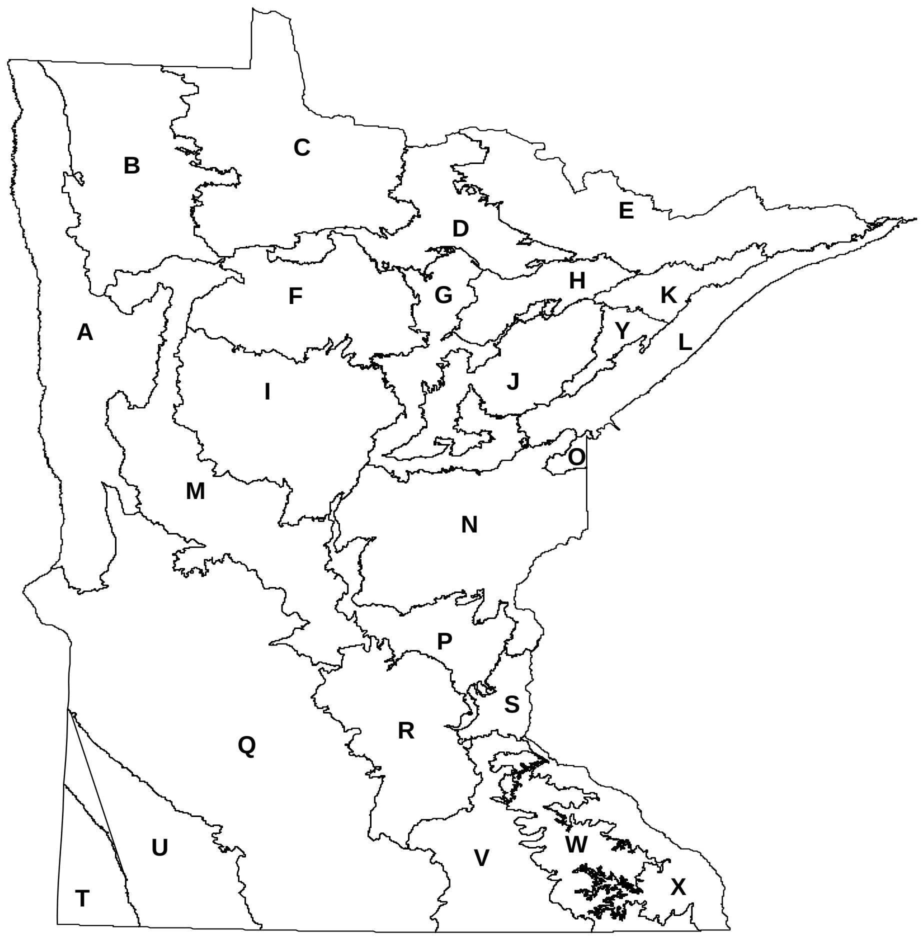


Figure 5b.



ECS Subsections - V99a

A - Red River Prairie
B - Aspen Parklands
C - Agassiz Lowlands
D - Littlefork-Vermilion Uplands
E - Border Lakes
F - Chippewa Plains
G - St. Louis Moraines
H - Nashwauk Uplands
I - Pine Moraines & Outwash Plains
J - Tamarack Lowlands
K - Laurentian Uplands
L - North Shore Highlands
M - Hardwood Hills
N - Mille Lacs Uplands
O - Glacial Lake Superior Plain
P - Anoka Sand Plain
Q - Minnesota River Prairie
R - Big Woods
S - St. Paul-Baldwin Plains and Moraines
T - Inner Coteau
U - Coteau Moraines
V - Oak Savanna
W - Rochester Plateau
X - The Blufflands
Y - Toimi Uplands
Z - St. Croix Moraine

The ELC and the PCC both explained a modest amount (22%) of the variation in lakes assigned by our plant cover groups classification. Many Ecological Lake Classes have a propensity for certain plant cover groups; however, some ELC's, such as Class 34, are comprised of a relatively even distribution of plant cover groups (Table 3). Likewise, plant cover Groups 2 and 4 (high frequency plant cover in north-central Minnesota lakes) almost always corresponded with plant community types 1, 3, and 16; whereas, plant cover Groups 1 and 3 (low to moderate frequency plant cover in southern Minnesota lakes) were rather was broadly distributed over a number of plant community types (Table 4).

Fish catch per effort

Catch per effort of each fish species in the model lakes and verification lakes were similar (Table 5). Zero CPE occurred for all species, and CPE was highly variable (coefficient of variation values exceeding 100%). Approximately 52% percent of the variation in fish CPE was accounted for by the three principal components in PCA (Table 6). The first principal component (PC1), explaining 23.4% of the variation in the data set, described a gradient among lakes ranging from those with high CPE of common carp, black bullhead, and black crappie (+ correlations) to lakes with high CPE of northern pike, pumpkinseed, and bluegill (- correlations). Thus, lower PC1 scores favored the more phytophilic fish species than those with higher PC1 scores. The

Table 3. Cross classification of the 640 lakes classified in this study to plant cover group by those classified by ecological lake class using physical-chemical variables (MNDNR unpublished data).

		Lake Class																						
Plant Group	n	20	21	22	23	24	25	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
1	64	0	3	0	0	15	2	0	0	0	3	1	0	0	4	0	1	2	5	0	2	8	2	16
2	143	3	1	7	28	5	16	12	5	16	3	14	7	3	7	2	1	1	3	7	0	1	0	1
3	126	0	0	1	0	52	3	8	0	4	13	6	0	1	5	1	3	0	11	2	2	3	4	7
4	139	2	2	13	9	3	19	21	1	11	2	19	3	2	7	1	3	1	1	10	0	9	0	0
5	68	1	3	0	0	12	2	1	1	6	10	3	5	0	6	2	1	4	5	3	2	0	1	0
6	100	0	1	16	15	10	7	13	2	2	3	7	4	1	6	2	0	0	5	1	0	4	0	1
Total	640	6	10	37	52	97	49	55	9	39	34	50	19	7	35	8	9	8	30	23	6	25	7	25

Table 4. Cross classification of the 640 lakes classified in this study to plant cover groups by those classified by Reschke et al. (2005) to plant community type. A summary description of these plant community classes is provided in Appendix I.

