IMPLEMENTATION AND INTERPRETATION OF LAKES ASSESSMENT DATA FOR THE UPPER MIDWEST

Final Report to U.S. EPA

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INTRODUCTION

Lake assessment and condition monitoring is a continuing goal of both the US EPA as well as state and local units of government. Often the goal of the assessment is quite different between these organizations. EPA, for example, is interested in examining lakes across a region or from a national perspective in terms of overall health and condition of the lacustrine resource. The questions are broad and general and at a scale that sometimes appears inappropriate or even uninteresting to state environmental agencies, local units of government, or citizen-based lake associations. National or regional EPA questions are in sharp contrast to the questions of local government or the public. Local questions are more often focused on "how is my lake doing? Is it healthy? Does it have a healthy fish community? Does it have a diverse macrophyte community? Is my lake aesthetically pleasing and does it enhance our community"? While somewhere in the middle, state environmental agencies are often most focused on: Is this lake attaining its designated use? What are the water quality problems (e.g. point source versus non-point source inputs), how do we set phosphorus standards in lakes statewide, how do we manage the watersheds, implement and evaluate best management practices? What do we report to EPA for 305b and 303d lists?

With these diverse questions and multiple needs of resource managers, government, and citizens, lake assessment tools and monitoring must be robust and applicable to multiple scales. Simply developing general tools and defining broad scale relationships between lake metrics and stressor gradients that can be used at the nationwide level is really of only interest to one constituent group. For states to successfully implement a holistic lake assessment program, the methodology employed must be designed to produce data that is able to answer questions at multiple scales, ranging from those posed by local individual lake associations to National Clean Water Act questions of overall ecosystem condition and health.

In this study, we describe work that addresses three components of progress toward a whole lake and bioassessment strategy for application to Wisconsin lakes. Wisconsin has over 15,000 lakes and is representative of the northern Lakes area of the upper Mid-West that includes lakes in Minnesota and Michigan. The first component addresses issues of statistical methodology and geographic scale in development of a lakes classification framework for lake assessment. The second component evaluates relations between potential biological indicators, habitat-based indicators, and water quality based indicators and anthropogenic stressor variables. The third component tests concordance between stressor variables and three alternative sets of lake assessement tools based upon bioassessment, habitat, and traditional water quality measures of lake ecosystem condition. These tools will be evaluated for power and sensitivity to detect responses to anthropogenic stressors within defined lake classes at multiple spatial scales.

WATER QUALITY

Lake Classification, Reference Conditions, and Variables Explaining Trophic Status in Wisconsin Lakes

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Lake Classification

One of the objectives of this study was to establish a lakes classification system that addresses issues of statistical methodology and geographic scale in development of a lakes classification framework for lake assessment and monitoring. Lakes across the landscape, even within eco-regions, are naturally highly variable in terms of lake morphometry, landscape position, surface/groundwater interfaces, and soil conditions. An effective classification framework for use in lake assessment and monitoring should provide groupings or classes of lakes that have maximum within-class similarity (or minimum variance) across these conservative lake attributes that are not responsive to external change or perturbation. Classification systems that account for this variation can be used to group lakes subject to similar ecological processes, and thus provide an objective framework for setting expectations for responses to anthropogenic impacts across stressor gradients.

Mixed or Stratified

Lakes will be placed into the stratified category if they stratify throughout the summer or if they undergo intermittent stratification. In the current WI DNR lake classification system, 18 feet maximum depth is used as the criteria for stratification and aquatic plant potential; lakes over 18 feet are classified as stratified during the summer and lakes less than 18 feet are classified as mixed, with the potential for the majority of the lake to contain rooted aquatic plants. This doesn't consider that area and depth play a role in whether a lake permanently or intermittently stratifies during the summer.

Several models for predicting lake stratification based on depth and area have already been developed including Lathrop and Lillie's thermal stratification equation (1980), the Osgood Index (Osgood 1988), and the Minnesota "lake geometry ratio" (Heiskary and Wilson 2005).

The classification system that seems to work best with the available Wisconsin data is the Lathrop and Lillie (1980) thermal stratification equation. The equation used to separate stratified and mixed lakes is:

$$\frac{\text{Maximum Depth (meters)} - 0.1}{\text{Log}_{10}\ \text{Lake Area (hectares)}}$$

A value >3.8 predicts a stratified lake. We used this equation to categorized lakes as either stratified or mixed. We recognize that some lakes classified as stratified will in fact occasionally mix during the summer.

Hydrology

The second measure to consider is the lake hydrology (seepage or drainage). Lake hydrology classification is based on the inflow/outflow of surface water and lake watershed size. A lake with no surface water inflow or outflow is a seepage lake. Seepage lakes receive water primarily through precipitation and seepage into the lake from groundwater although there may be some overland sheet flow into the lake from runoff. If there is surface water flow into and/or out of a lake from a river or stream the lake is classified as a drainage lake.

An additional category for drainage lakes is based upon the size of the watershed. If the lake's watershed is less than 4 square miles, it is classified as a headwater drainage lake. If the watershed is greater than 4 square miles, it is classified as a lowland drainage lake. The size of the watershed for a seepage lake is not used in the classification scheme because seepage lakes generally have small watershed sizes.

This classification scheme results in 6 lake classes. They are:

1. Headwater, shallow drainage
2. Headwater, deep drainage
3. Lowland, shallow drainage
4. Lowland, deep drainage
5. Shallow seepage
6. Deep seepage

Figure 1 shows the breakdown of the 6 lake classes.

Water Quality

Environmental Characteristics

The environmental characteristics thought to affect water quality were compiled for each watershed as well as the 100 m buffer from the edge of each lake. Five land use variables were quantified for each scale of analysis. The variables used are:

- *House Density* (houses/km^2)
- *Agricultural Land* (%) included grassland/herbaceous, pasture/hay, and cultivated crops
- *Disturbed* (%) included developed, barrenland , pasture/hay, and cultivated crops
- *Undisturbed* (%) included open water, forest, and wetlands
- *Impervious surface* (%)
- *Forest Canopy* (%)

Data for housing density was obtained from the 2001 U.S. census (Radeloff et al. 2005) and the other data was obtained using the 2001 National Land Cover Database.

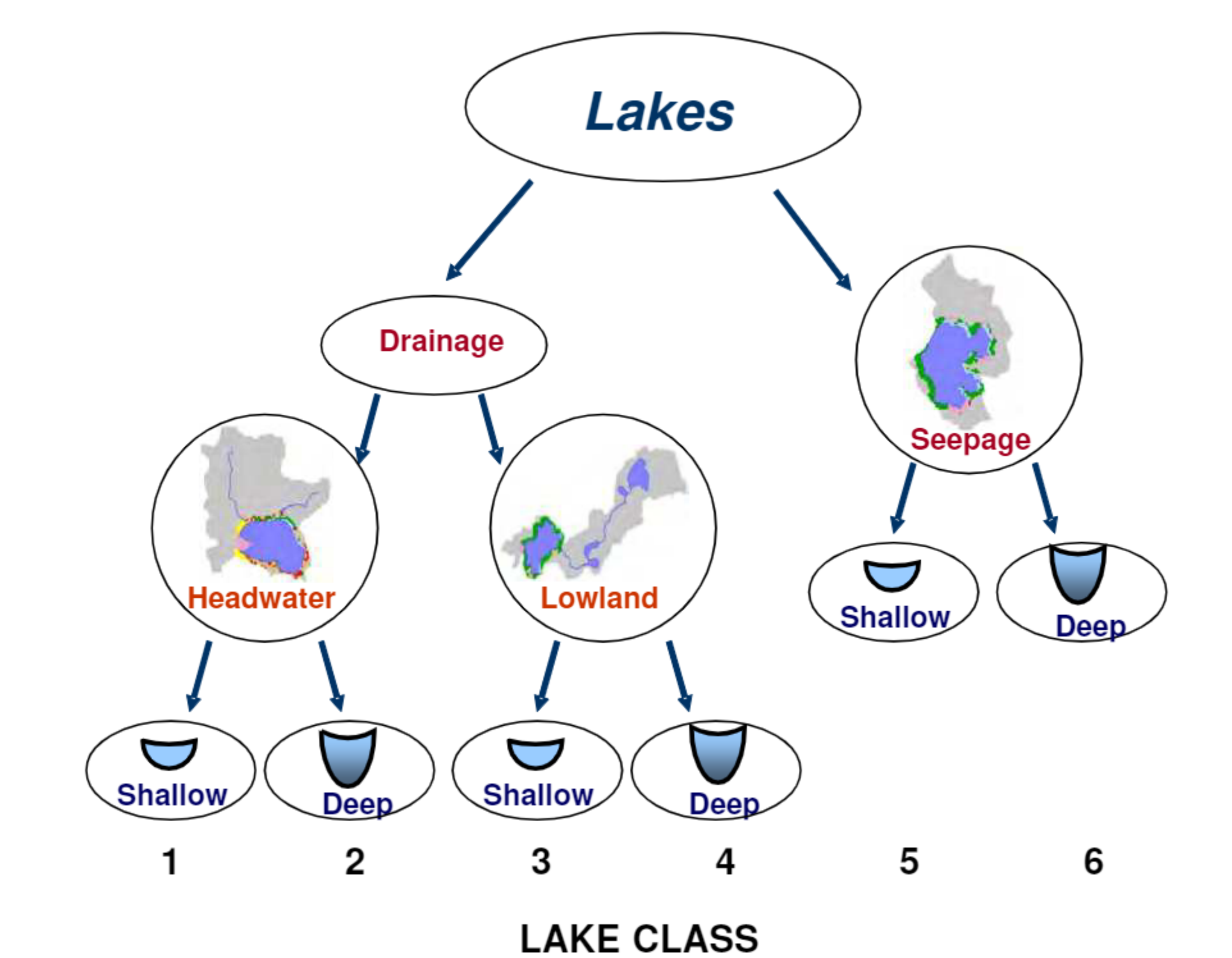


Figure 1. Schematic of the lake classification used in this study.

Water Chemistry

Lake data used in this study was obtained from a statewide database containing information collected by WDNR personnel and citizen volunteers. Secchi data was collected by onsite observers. Phosphorus data was analyzed at the Wisconsin State Laboratory of Hygiene and was rigorously QA/QCed. Data included in this study were collected between 2002-07 and at least 3 samples had to have been collected within a year between the months of July and September, inclusively. For this portion of the study phosphorus data from 177 lakes were used. Lake geographical distribution is shown in Figure 2.

Lakes were divided into the 6 lake classes previously described as well as well as Level III eco-regions (Omernick et al. 2000). Although Wisconsin contains 5 ecoregions (Figure 2), only 3 of them contain a significant number of lakes. These ecoregions are Southeastern Wisconsin Till Plains (SWTP), Northcentral Hardwood Forest (NCHF), and Northern Lakes and Forests (NLF). The small number of lakes in the ecoregions Driftless Area and Corn Belt and Northern Great Plains were included in the NCHF ecoregion.