		Plant Community Class								
Plant Cover Types	Total	1	3	16	40	42	59	66	117	134
1	64	0	9	0	8	8	3	18	7	11
2	143	32	21	83	1	0	0	6	0	0
3	126	19	5	29	45	0	0	6	14	8
4	139	78	10	44	3	0	0	3	1	0
5	68	12	25	4	23	3	0	0	1	0
6	100	14	11	56	8	0	0	9	2	0
All	640	155	81	216	88	11	3	42	25	19

Table 5. Gill net catch per unit effort (CPE) of northern pike, yellow bullhead, yellow perch, walleye, and black bullhead, and trap net CPE of pumpkinseed, bluegill, rock bass, bowfin, white sucker, black crappie, and common carp in model (n = 540) and verification (n = 100) lakes.

	Model lakes				Verification lakes			
	Mean	Median	Range	C.V.	Mean	Median	Range	C.V.
Northern pike	7.4	6.5	0 – 35.4	67.5	5.7	4.8	0 – 25.2	85.5
Pumpkinseed	3.9	2.3	0 – 65.7	146.6	2.9	1.9	0 – 13.6	110.0
Bluegill	33.8	21.6	0 - 352	116.7	28.6	21.5	0 – 140.1	94.3
Yellow bullhead	3.8	0.8	0 – 85.7	214.7	2.6	0.3	0 – 90.7	366.4
Rock bass	1.0	0	0 – 28.3	272.9	0.6	0	0 – 12.5	273.5
Bowfin	0.4	0.2	0 – 3.9	144.5	0.4	0.1	0 – 3.4	157.0
White sucker	0.4	0.1	0 – 20.3	329.7	0.4	0.1	0 – 4.1	173.1
Yellow perch	18.1	8.5	0 – 275.5	152.1	18.6	10	0 – 163.5	145.0
Walleye	4.1	2.6	0 – 38.7	117.5	4.9	2.8	0 – 29.0	129.5
Black crappie	5.5	1.6	0 – 125.0	219.1	7.1	2.4	0 – 157.9	251.7
Black bullhead	15.3	0.7	0 – 380.0	256.2	16.5	0.8	0 – 300.3	268.3
Common carp	0.9	0	0 – 114.0	634.7	0.8	0	0 – 10.7	257.8

Table 6. Correlation coefficients between catch per effort of 12 fish species and 3 principal component (PC) loadings (n = 540). Also shown are the eigenvalues and percent of variation in the data set accounted for by each of the first 3 principal components.

Species	PC 1	PC 2	PC 3
Northern pike	-0.60	-0.04	0.33
Pumpkinseed	-0.54	0.10	0.49
Bluegill	-0.50	-0.23	0.51
Yellow bullhead	-0.49	-0.13	0.24
Rock bass	-0.41	0.62	-0.14
Bowfin	-0.11	0.05	0.43
White sucker	0.25	0.72	0.10
Yellow perch	0.38	0.49	0.42
Walleye	0.32	0.70	0.26
Black crappie	0.51	-0.45	0.41
Black bullhead	0.64	-0.25	0.30
Common carp	0.72	-0.12	0.22
Eigenvalue	2.814	1.998	1.445
Percent of variation	23.5	16.7	12.0

second principal component (PC2) explained 16.7% of the variation in the data set, and described a gradient ranging between high CPE of white sucker, walleye, and rock bass (+ correlations) to high CPE of black crappie (- correlation) that occurs after removing the variation explained by PC1. Finally, the third principal component (PC3), which described 12.0% of the variation in fish CPE, appeared correlated with CPE of bluegill and pumpkinseed.

Plant cover – fish abundance relationships

Plant cover factors explained a considerable amount of variation in CPE of several fish species (Table 7). The highest R^2 (51%) was for the linear model using the first principal component of fish abundance (PC1) as the response variable; all plant cover factors and interaction terms were significant in this model except for the cover type x littoral area interaction (Table 8). Models for most species and the two fish abundance principal components appeared robust and repeatable because they explained similar amounts of variation (R^2) in both the model and verification sets of lakes (Table 7).

Table 7. Amount of variation (R^2) in principal components (PC) 1 and 2, and catch per effort of northern pike, pumpkinseed, bluegill, yellow bullhead, rock bass, bowfin, white sucker, yellow perch, walleye, black crappie, black bullhead, and common carp explained by linear models with all plant cover factors for model and verification lakes. In addition, variation explained by Ecological Lake Class (ELC classes 24, 25, 27, 4, and 43; MNDNR unpublished data)), Plant Cover Groups (PCG 1-6; this study), and Plant Community Classes (PCC classes 1, 16, 40, 42, 59, 66, 117, 134; Reschke et al. 2005);) and by ELC and PCG and by PCC and PGC among a subset of 261 lakes. One-way ANOVA was used to determine the variation explained singly by PGC, ELC, and PCC and two-way ANOVA was used to determine the variation explained by PGC and PCC, and PGC and ELC.

Principal Component / Fish Species	Linear Model (Model set n=540)	Linear Model (Verification set n=100)	Plant Cover Group (PCG)	Plant Community Class (PCC)	Ecological Lake Class (ELC)	PCG and PCC	PCG and ELC
PC1	51	54	42	37	37	48	53
PC2	36	37	16	15	36	21	39
Northern pike	23	31	15	9	8	15	16
Pumpkinseed	16	9	15	12	6	18	15
Bluegill	10	15	7	8	10	10	13
Yellow bullhead	15	6	7	8	7	10	10
Rock bass	28	32	20	19	42	26	43
Bowfin	14	14	6	2	6	7	12
White sucker	15	9	3	1	12	3	12
Yellow perch	16	10	6	5	11	9	14
Walleye	43	51	9	10	36	16	40
Black crappie	28	15	27	27	28	34	33
Black bullhead	29	33	23	23	37	28	41
Common carp	45	44	35	29	26	41	41

Table 8. Linear statistical models fitted with least squares for predicting the effects of plant cover factors (Plant Cover Group, wind-wave energy, percent littoral area, and alkalinity) on fish catches (principle components 1 and 2; $\log_{10}$ +1 catch per effort of northern pike, pumpkinseed, bluegill, yellow bullhead, rock bass, bowfin, white sucker, yellow perch, walleye, black crappie, black bullhead, and common carp) in Minnesota DNR lake surveys. Model set = 540 lakes and verification set = 100 lakes.

PC1

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	804.8548	34.994	25.3641	<0.0001
- plant cover group (PCG)	5	367.3731		53.2558	<0.0001
- littoral	1	14.9895		10.8647	0.001
- alkalinity	1	6.5714		4.7631	0.030
- wind-wave energy	1	20.8295		15.0976	<0.0001
- PCG * littoral	5	2.6442		0.3833	0.860
- PCG * alkalinity	5	38.7292		5.6143	<0.0001
- PCG * wind-wave energy	5	26.8929		3.8985	0.0018
Error	516	711.9024	1.380		
Total	539	1516.7571			

PC2

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	421.3999	18.322	14.4187	<0.0001
- plant cover group (PCG)	5	134.7594		21.2104	<0.0001
- littoral	1	24.0530		18.9291	<0.0001
- alkalinity	1	1.3049		1.0269	0.3114
- wind-wave energy	1	76.2692		60.0219	<0.0001
- PCG * littoral	5	22.1855		3.4919	0.0041
- PCG * alkalinity	5	4.8465		0.7628	0.5769
- PCG * wind-wave energy	5	15.7339		2.4764	0.0313
Error	516	655.6760	1.2707		
Total	539	1077.0795			

Northern Pike

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	11.5834	0.504	7.9025	<0.0001
- plant cover group (PCG)	5	4.3213		13.5611	<0.0001
- littoral	1	1.5891		24.9346	<0.0001
- alkalinity	1	0.1467		2.3012	0.130
- wind-wave energy	1	0.0287		0.4499	0.503
- PCG * littoral	5	0.7518		2.3593	0.039
- PCG * alkalinity	5	0.9727		3.0526	0.010
- PCG * wind-wave energy	5	1.0371		3.2546	0.007
Error	516	32.8851	0.064		
Total	539	44.4687			

Pumpkinseed

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	12.4998	0.543	5.350	<0.0001
- plant cover group (PCG)	5	4.8822		9.6284	<0.0001
- littoral	1	1.4905		4.8717	0.0278
- alkalinity	1	0.0468		0.4615	0.4972
- wind-wave energy	1	0.0859		0.8469	0.3579
- PCG * littoral	5	0.7051		1.3906	0.2262
- PCG * alkalinity	5	0.5422		1.0694	0.3764
- PCG * wind-wave energy	5	0.3861		0.7615	0.5779
Error	516	52.3290	0.101		
Total	539	64.8288			

Table 8. Continued

Bluegill

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	19.7271	0.858	3.6983	<0.0001
- plant cover group (PCG)	5	8.6397		7.4467	<0.0001
- littoral	1	0.1976		0.8515	0.3566
- alkalinity	1	0.0728		0.3139	0.5756
- wind-wave energy	1	0.7069		3.0466	0.0815
- PCG * littoral	5	1.3492		1.1629	0.3263
- PCG * alkalinity	5	4.3733		3.7694	0.0023
- PCG * wind-wave energy	5	2.5010		2.1555	0.0577
Error	516	119.7341	0.232		
Total	539	139.4611			

Yellow bullhead

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	18.7557	0.816	5.2183	<0.0001
- plant cover group (PCG)	5	4.6203		5.9070	<0.0001
- littoral	1	3.8253		24.4527	<0.0001
- alkalinity	1	0.5065		3.2379	0.0725
- wind-wave energy	1	0.4105		2.6241	0.1059
- PCG * littoral	5	2.2062		2.8206	0.0159
- PCG * alkalinity	5	2.6139		3.3418	0.0056
- PCG * wind-wave energy	5	0.9125		1.1666	0.3244
Error	516	80.7215	0.1564		
Total	539	99.4972			

Rock bass

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	10.7993	0.4695	10.0693	<0.0001
- plant cover group (PCG)	5	6.3470		27.2228	<0.0001
- littoral	1	1.1143		23.8958	<0.0001
- alkalinity	1	0.0628		1.3473	0.2463
- wind-wave energy	1	0.1879		4.0293	0.0452
- PCG * littoral	5	0.8781		3.7662	0.0023
- PCG * alkalinity	5	0.2598		1.1144	0.3516
- PCG * wind-wave energy	5	0.2420		1.0380	0.3944
Error	516	24.0612	0.0466		
Total	539	34.8606			

Bowfin

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	2.0727	0.0901	4.6878	<0.0001
- plant cover group (PCG)	5	1.1028		11.4736	<0.0001
- littoral	1	0.0818		4.2529	0.0397
- alkalinity	1	0.0379		1.9702	0.1610
- wind-wave energy	1	0.1955		10.1672	0.0015
- PCG * littoral	5	0.1375		1.4307	0.2115
- PCG * alkalinity	5	0.0995		1.0347	0.3964
- PCG * wind-wave energy	5	0.1751		1.8219	0.1068
Error	516	9.9194	0.0192		
Total	539	11.9921			

Table 8. Continued

White sucker

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	7.7224	0.3358	5.1794	<0.0001
- plant cover group (PCG)	5	0.7975		2.4606	0.0322
- littoral	1	0.5873		8.7506	0.0032
- alkalinity	1	0.2800		4.3202	0.0382
- wind-wave energy	1	1.2114		18.6869	<0.0001
- PCG * littoral	5	0.5208		1.6069	0.1565
- PCG * alkalinity	5	0.5556		1.7142	0.1296
- PCG * wind-wave energy	5	0.8678		2.6774	0.0211
Error	516	33.4498	0.0648		
Total	539	41.1722			

Yellow perch

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	33.5891	1.4604	5.5297	<0.0001
- plant cover group (PCG)	5	6.1628		4.6670	0.0004
- littoral	1	1.3357		5.0576	0.0249
- alkalinity	1	1.0670		4.0403	0.0449
- wind-wave energy	1	5.4799		20.7498	<0.0001
- PCG * littoral	5	2.0966		1.5877	0.1618
- PCG * alkalinity	5	0.4766		0.3609	0.8752
- PCG * wind-wave energy	5	0.5974		0.4524	0.8116
Error	516	136.2749	0.2641		
Total	539	169.8640			

Walleye

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	33.5513	1.4586	18.8782	<0.0001
- plant cover group (PCG)	5	1.4552		3.7664	0.0023
- littoral	1	0.1118		1.447	0.2296
- alkalinity	1	0.5651		7.3133	0.0071
- wind-wave energy	1	11.9848		155.099	<0.0001
- PCG * littoral	5	0.4698		1.2159	0.3003
- PCG * alkalinity	5	0.1416		0.3665	0.8715
- PCG * wind-wave energy	5	0.7356		1.9040	0.0920
Error	516	39.8722	0.0773		
Total	539	73.4235			