The NLF ecoregion contained most of the lakes (112) while NCHF had the fewest (27 lakes). The lakes were not evenly distributed across the lake classes (Table 1). Class 4 (lowland, deep, drainage) had the most lakes followed closely by Class 3 (lowland, shallow, drainage). The classes with the fewest lakes were Class 1 (upland, shallow, drainage) and Class 5 (shallow seepage). Because this dataset did not contain adequate representation of all lake classes within the ecoregions we were not able to perform an analysis on each class within the ecoregions. Instead lakes were combined within ecoregions regardless of class or classes were combined regardless of ecoregion.

The lakes with the largest surface area tended to be in the NLF ecoregion where the median size was 137 ha (Table 2). The deepest lakes tended to be in the SWTP ecoregion although all ecoregions contained deep and shallow lakes. The dataset contained the deepest natural lake in the state

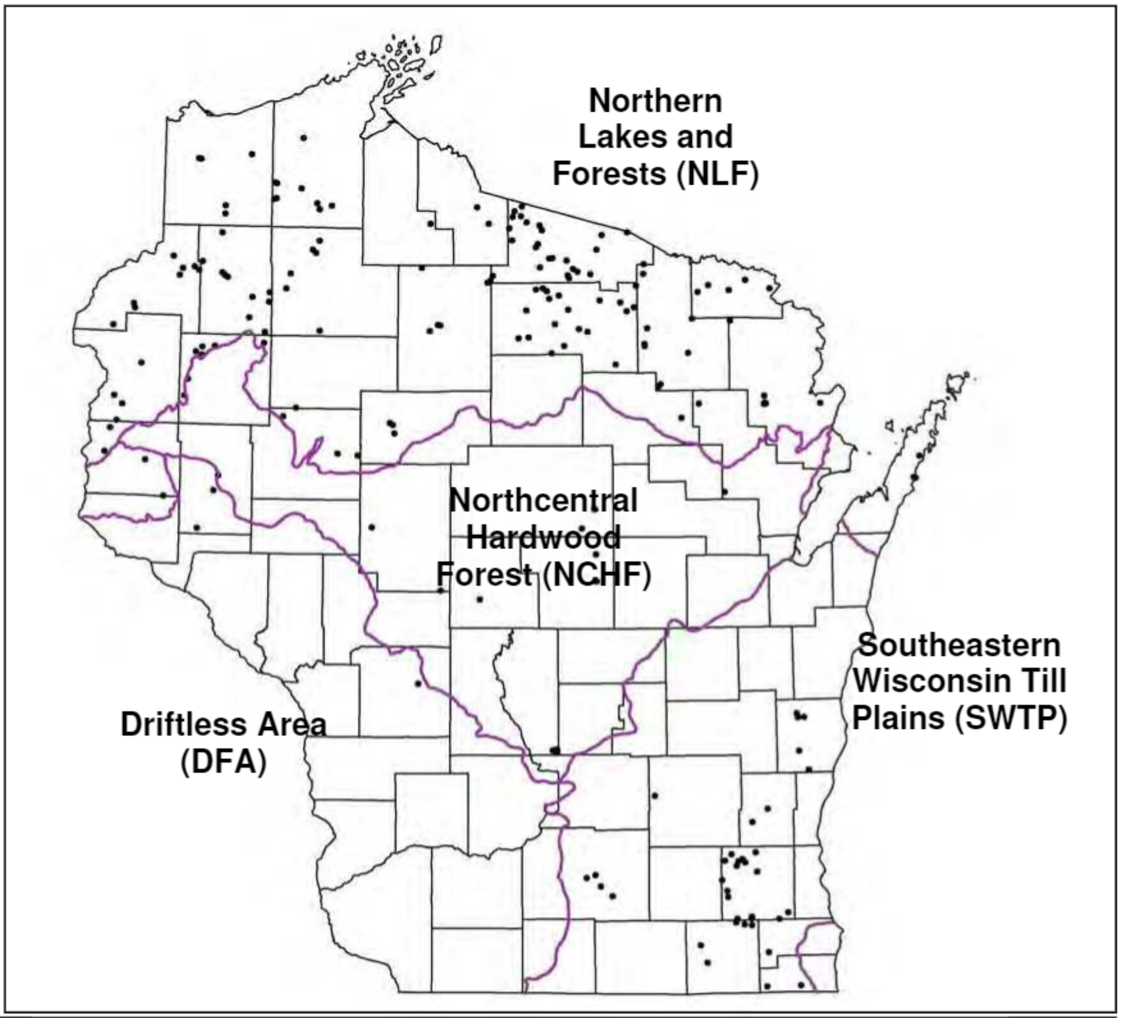


Figure 2. Location of the 177 lakes used in the water quality portion of the study. The level III ecoregion boundaries are also shown.

Table 1. Number of lakes in each lake class by ecoregion.

Class	SWTP	NCHF	NLF	TOTAL
1	5	1	10	16
2	8	1	14	23
3	7	10	24	41
4	11	5	32	48
5	1	2	11	14
6	6	8	21	35
TOTAL	38	27	112	177

SWTP = Southeatern Wisconsin Till Plains
NCHF = Northcentral Hardwood Forest
NLF = Northern Lakes and Forest

(Green Lake, Green Lake County) which has a maximum depth of 36.3 m.

The lake class with the largest lakes was lowland drainage lakes. In general, upland drainage lakes and seepage lakes were of similar size, regardless of lake depth (Table 3). The classification system segregates lakes into deep and shallow. Seepage lakes tended to be shallower while drainage lakes tended to be deeper.

Even though seepage lakes were not segregated by watershed size, their median watershed size was similar to upland drainage lakes. This was despite the fact that the maximum watershed size of both classes of seepage lakes was much larger than upland drainage lakes. This means that in terms of watershed size, seepage and upland drainage lakes could be classified similarly. The lakes in the NCHF ecoregion had somewhat larger watersheds than the other ecoregions but the distribution is skewed and median values were more similar.

The percentage of landuse in agriculture was smallest in the NLF ecoregion (Table 2). This is as expected since the climate and soils are generally not conducive for agriculture in the northern part of Wisconsin. The lakes in the other two ecoregions had similar amount of agriculture in their watersheds with the mean and median values near 50%. Lowland, shallow, drainage and deep seepage lakes tended to have the most agricultural in their watersheds.

Lakes in the NCHF ecoregion tended to have higher summer phosphorus values than the other two ecoregions. The median value for NCHF ecoregion was 52 µg L^{-1} while it was 21-22 µg L^{-1} for the other ecoregions (Figure 3a). As would be expected the worst water clarity was in the NCHF ecoregion (Figure 3b) with the median Secchi depth being 1.6 m. The best water clarity was in the NLF ecoregion (2.7 m) while in the SWTP ecoregion the median Secchi depth was 2.0 m.

The lake class with the lowest summer phosphorus concentration was deep seepage lakes, Class 6 with a median value of 15 µg L^{-1}. The lake class with the highest phosphorus concentrations

Table 2. Summary statistics by Ecoregion.

	Ecoregion	No. of Lakes	Mean	Median	Maxi-mum	***Minimum***
Size (ha)	SWTP	38	270	110	1325	22
	NCHF	27	193	100	745	20
	NLF	112	254	137	1451	32
Max Depth (m)	SWTP	38	12.0	11.4	36.3	1.2
	NCHF	27	10.0	8.5	32.3	1.8
	NLF	112	11.7	9.9	32.0	2.4
Secchi (m)	SWTP	38	2.2	2.0	5.1	0.2
	NCHF	27	1.8	1.6	4.2	0.4
	NLF	112	3.1	2.7	8.0	0.8
TP ($\mu g\ L^{-1}$)	SWTP	38	49	22	584	7
	NCHF	27	91	52	501	13
	NLF	112	26	21	149	6
Watershed (mi^2)	SWTP	38	45	5	402	1
	NCHF	27	158	7	1761	1
	NLF	112	32	4	848	1
Watershed ag (%)	SWTP	38	47	50	78	3
	NCHF	27	42	46	78	7
	NLF	112	5	2	42	0

SWTP = Southeastern Wisconsin Till Plains
NCHF = Northcentral Hardwood Forest
NLF = Northern Lakes and Forests

was Class 3, lowland, shallow drainage lakes (Figure 4a). In general, seepage lakes tended to have lower phosphorus levels while shallow drainage lakes had the highest concentrations. These latter types of lakes also had the greatest range of phosphorus concentrations. The best water clarity was found in lakes in Classes 2 and 6 (Figure 4b). These are deep, highland, drainage and deep seepage lakes. These lakes also had the greatest range of Secchi values. The lakes with the lowest Secchi depths were shallow, drainage lakes.

Table 3. Summary statistics by lake class.

	Class	No. of Lakes	Mean	Median	Maximum	Minimum
Size (ha)	1	16	103	97	184	24
	2	23	127	116	387	33
	3	41	372	207	1451	47
	4	48	381	253	1373	34
	5	14	103	91	339	32
	6	35	124	78	450	20
Max Depth (m)	1	16	5.3	5.9	7.9	2.4
	2	23	16.2	13.7	36.3	7.9
	3	41	5.7	5.5	11.9	1.2
	4	48	15.9	15.4	32.0	7.6
	5	14	5.0	4.7	7.3	3.0
	6	35	14.6	12.2	32.3	6.4
Secchi (m)	1	16	1.8	1.7	3.9	0.4
	2	23	3.5	3.3	6.1	1.6
	3	41	1.6	1.7	3.2	0.2
	4	48	2.9	2.6	8.0	1.0
	5	14	2.7	2.6	3.9	0.3
	6	35	3.6	3.4	7.0	0.8
TP (µg L^{-1})	1	16	66	29	584	11
	2	23	19	17	39	8
	3	41	65	33	501	7
	4	48	33	23	151	9
	5	14	21	18	41	12
	6	35	36	15	403	6
Watershed (mi^2)	1	16	2	2	4	1
	2	23	2	2	4	1
	3	41	121	27	1761	4
	4	48	89	16	1677	4
	5	14	6	1	60	1
	6	35	4	2	58	1
Watershed ag (%)	1	16	18	2	76	0
	2	23	18	6	73	0
	3	41	24	12	78	0
	4	48	17	6	58	0
	5	14	16	7	55	0
	6	35	23	20	78	0

Class 1 highland, shallow drainage lakes
Class 2 highland, deep drainage lakes
Class 3 lowland, shallow drainage lakes
Class 4 lowland, deep drainage lakes
Class 5 shallow seepage lakes
Class 6 deep seepage lakes