Black Crappie

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	31.407	1.367	10.259	<0.0001
- plant cover group (PCG)	5	21.507		32.3139	<0.0001
- littoral	1	0.1098		0.8255	0.364
- alkalinity	1	0.0001		0.0007	0.980
- wind-wave energy	1	0.0112		0.0838	0.772
- PCG * littoral	5	1.0396		1.5619	0.169
- PCG * alkalinity	5	0.9430		1.4169	0.217
- PCG * wind-wave energy	5	0.8719		1.3100	0.258
Error	516	66.6853	0.133		
Total	539	100.0923			

Black bullhead

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	76.8774	3.3425	10.4918	<0.0001
- plant cover group (PCG)	5	40.5599		25.4628	<0.0001
- littoral	1	1.0623		3.3344	0.0684
- alkalinity	1	4.2302		13.2784	0.0003
- wind-wave energy	1	0.6691		2.1003	0.1479
- PCG * littoral	5	1.0493		0.6587	0.6550
- PCG * alkalinity	5	5.2488		3.2951	0.0061
- PCG * wind-wave energy	5	3.1911		2.0033	0.0767
Error	516	164.3877	0.3186		
Total	539	241.3651			

Table 8. Continued

Common carp

Source	df	Sum of Squares	Mean Square	F Ratio	Prob. > F
Model	23	14.6415	0.6366	20.3542	<0.0001
- plant cover group (PCG)	5	5.6942		36.4135	<0.0001
- littoral	1	0.0732		2.3417	0.1266
- alkalinity	1	0.3528		11.2818	0.0008
- wind-wave energy	1	0.6715		21.4706	<0.0001
- PCG * littoral	5	0.1281		0.8190	0.5364
- PCG * alkalinity	5	0.0620		0.3965	0.8513
- PCG * wind-wave energy	5	0.5946		3.8022	0.0022
Error	516	16.1381	0.0313		
Total	539	30.7796			

Much of the differences in CPE of individual fish species among Plant Cover Groups were reflected in differences in PC1 scores (Table 9). Lakes in PCG 1 had higher PC1 values and high CPE of black bullhead, common carp, and black crappie. Differences in mean PC1 values among the remaining plant cover groups were not as large, but followed a gradient from highest in lakes with lower occurrences and diversity of cover types (PCG 1 and 3) to those with high occurrences of many different cover types (PCG 2 and 4). CPE of northern pike and pumpkinseed was lower in PCG 1 and higher in PCG 4 (Table 9).

Abundances of individual fish species responded differently to other plant cover factors (Table 8). Higher littoral area favored species with low PC1 scores (i.e., northern pike, pumpkinseed, and yellow bullhead), and had an insignificant or a small effect on species with high PC1 scores (i.e. walleye, black crappie, and common carp). Littoral area was generally negatively associated with most species that had high PC2 scores (i.e., rock bass, white sucker, and yellow perch). Wind-wave power was positively associated with higher catches of fish with high PC2 scores, especially walleye. In general, the effects of alkalinity and interaction terms in the linear models were weak. However, alkalinity did affect fish species with large PC1 scores, especially black bullhead and common carp.

Plant cover group explained considerable variation in fish CPE among Minnesota lakes, similar to that explained by the ELC and by PCC (Table 7). PCG accounted for a little more of the variation in the PC1 gradient than PCC, and more of the variation in CPE of northern pike and common carp. Little additional variance was explained by adding PCG to PCC in a two-way ANOVA model, which indicates that they are similarly associated with differences among lakes with respect to their fish populations. Although PCG and ELC explained about the same amount of variation in fish CPE among lakes, they differed in how they were associated with fish species. In general, PCG explained more of the variation in PC1 than ELC and less of the variation in PC2. Therefore, as might be expected, more variation in fish CPE was explained using both PCG and ELC as explanatory variables in two-way ANOVA models. When comparing results of the two way ANOVA PCG-ELC model with our linear model summarizing plant cover effects (PCG with the three key environmental factors related to the density and distribution of plant cover), it should be noted that the two way PCG-ELC ANOVA only performed better for two fish species, rock bass and black bullhead (Table 7). Therefore, the abundance of these two species is more related to factors other than plant cover.

Discussion

Our findings clearly show associations between fish populations and plant structure among Minnesota lakes. Plant cover frequency explains a considerable amount of variation in fish CPE associated with a

Table 9. Least square means of principal components (PC) 1 and 2, and catch per effort of northern pike (NOP), pumpkinseed (PMK), bluegill (BLG), yellow bullhead (YEB), rock bass (RKB), bowfin (BOF), white sucker (WTS), yellow perch (YEP), walleye (WAE), black crappie (BLC), black bullhead (BLB), and common carp (CAP) in six plant classification groups; means with the same letter within vertical groupings did not differ (*P* > 0.05; Tukey's Honestly Significant Difference tests).

Plant Classification Group	PC 1	PC 2	NOP	PMK	BLG	YEB	RKB	BOF	WTS	YEP	WAE	BLC	BLB	CAP
1	2.46a	-0.42cd	2.5c	1.0c	7.7c	0.4c	<0.1b	0.1c	1.0ab	14.5a	3.9ab	6.3a	15.9a	1.7a
2	-0.80d	0.17bc	6.8ab	2.9ab	20.6ab	2.5a	0.7a	0.3bc	1.1ab	4.9c	1.9bc	1.2b	1.0d	0.1d
3	0.54b	-0.73d	5.3b	2.4b	28.7a	1.4b	<0.1b	0.4ab	0.8b	8.0b	2.5abc	5.6a	6.4b	0.5b
4	-0.78d	0.64a	8.1a	3.9a	15.9b	1.6ab	0.9a	0.5a	1.3a	9.0ab	2.6abc	1.3b	1.0d	0.1d
5	0.07bc	-0.58d	5.8ab	2.8ab	24.0ab	1.5abc	<0.1b	0.6a	0.8ab	8.7ab	1.2c	3.2a	4.1bc	0.4bc
6	-0.24c	0.47ab	6.0ab	1.9bc	23.5ab	1.4ab	0.8a	0.1c	1.2ab	8.7ab	4.4a	1.3b	1.9cd	0.2cd

dominant fish community gradient among Minnesota lakes, a gradient that differentiates between phytophyls and benthic omnivores. These findings are consistent with those of Radomski and Goeman (2001) that showed the reduction of emergent plant cover types resulted in decreased abundances of phytophilic species such as bluegill and northern pike. Our findings are also consistent with those of Drake and Valley (2005) that showed phytophylic species in higher abundance with greater plant diversity. In general, plant cover type frequency was more powerful for explaining variation in fish CPE than the other plant cover factors we analyzed (i.e., plant littoral area, alkalinity, and wind-wave energy). Even though the frequency distribution of plant types among MN DNR lake surveys is quite variable, such information can be valuable for evaluating the effects of plant community change on fish populations in Minnesota lakes.