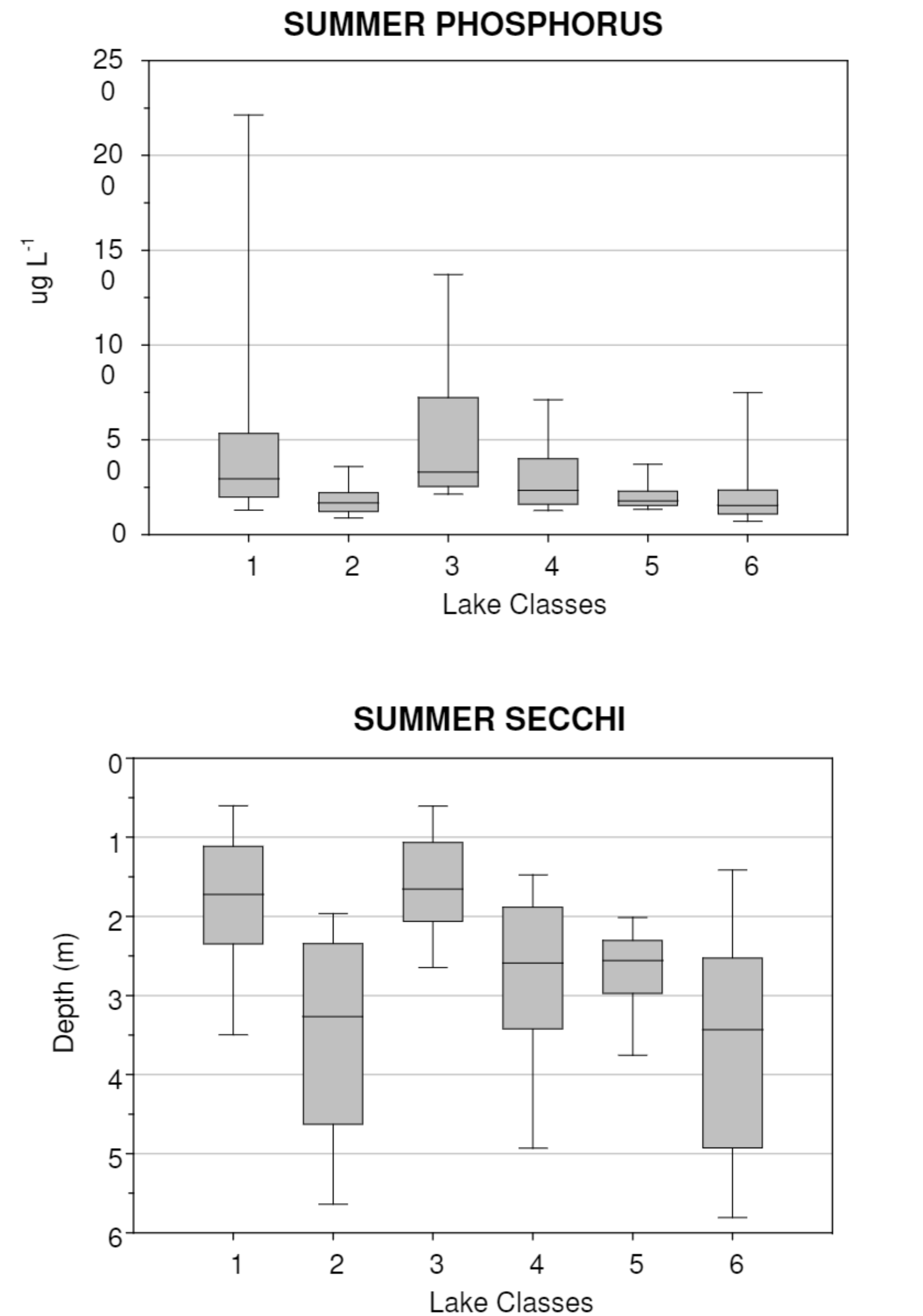


Figure 3. Summer phosphorus and Secchi distribution for the 6 lake classes.

Main variables for determining phosphorus

The lake's morphometry statistics as well as the anthropogenic stressors around the lakes were used to construct a model to best predict summer phosphorus concentrations. The variables phosphorus, lake size, and watershed area were skewed with a few large values and many small values; these variables were log transformed. A regression tree analyses was performed to determine which variables were the best determinants of phosphorus concentration. The most important variables were the size of the watershed, amount of agriculture in the watershed, and maximum depth. The addition of other variables did not appreciably improve the model.

Adding the categorical factors ecoregion and hydologic type (drainage or seepage) improved the model. Since the amount of agriculture in the watershed was disproportionally distributed among the ecoregions (NLF had very little agriculture), this variable was not used in the final model. Two linear regression models were developed. One was for drainage lakes and the other model was for seepage and spring fed lakes.

Drainage lakes:

$$\text{Log } P_{\text{Predicted}} = 1.471 + 0.0820 \text{ Log (watershed area)} - 0.0044 \text{ max depth} + 0.0053 \text{ \%ag in watershed} \quad (1)$$

Seepage lakes:

$$\text{Log } P_{\text{Predicted}} = 1.304 + 0.0820 \text{ Log (watershed area)} - 0.0044 \text{ max depth} + 0.0053 \text{ \%ag in watershed} \quad (2)$$

$R^2 = 0.38$

These models indicated that higher phosphorus concentrations occurred with larger watersheds, with increasing area of the watershed devoted to agricultural production, and in shallower lakes. Comparison of the y-intercept reveals that drainage lakes naturally have higher phosphorus levels than seepage lakes. It is interesting that the amount of agriculture in the 100 m buffer area was not a strong predictor. This may be in part because most of the lakes had very little agricultural within 100 m of the shore. Instead this land has generally been converted to home sites.

This modeling indicates that lake classes with the highest phosphorus concentrations tend to be lowland drainage lakes and that shallow lakes tend to have higher phosphorus concentrations than deep lakes. This model agrees with the empirical data where Class 3 lakes had the highest phosphorus levels. This class of lakes had the largest watershed size and generally the shallowest water depth. This lake class in the NCHF ecoregion had the highest phosphorus concentrations as these lakes had a relatively high amount of agriculture in their watersheds. Examination of Table 2 explains why lakes in the NCHF tend to have the highest phosphorus concentrations. These lakes tend to have the largest

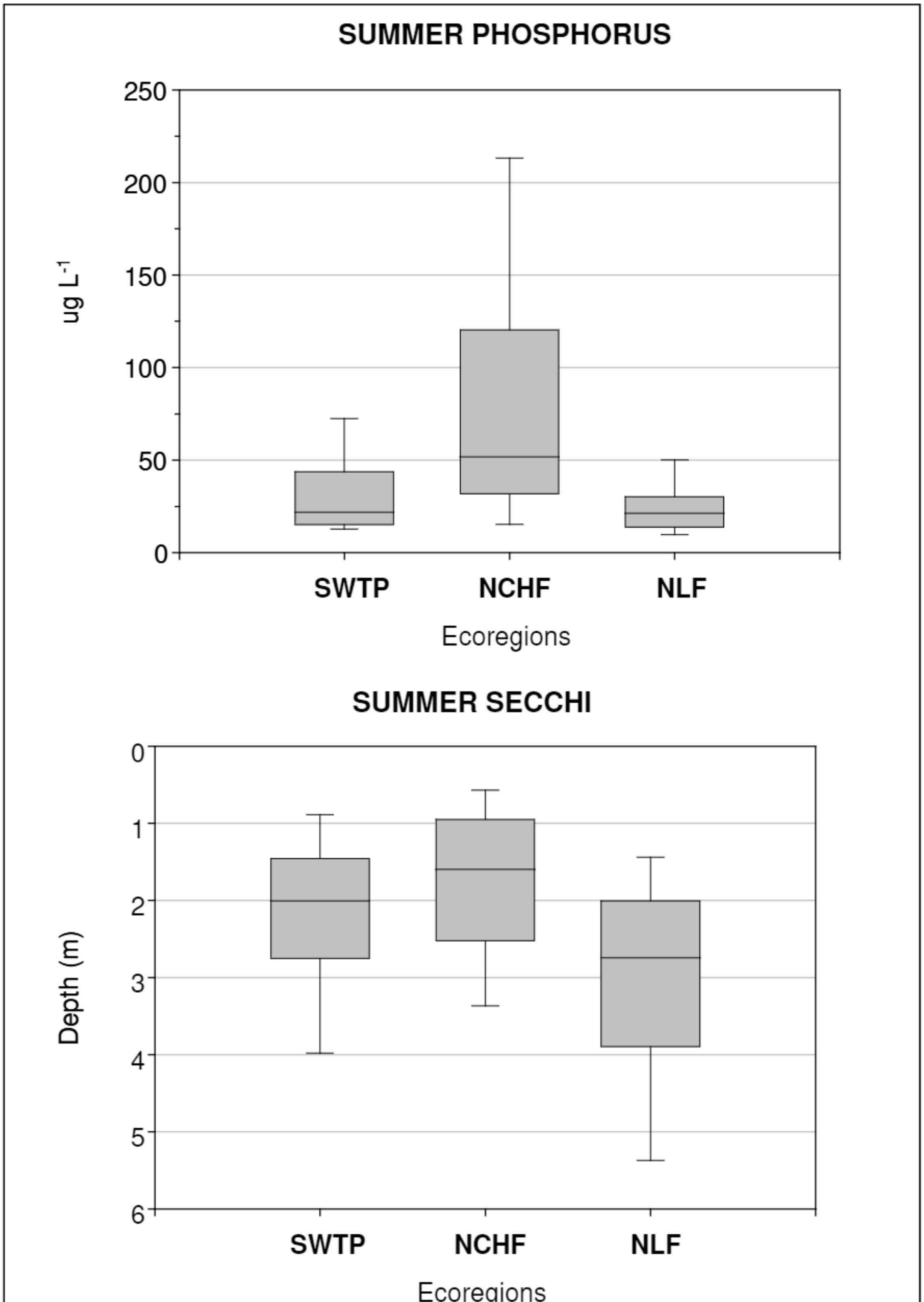


Figure 4. Summer phosphorus and Secchi distribution for the 3 lake bearing ecoregions in Wisconsin.

watershed and the shallowest depths. These lakes tend to have a similar amount of agriculture in their watersheds compared with lakes in the SWTP ecoregion but NCHF lakes tend to be shallower, resulting in their high phosphorus levels.

Reference Conditions

Reference conditions for the lake classes were determined using historical diatom assemblages. Sediment cores were collected from over 100 lakes and the diatom assemblages were determined in the surface and bottom samples. The surface samples were assumed to represent conditions over the last 2-3 years while the bottom samples represented pre-settlement conditions. In Wisconsin pre-settlement is prior to the mid-1800s.

For the analysis, lakes were divided into deep and shallow lakes based upon whether they were deeper or shallower than a maximum depth of 18 feet. An exploratory analysis using canonical correspondence analysis (CCA) with downweighting of rare species was performed using CANOCO version 4.5 (ter Braak and Ŝmilauer 2002). This is a direct gradient technique, that simultaneously represents sites, environmental variables and diatom taxa in low dimensional space (ter Braak 1986). Species are assumed to have unimodal response surfaces and the axes are constrained to be linear combination of the environmental variables.