Associations between plant cover and CPE are probably affected by the biology of different fish species and life stages. Different life stages may benefit from different plant forms; consequentially, higher diversity of cover types will be more beneficial for many species. For example, young bluegills are commonly observed in dense vegetation, while larger bluegills frequent much sparser vegetation (Baumann and Kitchell, 1974). Additionally, some of the observed associations between fish CPE and plant cover could also be explained by fish directly altering the type and frequency occurrence of plant cover in lakes. Benthivorous fish can cause physical damage by uprooting and consumping plants. Furthermore, increased nutrients generated from these activities can trigger a trophic cascade, whereby increases in planktonic algae shade out various plant cover types. For example, common carp and black bullheads are both known to physically uproot plants and increase turbidity (Parkos et al. 2003). High populations of planktivorous fish such as fathead minnow, sunfish, and crappie have also been shown to trigger a trophic cascade resulting in increased algal biomass that decreases macrophyte complexity in lakes (Shapiro and Wright 1984; Zimmer et al. 2001).

Our results showing the effects of wind-wave power, littoral area, and alkalinity on CPE of fish in Minnesota lakes were consistent with the biology of these species. Alkalinities tend to be higher in shallow southwest Minnesota lakes that are often dominated by algae blooms that limit vascular plant cover. Common carp and black bullhead are common in algal dominated lakes, and may contribute to the switch from vascular plant cover to algal domination (Braig and Johnson 2003). Northern pike were strongly associated with littoral (plant habitat) area. Northern pike are top predators that feed by concealment and ambush (Eddy and Underhill 1974), a tactic that would favor lakes with large areas of plant cover. Wind-wave power had a strong association with the fish community gradient described by PC2 and with walleye CPE in particular. Because PCG was not very influential on walleye CPE, we assume the effect of wind-wave power affects walleye in other ways besides its effect on plant communities. Spawning walleye typically require substrates free of silt and periphyton (Newburg 1975) that could be fostered by wave action in shoal areas. In fact, Newburg (1975) stated that lakes less than 243 ha were unlikely to have sufficient wave action to keep spawning shoals clean. As predators, walleye may also obtain an advantage over prey that becomes disorientated and vulnerable due to wave action.

This study was limited to widely distributed fish species that are commonly captured in standardized MNDNR lake survey nets, so we are unable to make conclusions about entire fish communities in Minnesota lakes. There are insufficient data for some fish species because they are not vulnerable to standardized lake survey sampling gear (e.g., largemouth bass have been shown to have strong associations with aquatic plant cover). Many fish species (e.g. minnow, darters, some *Lepomis* spp.) are seldom captured by either gill or trap netting, and could be expected to have indirect effects as forage or competitors to the species we analyzed. Some fish species not commonly captured in our nets were probably rare because of more specific habit requirements. Because of these specific habitat requirements, analysis of plant habitat associations for these species could be especially valuable for identifying the effects of natural or human induced plant community change. Additional analysis using presence and absence data for uncommon and nongame fish species may provide insight into the associations of these species with variation in plant cover among Minnesota lakes.

Despite the high level of statistical significance of our models of fish catches in Minnesota lakes using plant cover data, a lot of unexplained variation remains in fish catches. Much of this unexplained variation could simply be the result of sampling or measurement error. The physical variables that Schupp (1992) used to model fish populations in Minnesota lakes had a comparable amount of unexplained variation. Schupp (1992) cited varying year class strengths and seasonal effects as contributing to the unexplained error in models of fish abundance in Minnesota lake survey data. Cross et al. (1995) documented a seasonal affect in trap net CPE of bluegill in standardized MNDNR lake surveys that could account for 40% of the variation in the data. High variation is typical for CPE data, and this results in low statistical power for detecting differences among lakes without very large sample sizes (Krueger et al. 1998). An advantage of using a large data set of net catches, such as the MNDNR lake survey data set, is that it provides enough statistical power to identify some of the relationships that exist among lakes despite the large unexplained error associated with net catches.

The results of our study should be interpreted cautiously because it is a large-scale observational study without controls on factors correlated with our plant cover variables that could also explain variation in fish populations. For example, the length of growing season and water temperatures could affect fish populations, and follow similar north-south geographic gradient to the distribution of plant cover types, wind-wave energy, and alkalinity. Differences in watershed characteristics may affect both fish and aquatic plants. Water levels tend to bounce erratically in lakes with large watersheds (drainage) in response to short-term surface runoff; whereas, lakes without outlets (seepage) generally respond more to longer term variation in precipitation that alters the water table leading to extended periods of very high or low water levels. Water level changes are known to influence plant cover (Wilcox and Meeker 1992). Differences in fish populations may also be related to watershed differences. For example, various types of flooded habitats in water bodies connected through lake watersheds can affect species such as northern pike and common carp (Navarro and Johnson 1992). Additional research is needed to identify plant species associations characteristic of particular physiochemical regimes in lakes (water level regime, alkalinity and other chemical and nutrient dynamics, substrates and sedimentation, wind-wave energy, temperature, sunlight, slope, aspect). This information could then be used to separate the effects of these same physical-chemical factors on fish from their indirect effects through plants.

Management strategies aimed at maintaining native plant habitat conditions in harmony with natural conditions can be effective for protecting fish populations. Lake management that reduces the frequency occurrence of diverse plant cover types is likely to influence fish populations. Efforts to protect and enhance aquatic plant habitats for fish entail both site specific and broad-scale approaches. At the site-scale, existing plant communities in Minnesota lakes can be protected through MNDNR shoreland and aquatic plant management regulations. In addition, MNDNR aquatic management areas and a shoreland restoration program have been initiated to address plant habitat losses starting at the site-scale. However, broad-scale land use (Reschke et al. 2006) and watershed influences (Cross and McInerny 2001) ultimately overwhelm any work done at the site-scale, so it is critical these factors are addressed prior or concurrent to site-scale efforts. Although broad-scale factors such as nutrient loading, siltation, chemical pollution, invasive species, and altered hydrology are commonly outside the direct control of fish managers, they can have pervasive consequences on fish abundance and community composition.