CCA with forward selection was performed in order to identify the significant environmental variables that explain significant variation in the diatom species. Forward selection orders the environmental variables according to the amount of variance they explain in the species data and their significance was tested using Monte Carlo testing with 499 unrestricted permutations. All of the environmental variables were $\log_{10}$ transformed. The number 1 was added to the values before they were log transformed to eliminate problems with negative values.

Weighted averaging regression and calibration were performed using WACALIB version 3.3 (Line et al. 1994) with 999 bootstrap cycles. This procedure produced diatom transfer functions that were applied to the diatom assemblages in the sediment core samples. Bootstrapping allows the statistical significance to be determined for the transfer functions. The root mean square error (RMSE) was determined for each of the transfer functions.

The results of the CCA for the shallow lakes are given in Table 4. For shallow lakes the eigenvalues of CCA axis 1 (0.43) and axis 2 (0.38) capture 8.4 % of the cumulative variance in the species data. For deep lakes the statistics were better than for shallow lakes. The results of the CCA for deep lakes are given in Table 5. For deep lakes the eigenvalues of CCA axis 1 (0.55) and axis 2 (0.43) capture 9.5 % of the cumulative variance in the species data.

Table 4. Summary statistics for the first four axes of the CCA for the shallow lakes.

CCA axes	*1*	*2*	*3*	**4**
Eigenvalues	0.43	0.38	0.24	0.19
Species-environment Correlations	0.89	0.90	0.84	0.77
Cumulative %variance:				
- of species data	4.4	8.4	10.9	12.9
-of species-environmental relationship	30.8	58.3	75.8	89.7

Table 5. Summary statistics for the first four axes of the CCA for the deep lakes.

CCA axes	*1*	*2*	*3*	**4**
Eigenvalues	0.55	0.43	0.40	0.26
Species-environment Correlations	0.92	0.91	0.86	0.72
Cumulative %variance:				
- of species data	5.3	9.5	13.3	15.9
-of species-environmental relationship	29.7	53.0	74.3	88.5

For both shallow and deep lakes the significant environmental variables were phosphorus, Secchi depth, alkalinity/pH, and color (Figure 5). The pH variable was dropped as it covaries with alkalinity.

The relationship of observed versus diatom-inferred phosphorus are shown in Figure 6. For shallow lakes the median P value was 18 µg L^{-1} and a root mean squared error of prediction (RMSEP) of 0.28 log 10 µg L^{-1}. For the deep lakes the median P value was 15 µg L^{-1} and a root mean squared error of prediction (RMSEP) of 0.32 log 10 µg L^{-1}.

The sediment top/bottom diatom assemblage was analyzed from 134 natural lakes in Wisconsin (Figure 7) to determine historical phosphorus concentrations. The lakes were divided amongst the 6 lake classes. The most numerous lakes were in class 4 which are deep, lowland drainage lakes. This is the lake class with the most lakes in the state. The least common were class 3 which are shallow, lowland, drainage lakes. Many lakes in this class are reservoirs and there are not a lot of natural lakes in this class. In all of the lake classes, the phosphorus concentration in the top sample (current concentration) was higher than the historical (bottom) phosphorus concentration. In some lakes the present day concentration is the same as the historical value, but within each class historical levels

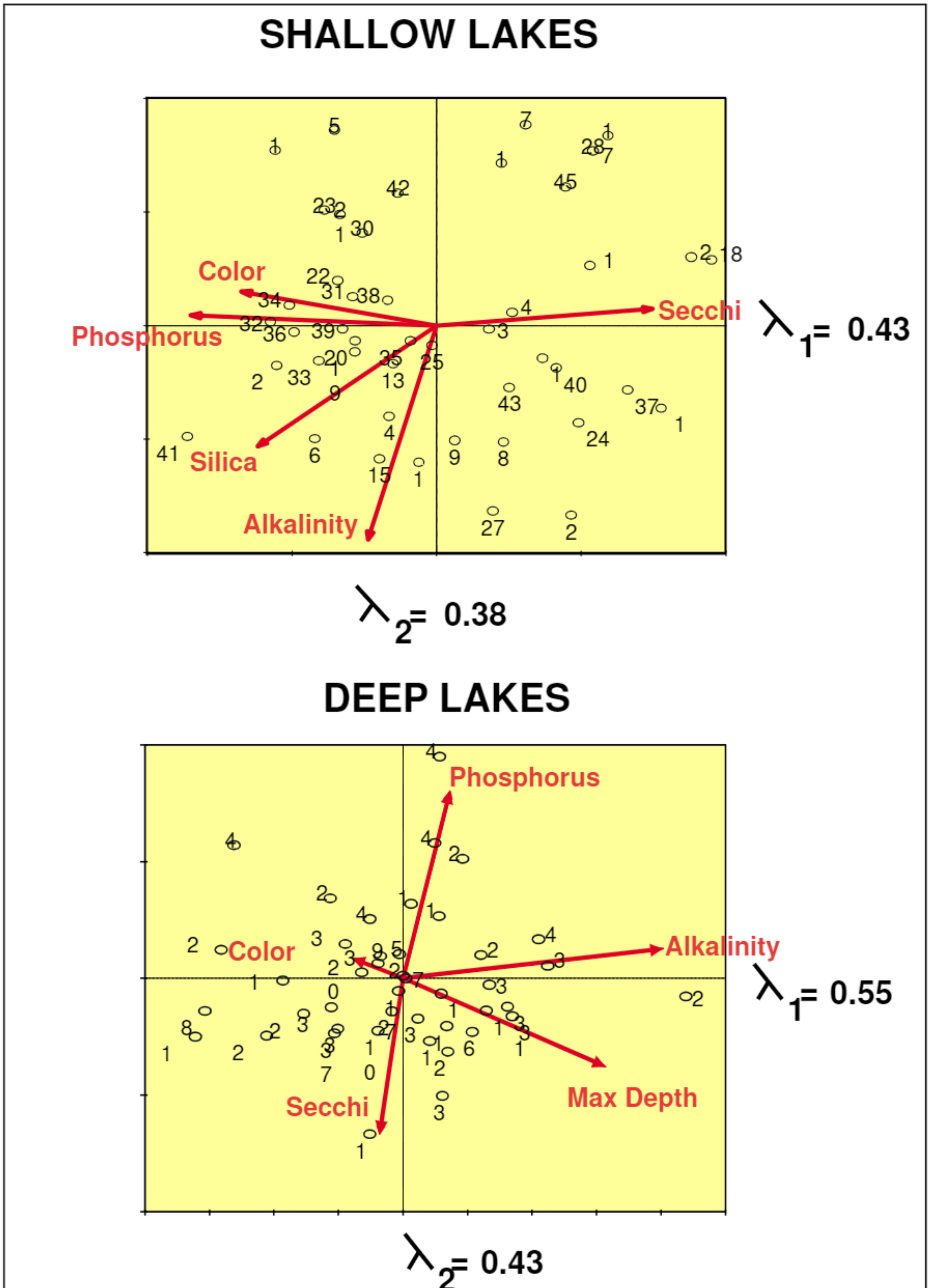


Figure 5. CCA ordination plots of sample lakes. The significant environmental variables are shown as arrows.

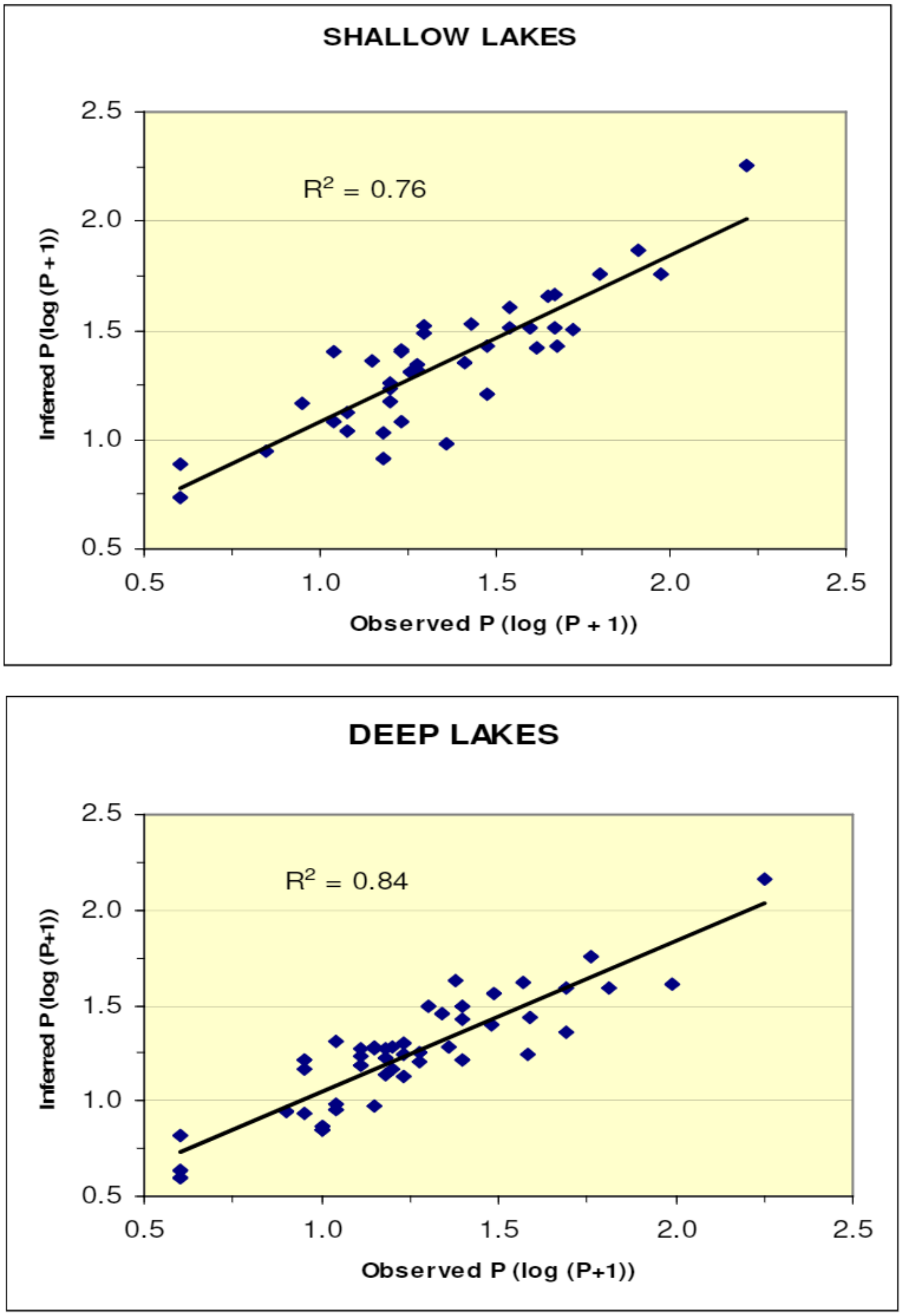


Figure 6. The relationship between observed and diatom inferred summer phosphorus for shallow and deep lakes.

were lower. The concentration in the bottom sample was used to establish reference phosphorus concentrations for the lake classes (Table 6). Although we are maintaining 6 lake classes, the paleolimnological investigation indicates that perhaps some of these classes could be collapsed. For example, the historical P concentrations for seepage lakes were nearly identical between deep and shallow lakes. For drainage lakes, depth was important but the position in the landscape was not important.