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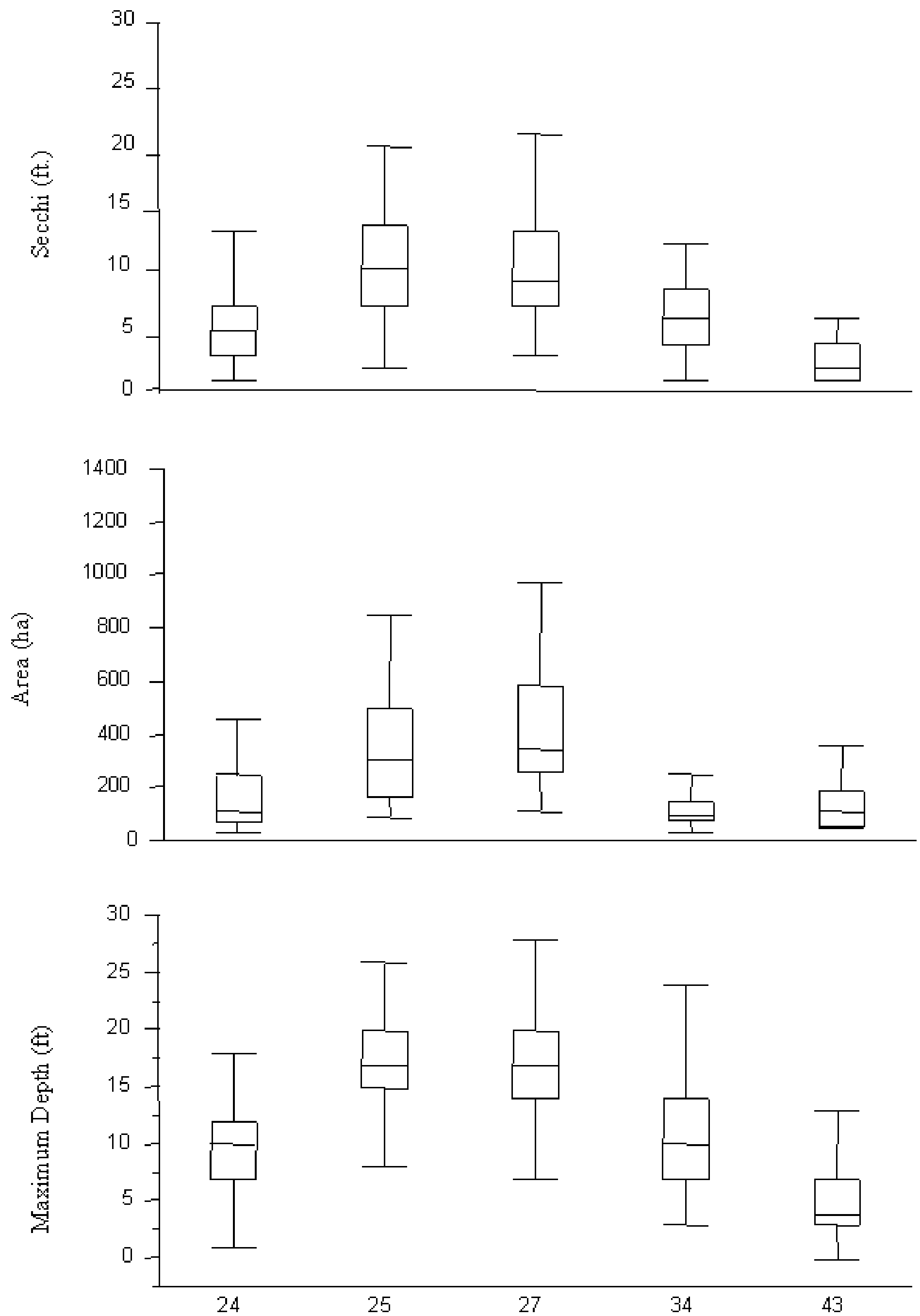
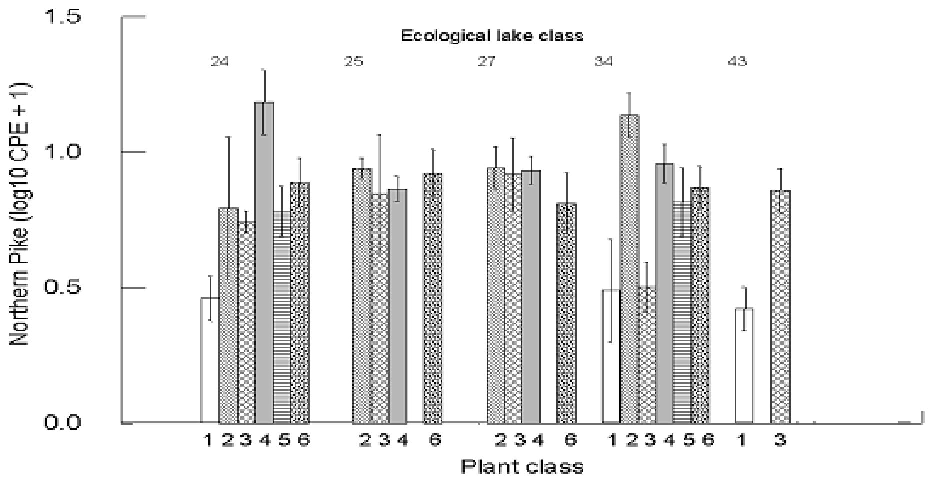
Appendix I. Composition of plant community types classified by Reschke et al. (2005) from MNDNR Fisheries Lake Survey plant transect data. Shown are the sum of importance values for each plant community class and taxon with highest importance values.