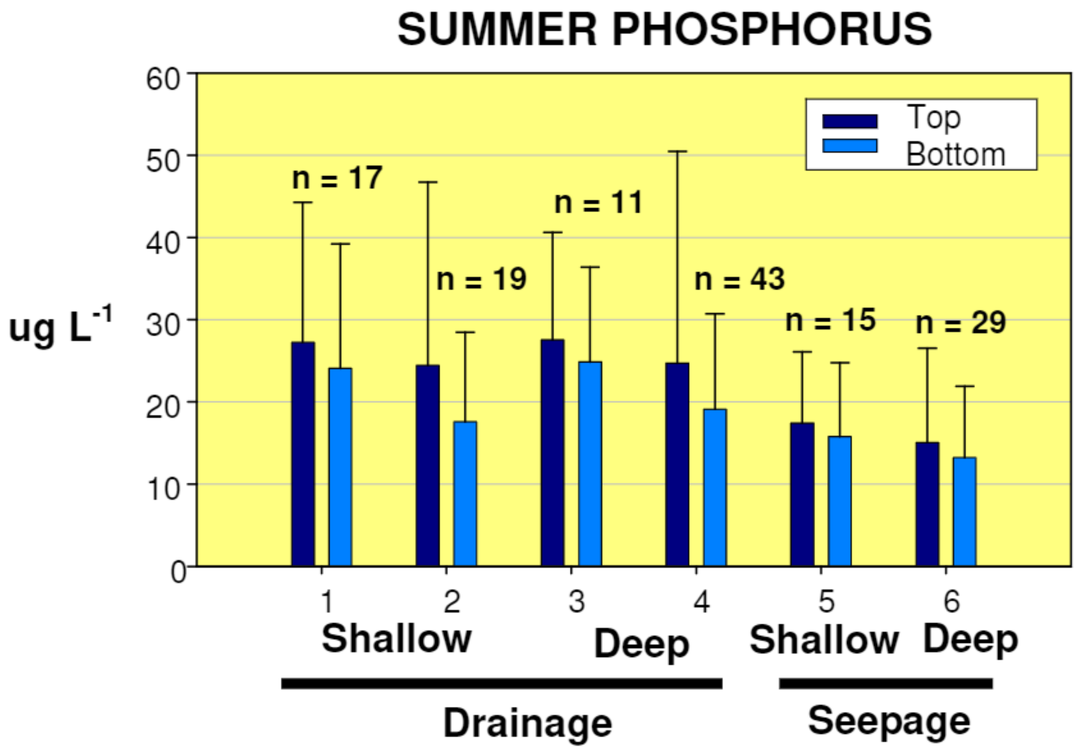
Table 6. Reference concentrations for summer mean phosphorus (µg L^{-1}) for each lake class and the three lake bearing ecoregions.

CLASS	REFERENCE
1	24
2	18
3	25
4	19
5	16
6	13

ECOREGION	REFERENCE
SWTP	19
NCHF	21
NLF	17

The differences in the variables that determine the historical phosphorus values and present day concentrations indicate the importance of anthropogenic influences. A lake's phosphorus concentration in presettlement time was determined by its hydrologic type, and for drainage lakes maximum depth was an important variable. With the landscape having little impact from anthropogenic sources, the size of the lake's watershed was not an important determining factor in the phosphorus concentration of drainage lakes. Now that the landuse in the watersheds has been altered, the size of the watershed as well as the amount of agriculture in the watershed are important factors in determining the water quality of a lake, regardless of the lake's hydrology. While seepage lakes tend to have lower phosphorus levels, the size of their watershed is important.

Because of the importance of anthropogenic influences it is now necessary to have 6 lake classes based upon hydrologic type, watershed size, and maximum depth. For reference conditions only 4 classes are needed. These would be based upon hydologic type and maximum depth. Seepage and drainage lakes would only be separated between shallow and deep lakes.



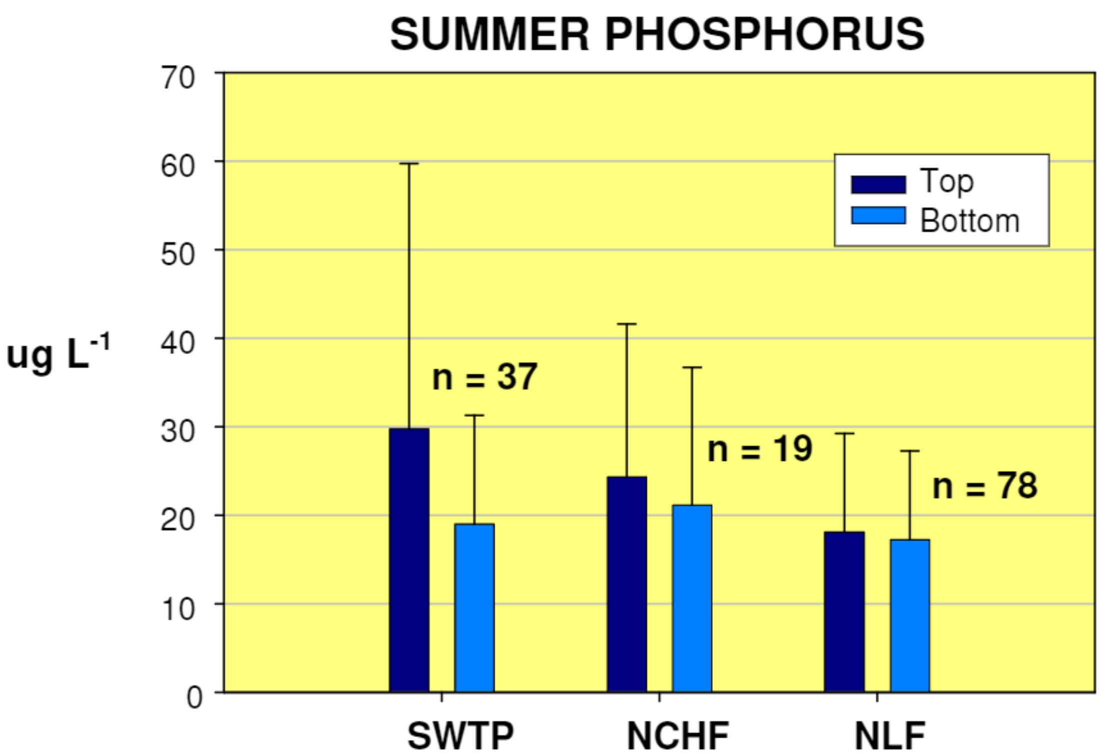


Figure 7. Diatom inferred summer phosphorus concentrations comparing present day levels with historical values by lake class (A) and ecoregion (B).

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MACROPHYTES

Explaining Variation in Submersed Aquatic Macrophyte Communities: Littoral Area, Ecoregion, Hydrological Type, and Landuse

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Introduction

Aquatic macrophytes serve important ecological roles in lentic ecosystems, and their presence or absence can alter the structure, function and composition of entire aquatic communities. (Scheffer 1998, Wetzel 2001). The impact of aquatic plants on dissolved oxygen concentrations, for example, can significantly change the nutrient and gas chemistry that determines habitat quality for aquatic animals on time courses as short as one day (Caraco et al. 2006). Even in lakes with relatively low macrophyte biomass, aquatic plants influence transparency, phytoplankton chl *a* and suspended solids (Havens, 2003). Furthermore, by providing refuge and food, and by determining habitat architecture, aquatic plants also directly affect the structure and composition of the rest of the aquatic community (Crowder and Cooper 1982).

Aquatic plant communities respond to both natural and human-induced sources of environmental variation. The literature is rich with accounts of the abundance, distribution, and community composition of aquatic macrophytes varying in response to water chemistry, trophic status, substrate composition, lake morphometry, climate, etc. (For review see Moyle 1945, also Duarte et al. 1986, Havens 2003, Schmieder and Lehmann 2004). Losses of or changes in assemblages of native submersed aquatic vegetation (SAV) have been documented in shallow freshwater, estuarine, and marine systems worldwide with increasing frequency. (Bayley et al. 1978, Rybicki and Carter 1986, Schloesser and Manny 1990, Kimber et al. 1995, Short and Wyllie-Echeverria 1996, Duffy and Baltz 1998, Hauxwell et al. 2001, Jennings et al. 2003, Rasmussen and Anderson 2005, Borman 2007, Canny 2007). Lately, many of these studies seem to indicate a significant impact of human-mediated disturbance on SAV. Increases in anthropogenic nutrient supply to inland and near shore waters, and the accompanying decline in water clarity resulting from blooms of nutrient-limited algae may be important factors contributing to loss of light-limited rooted macrophytes in freshwater environments (Chambers and Kalff 1985, Barko et al. 1986). In other cases, an increase in sediment loading and reduced water clarity as a result of shoreline development may affect rooted freshwater macrophytes (Barko et al. 1986). Infestations of non-native macrophytes, including Eurasian watermilfoil (*Myriophyllum spicatum* L.) and hydrilla (*Hydrilla verticillata* (L.f.) Royle) may also competitively exclude native freshwater macrophytes (Lind and Cottam 1969, Van et al. 1976, Titus and Adams 1979, Van et al. 1999, McFarland and Rogers 1998). Non-native herbivores, including grass carp (*Ctenopharyngodon idella* Val.) or the rusty crayfish (*Orconectes rusticus*), in addition to native herbivores (e.g., turtles, muskrats, waterfowl; Carter and Rybicki 1985), may also severely affect native SAV (Hestand and Carter 1978, Roberts et al. 1995, Wilson 2002). Human-induced disturbance as a result of anthropogenic alterations of landscapes have increasingly degraded water quality of adjacent aquatic systems.

In northern temperate lakes, studies have linked changes in landuse patterns to changes in SAV (Garrison and Wakeman 2000, Borman 2007, Canny 2007). However, the high degree of natural variation in lentic systems often complicates analysis and can obscure important trends. Thus, we attempted to identify the factors (physical, hydrological, geographical, and human-related) that most directly affected aquatic macrophyte community parameters. Following Emmons et al. (1999) and Breiman et al. (1997), we used a hierarchical regression tree approach combined with a classical multiple linear regression analysis to model the relationship between independent environmental and dependent macrophyte variables. Ultimately, by examining the comparative strength of different multiple linear regression models, we were able identify the factors most important in predicting the response of SAV. By identifying important natural variables that influenced SAV, we were able classify lakes into groups in which natural variation among lakes is minimized. These similar groups would be expected to respond similarly to landscape perturbations, allowing us a clear and straightforward look into whether and how human-mediated landscape disturbances impact aquatic macrophyte communities.