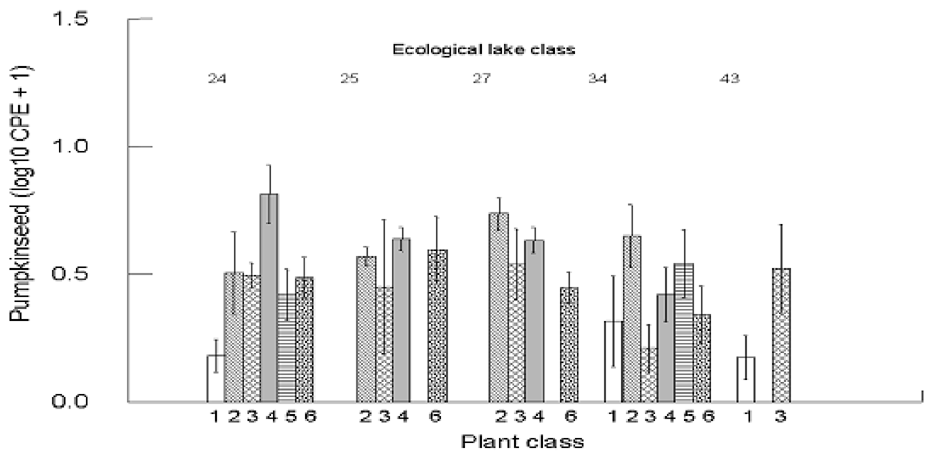
Plant Community Types	Sum of Species Importance Values	Dominant Species				
1	396	coontail	flatstem pondweed	Chara	yellow lily	northern milfoil
3	220	carex sp.	white lily	yellow lily	bushy pondweed	water shield
16	255	chara	bushy pondweed	flatstem	coontail	northern milfoil
40	215	coontail	elodea	Broad-leaf cattail	lesser duckweed	eurasian milfoil
42	37	broad-leaf cattail	narrow-leaf cattail			
59	121	carex	yellow lily			
66	148	algae	sago pondweed	northern milfoil	coontail	flatstem pondweed
117	97	elodea	curled-leaf pondweed	Algae	white lily	
134	79	sago pondweed	curled-leaf pondweed	Broad-leaf cattail		

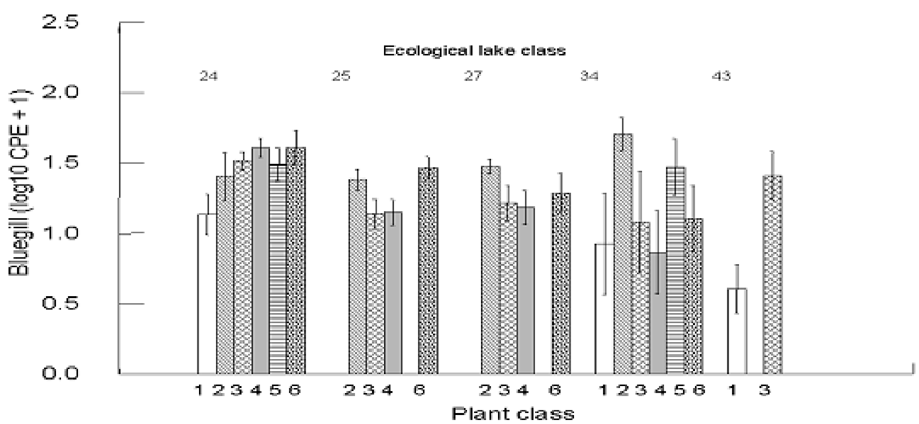
Appendix II. Box whisker plot (median, 25 percent quartile, 75 percent quartile, and range) describing Secchi disk transparency, surface area, and maximum depths of five Ecological Lake Classes (24, 25, 27, 34, 43) used in Appendix III.



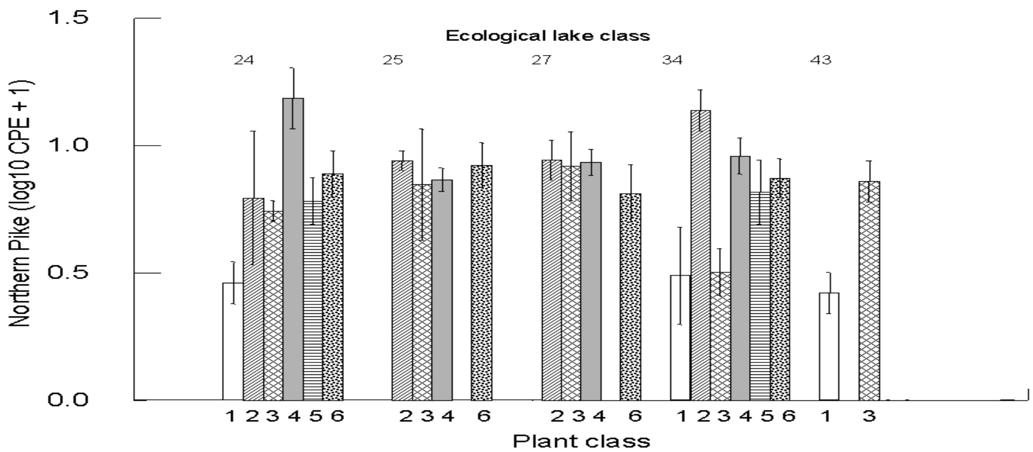
Appendix III. Catch per unit effort (CPE) of 12 selected fish species in 5 Ecological Lake Classes by Plant Cover Group. Vertical bars show standard error.

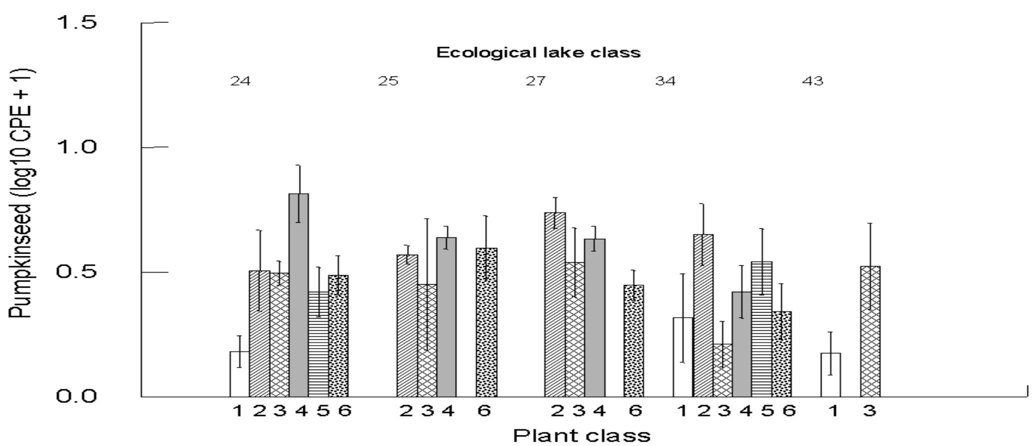


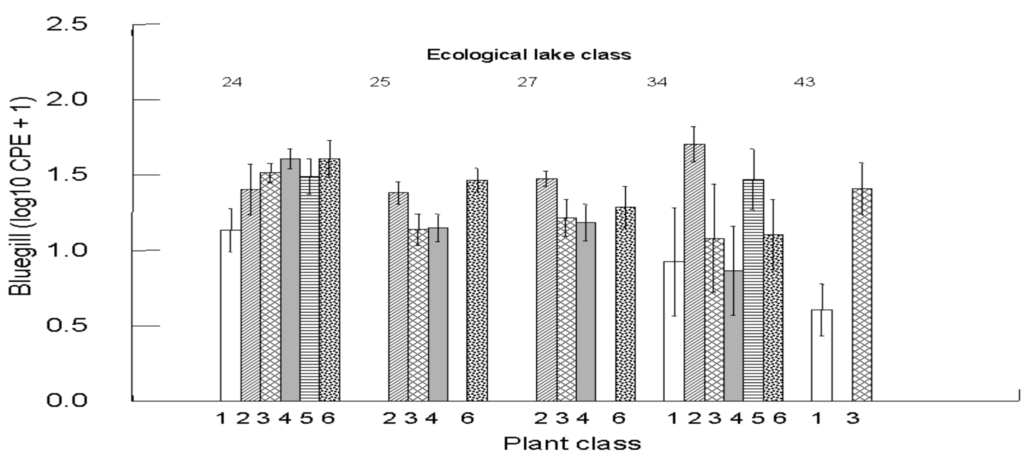




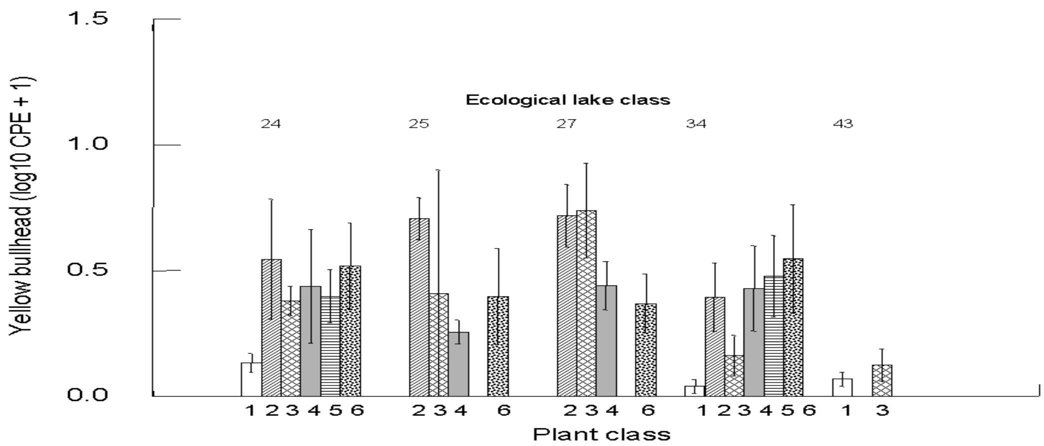
Appendix III. Continued.

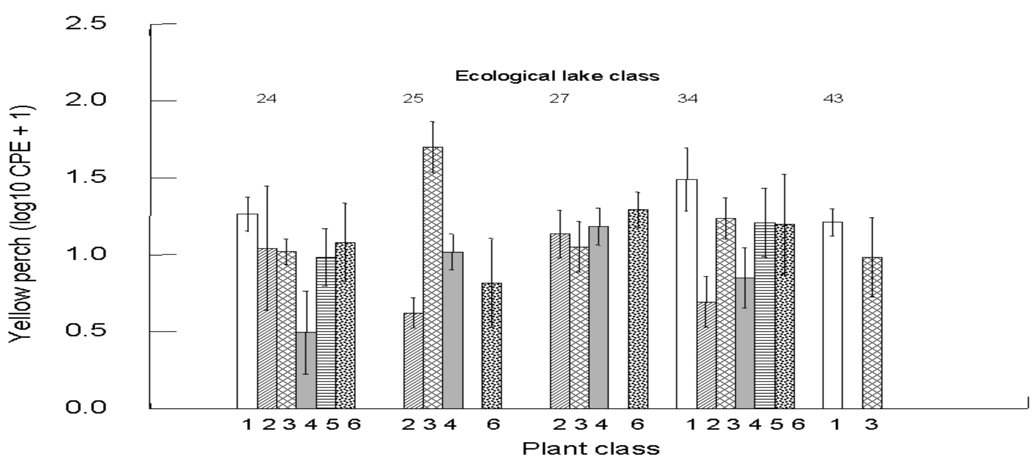


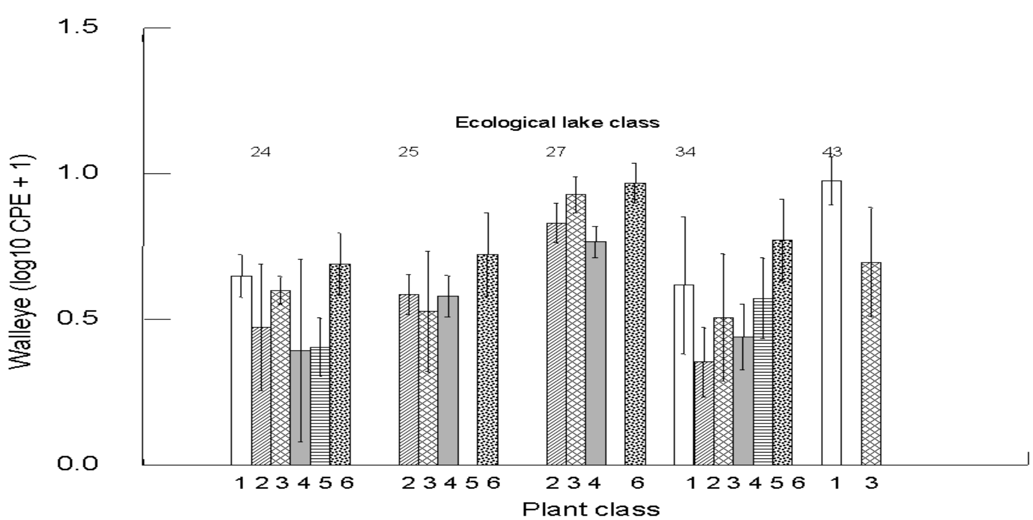




Appendix III. Continued.







Appendix III. Continued.