Materials and Methods

Using the Point-Intercept (PI) method described by Hauxwell et al. (*in preparation*), we gathered detailed SAV community distribution and abundance data on 193 Wisconsin lakes ranging from 12 to around 8,000 acres in size (Figure 1, Figure 2). We constructed a GIS-based sampling grid for each study lake, with number of points dependent on 1) estimated littoral area and 2) the shape of the shoreline. Littoral area was estimated using area of the lake shallower than 6 m as a proxy. We used the standard limnological shoreline development factor (SDF, the ratio of the length of the shoreline to the circumference of a circle equal in area to that of the lake) to divide lakes into three categories of complexity. Based on what we considered maximum effort, we set the number of sample points for each lake depending on littoral area and SDF, scaling the grid resolution to produce increasingly more points on lakes with larger littoral zones and lakes with more complex shorelines. From this information, we then generated a logarithmic equation relating number of grid points (y) to estimated littoral area (x) for each SDF complexity group. The PI method has been shown to be a fairly robust methodology, leading to asymptotic species accumulation curves in around 95% of systems surveyed (Mikulyuk et al. in review).

We collected species presence/absence data and depth from a boat at each point in the predetermined sampling grid. We used a double-headed rake on an adjustable pole to rake plants from a ~0.75 m-long swath of the bottom. We employed a similar rake attached to a rope to collect plants from sites deeper than 4.5 m. At each sample point we identified plants on the rake, as well as those detached from the bottom and floating, to species level following Crow and Hellquist (2000a, 2000b). We also recorded visual sightings of all plant species within a two-meter radius of each sample point.

From the PI data, we determined for each lake:

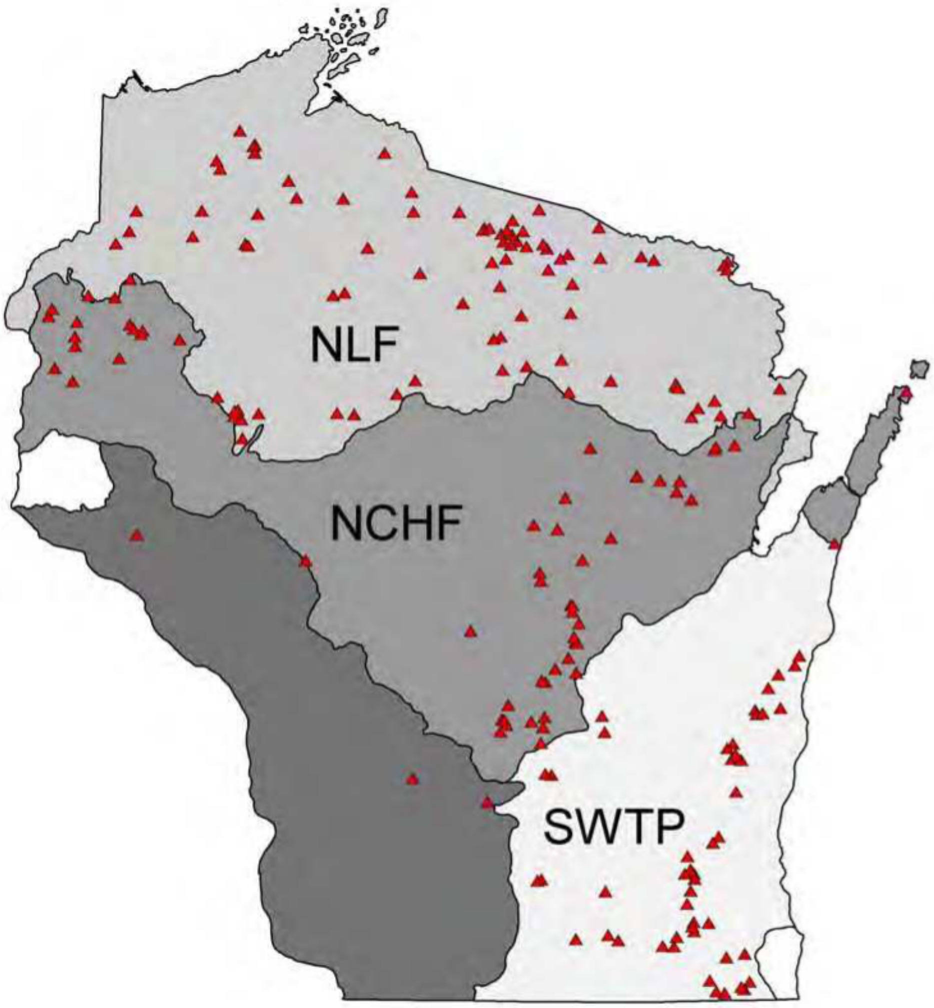

Figure 1. Map of Wisconsin showing locations of 193 study lakes and Level III ecoregion boundaries.

1) Maximum depth of plant growth (MDPG) as the greatest depth of all vegetated sample points. In order to ensure that MDPG remained a function of water quality and not lake morphometry, lakes where MDPG = maximum lake depth were excluded from the MDPG analyses.

2) Species richness as the total number of species found,

3) Nichols' Floristic Quality Index (FQI) as $FQI = (\overline{C})(\sqrt{N})$, where N = the total number of species, and $\overline{C}$ = the average coefficient of conservatism. Conservatism is defined as the estimated probability that a plant is likely to occur in a landscape that is believed to be relatively unaltered from presettlement conditions (Nichols 1999). Conservatism values range from 0 (most tolerant) to 10 (most sensitive),

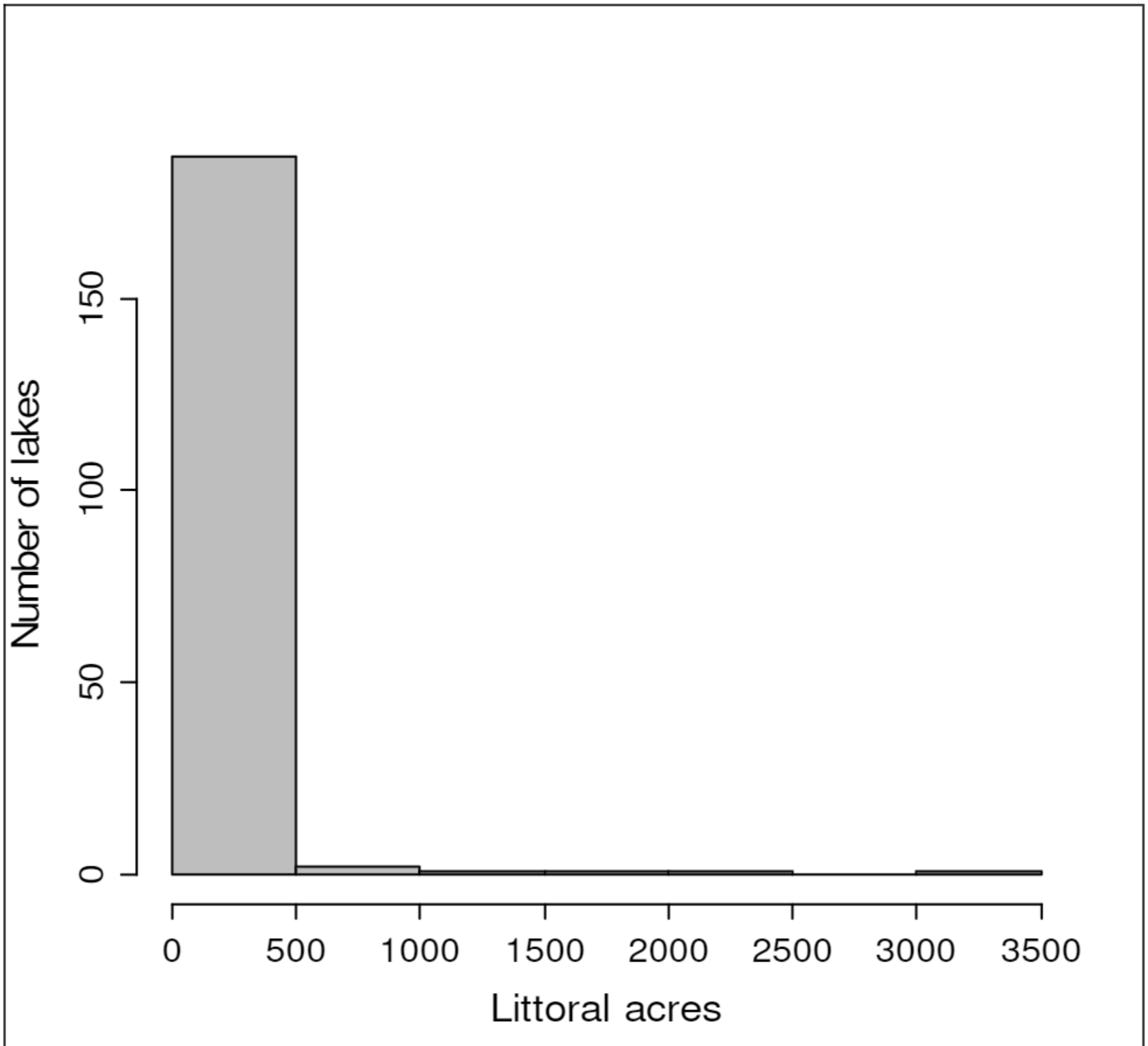

Figure 2. Littoral zone size distribution of study lakes.

4) Nichols' Aquatic Macrophyte Community Index (AMCI), a scaled index based on seven parameters including: maximum depth of plant growth, percentage of the littoral area vegetated, Simpson's diversity index, relative frequency of submersed species, taxa number and relative frequency of exotic species (Nichols et al. 2000).

Plant-based biotic indices such as FQI and AMCI vary over gradients of environmental conditions, demonstrating the ability of plant populations to accurately reflect larger ecosystem processes by responding to changes in trophic state, disturbance regime, and landuse. We would expect both of these indices to decrease with increasing levels of disturbance.

Predictor Variables

Physical and geographic characteristics

In defining a possible classification scheme, we identified several predictor variables we expected would influence SAV metrics. Strong evidence confirms time and again the existence of a species-area relationship in terrestrial ecosystems, but in lake systems, current studies only inconsistently relate species diversity to lake surface area (Friday 1987, Oertli et al. 2002). In order to examine the species-area relationship in our dataset, we considered littoral area as opposed to lake surface area, as we felt that the size of the colonizable area would more likely significantly impact total species richness. Lake size varied similarly in each ecoregion and lake class. We also considered Level III ecoregions, which Omernik et al. (2000) define as "geographical areas within which the biotic and abiotic components of terrestrial and aquatic ecosystems exhibit different but relatively homogeneous patterns in comparison to that of other areas." Lake hydrology is also likely to have an effect on the plant communities. Lakes are grouped into type classes based on their landscape position and connection to the surface water drainage network. (See Classification and Reference Condition section for details.) Lakes by ecoregion and class are listed in Table 1.

TABLE 1. Distribution of study lakes by lake type and ecoregion.

	SWTP	NCHF	NLF	other	All Lakes
Seepage	**16**	**30**	**41**	**1**	**88**
Deep	*14*	*21*	*37*	*1*	*4*
Shallow	*2*	*9*	*4*	*0*	*15*
Headwater	**13**	**15**	**18**	**1**	**47**
Deep	*12*	*10*	*11*	*1*	*34*
Shallow	*1*	*5*	*7*	*0*	*13*
Lowland	**18**	**11**	**22**	**2**	**53**
Deep	*15*	*9*	*14*	*0*	*38*
Shallow	*3*	*2*	*8*	*2*	*15*
Unclassifiable	**1**	**1**	**3**	**0**	**5**
All Lakes	48	57	84	4	***193***

Landuse Data

We identified two scales on which to evaluate the impact of landuse: the local, or buffer level as well as the larger watershed scale. To evaluate the effect of development at the nearshore level, we used GIS to delineate a 100-m buffer around each lake. We also delineated lake watersheds based on water flow direction and topography. We then analyzed the specific types of landuse present at both scales for all lakes studied. Much of the landuse data was derived from the 2001 and the 2006 version of the National Land Cover Database (NLCD). The NLCD uses classification algorithms to interpret satellite data from Landsat Thematic Mapper imagery, producing a raster coverage with resolution of 30m in which the primary type of land use is designated for each pixel (Homer et al., 2007) (Table 2). This information allowed us to determine the proportion of land in the buffer and watershed areas that fell into various landuse categories. At the watershed scale, we considered both percent agriculture and percent urban development, and at the local buffer scale, we considered percent agriculture and percent urban development as well as percent forest canopy and percent impervious surface. Additionally, we used Radeloff et al.'s (2005) integrated NLCD and U.S. Census coverage to estimate house density in the buffer area.

TABLE 2. Landuse designations from the 2001 and 2006 National Land Cover Database (Homer et al. 2007).

Undisturbed	Disturbed
Open Water	Urban/Developed - Open Space
Deciduous Forest	Urban/Developed - Low Intensity
Evergreen Forest	Urban/Developed - Medium Intensity
Mixed Forest	Urban/Developed - High Intensity
Scrub/Shrub	Grassland/Herbaceous
Woody Wetlands	Pasture/Hay
Emergent Herbaceous Wetland	Cultivated Crops
	Barren

Data analysis

We used a multiple linear regression approach to define models predicting SAV community parameters. We log-transformed the littoral area because of its highly skewed distribution (Figure 2); its relationship to other variables was more nearly linear on this scale. As a result of unbalanced sample sizes, we considered only lake type (seepage, headwater, or lowland drainage lake) and did not include the class variable describing depth. As an exploratory step, coplots (plots showing the relationship of two variables at several levels of another), linear regression, and analysis of variance were used to examine the influence of size, type, and ecoregion on the plant response variables. Using the statistical software R (R Development Core Team 2008) and the package rpart (Therneau et al. 2008), we used a form of binary recursive partitioning to grow regression trees in order to identify influential predictor variables. This stepwise process involves a series of dichotomous splits that partition the data into increasingly homogeneous subsets, using a single predictor variable to determine each split. Because each split is determined by the predictor variable that produces the two most homogeneous subsets at that stage (with respect to the response variable), the resulting tree may use any number of the potential predictors. To avoid overfitting, cross-validation was used to prune the original tree to a smaller size, depending on the cross-validation error rate. Finally, by using the information gained in all exploratory analyses, we tested numerous multiple linear models and evaluated their relative empirical support using Akaike's Information Criterion (AIC) (Akaike 1974).

Results

Plant community parameters measured in the 193 study lakes were variable (Table 3) and ranged widely (MDPG from 0.91m - 12.04m, 2-42 species, FQI scores from 3 – 39.97, and AMCI from 22-68). There was a highly significant positive linear relationship between log-transformed lake littoral area and species richness (adjusted $r^2 = 0.28$; $P < 0.0001$) log-transformed lake littoral area and FQI (adjusted $r^2 = 0.18$; $P < 0.0001$) (Figure 3), and a significant relationship between log-transformed littoral area and MDPG (adjusted $r^2 = 0.02$; $P = 0.048$), and between log-transformed littoral area and AMCI (adjusted $r^2 = 0.02$; $P = 0.02$). Similarly, the factors ecoregion and lake class both had a significant effect on many response variables (Table 4).

TABLE 3. Response variables measured in study lakes, N = 193.

All lakes	Species Richness	MDPG (m)	FQI	AMCI
Min	2	0.9	3.0	22
1st quartile	13	3.5	20.3	48
Median	17	4.9	25.2	52
Mean	17	5.1	24.8	52
3rd quartile	22	6.5	30.2	58
Max	42	12.0	39.0	68
Standard deviation	7.3	2.1	6.8	8.4
Variance	53.8	4.4	46.6	70.1

TABLE 4. Summary table of ANOVA results indicating significant effect of ecoregion and type on response variables.

		MDPG	Species Richness	FQI	AMCI
Ecoregion	F	3.62	4.07	26.9	24.51
	df	158	186	186	186
	p	0.03	0.19	< 0.0001	< 0.0001
Class	F	5.91	4.47	0.25	1.43
	df	159	186	186	186
	p	0.003	0.01	0.78	0.24

Ecoregion = Southeastern Wisconsin Till Plains, North Central Hardwoods, Northern Lakes and Forests
Class = Headwater (classes 1 and 2), Lowland Drainage (classes 3 and 4), Seepage (classes 5 and 6)

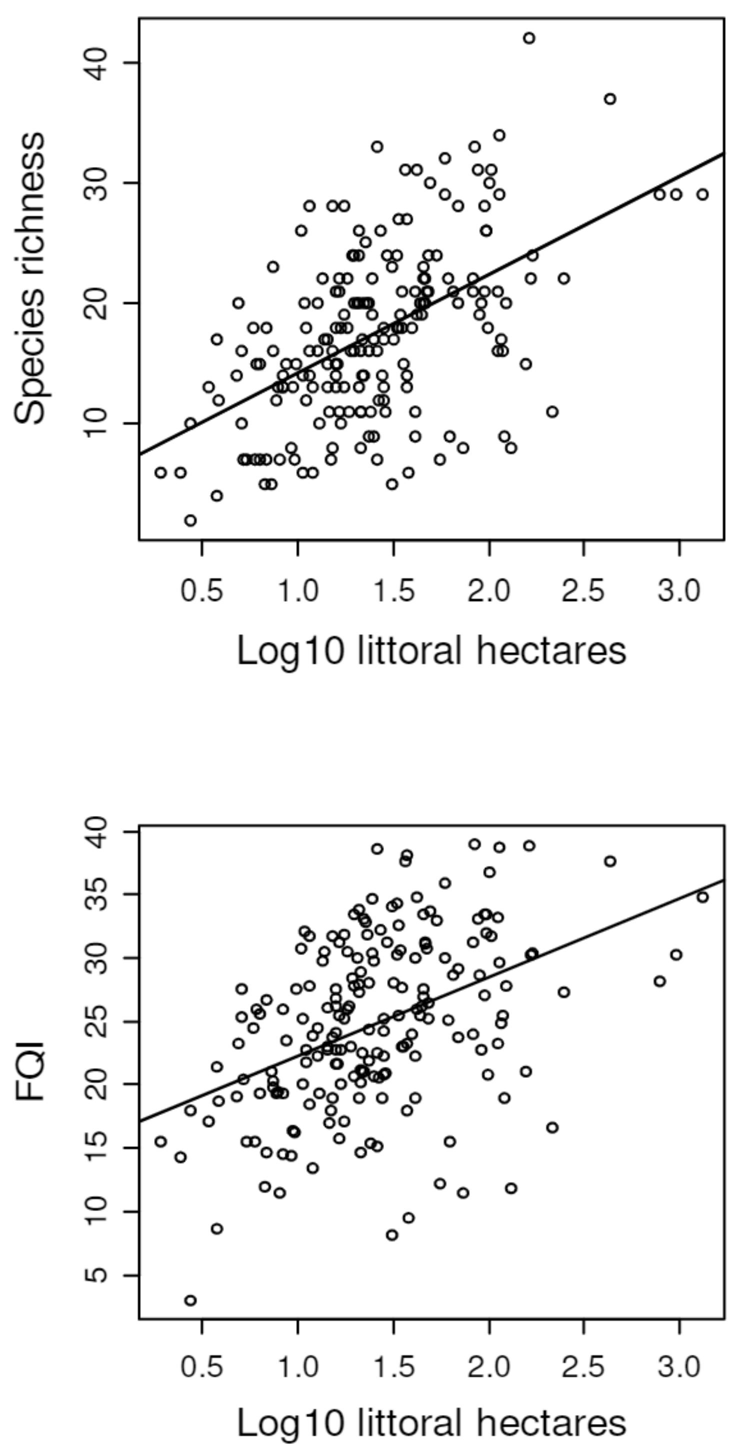

Figure 3. Top: Species-area relationship across entire data set. Linear model adjusted $r^2 = 0.28$, $F = 75.7$, $df = 191$, $P = 1.52e-15$. Bottom: Relationship between log10 littoral area and FQI. Linear model adjusted $r^2 = 0.18$, $F = 44$, $df = 191$, $P = 3.28e-10$.

Gradients of watershed and buffer development were not similar across ecoregions; the SWTP region tended to have lakes with higher levels of development whereas lakes in the NLF region were largely undeveloped (Figure 4). Though ultimately unimportant, this led us to consider the interactive factor of disturbance and ecoregion in our final model selection. When we analyzed all lakes as a single group, we saw a significant negative relationship between species richness (adjusted $r^2 = 0.02$, $P = 0.03$), FQI (adjusted $r^2 = 0.19$, $P < 0.0001$) and AMCI (adjusted $r^2 = 0.16$, $P = 0.0001$) and percentage of disturbed land in the watershed (Figures 5-7). However, adjusted r^2 values are quite low, revealing a high amount of variation not accounted for by disturbance level alone. When we segregated the lakes into smaller groups controlling for the variables of ecoregion and type, adjusted r^2 values increased dramatically, leading us to consider regression trees and multiple linear regression models.

Final pruned regression trees are shown in Figures 8-11. Based on the plots of the complexity parameters, trees were pruned to the number of nodes that would correspond to the lowest cross-validation error rate. Log_{10} littoral area is an important predictor variable in all trees, and all trees include some measure of buffer or watershed disturbance. Final trees did not include lake type as a factor, and ecoregion was only considered in the AMCI tree.

Based on these exploratory findings, we ran a number of multiple linear regression models and ranked their relative predictive strengths using a maximum likelihood procedure (Akaike's information criterion). The best models are shown in Tables 5-8, with competing models (within two points of the highest-scoring model) also listed. For all macrophyte variables explored, littoral area, ecoregion type, and %urban (buffer) were all present in the best models. None of the interactive factors we explored (size and ecoregion, size and lake class, ecoregion and lake class, etc) improved the strength of the models for any variable. Disturbance-related variables were important in explaining variation in plant community parameters; in fact, the most consistent trend was that all of the best models used disturbance variables at **both** the watershed and buffer scale. The way in which the disturbance factor was measured was variable, but as long as both local and watershed scales were considered, the linear models were notably improved.

Discussion

There was a significant effect of disturbance on macrophyte community parameters. Increased levels of disturbance were associated with decreases in the quality of the macrophyte community, as evinced particularly by the decline in FQI and AMCI scores. Even when taken at the statewide scale, the effect of, for example, watershed disturbance on richness, MDPG, FQI and AMCI was evident. However, it is also obvious that many disturbance-independent variables have a simultaneous effect on these same parameters. In any analysis that seeks to identify a response in the macrophyte community, it is paramount to recognize these effects and account for their influence on the observed variation. By accounting for the variability due to factors independent of disturbance by using a multivariate approach, we were better able to identify the effect of human perturbations.

TABLE 5

			Watershed		Buffer					R^2
Log10 littoral ha	**Ecoregion**	**Type**	**% Agriculture**				**% Agriculture**		**% Urban**	**0.199**
Log10 littoral ha	Ecoregion	Type		% Urban			% Agriculture		% Urban	0.191
Log10 littoral ha	Ecoregion	Type	% Agriculture				% Agriculture	% Impervious	% Urban	0.196
Log10 littoral ha	Ecoregion	Type	% Agriculture			House Density	% Agriculture		% Urban	0.195
Log10 littoral ha	Ecoregion	Type	% Agriculture					% Impervious	% Urban	0.188
Log10 littoral ha	Ecoregion	Type	% Agriculture		% Canopy		% Agriculture		% Urban	0.193
Log10 littoral ha	Ecoregion	Type	% Agriculture			House Density			% Urban	0.188
Log10 littoral ha	Ecoregion	Type	% Agriculture	% Urban			% Agriculture		% Urban	0.193

TABLE 6

			Watershed		Buffer				R^2
Log10 littoral ha	**Ecoregion**	**Type**	**% Agriculture**					**% Urban**	**0.306**
Log10 littoral ha	Ecoregion	Type		% Urban				% Urban	0.306
Log10 littoral ha	Ecoregion	Type	% Agriculture			% Agriculture		% Urban	0.308
Log10 littoral ha	Ecoregion	Type		% Urban		% Agriculture		% Urban	0.304
Log10 littoral ha	Ecoregion	Type	% Agriculture		% Canopy			% Urban	0.302
Log10 littoral ha	Ecoregion	Type	% Agriculture	% Urban				% Urban	0.302
Log10 littoral ha	Ecoregion	Type	% Agriculture				% Impervious	% Urban	0.302

TABLE 7

			Watershed		Buffer		R^2
Log10 littoral ha	**Ecoregion**	**Type**		**% Urban**	**% Agriculture**	**% Urban**	**0.395**
Log10 littoral ha	Ecoregion	Type	% Agriculture		% Agriculture	% Urban	0.392
Log10 littoral ha	Ecoregion	Type	% Agriculture	% Urban	% Agriculture	% Urban	0.391

TABLE 8

			Watershed		Buffer					R^2
Log10 littoral ha	**Ecoregion**	**Type**		**% Urban**			**% Agriculture**		**% Urban**	**0.242**
Log10 littoral ha	Ecoregion	Type	% Agriculture				% Agriculture		% Urban	0.235
Log10 littoral ha	Ecoregion	Type		% Urban			% Agriculture	% Impervious	% Urban	0.239
Log10 littoral ha	Ecoregion	Type	% Agriculture	% Urban			% Agriculture		% Urban	0.238
Log10 littoral ha	Ecoregion	Type		% Urban	% Canopy		% Agriculture		% Urban	0.238
Log10 littoral ha	Ecoregion	Type		% Urban		House Density	% Agriculture		% Urban	0.238

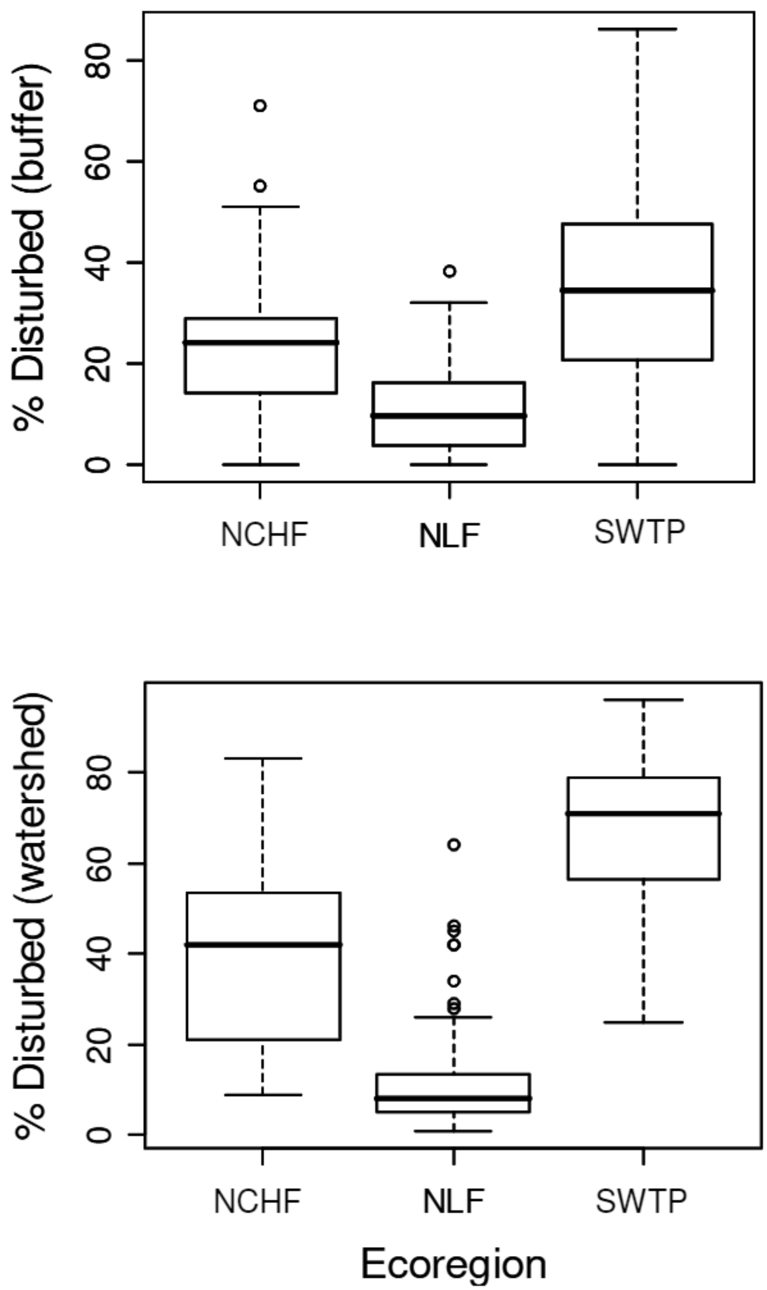

Figure 4. Distribution of disturbed watersheds and buffers across ecoregion.

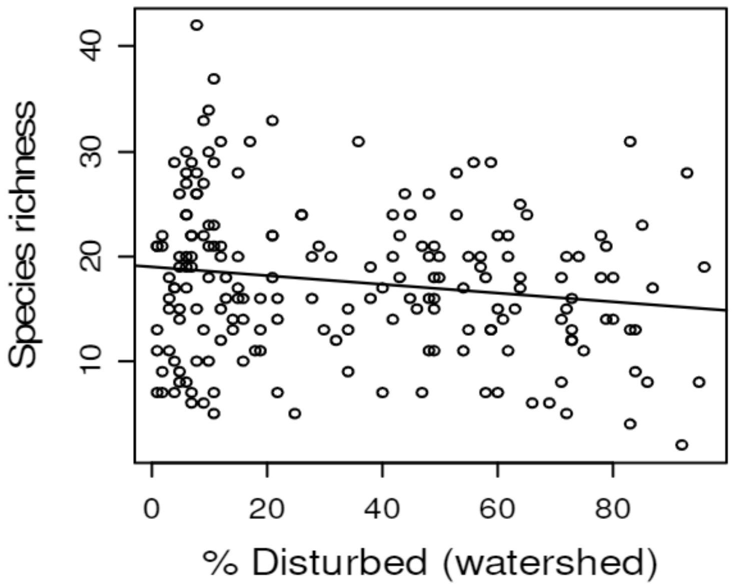

Figure 5. Species richness decreases with increasing watershed disturbance (adjusted $r^2 = 0.02$, $F = 4.91$, $df = 187$, $p = 0.03$).

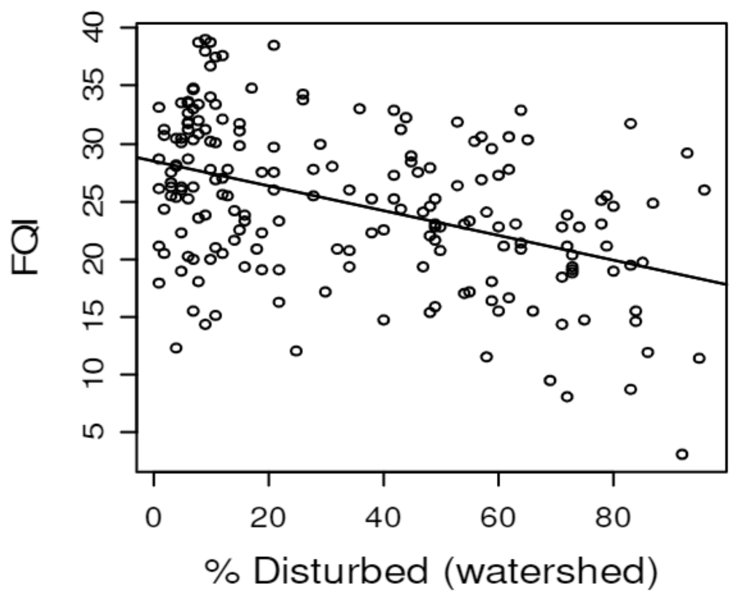

Figure 6. FQI decreases with increasing watershed disturbance (adjusted $r^2 = 0.19$, $F = 44.72$, $df = 187$, $P = 2.55^{e-10}$).

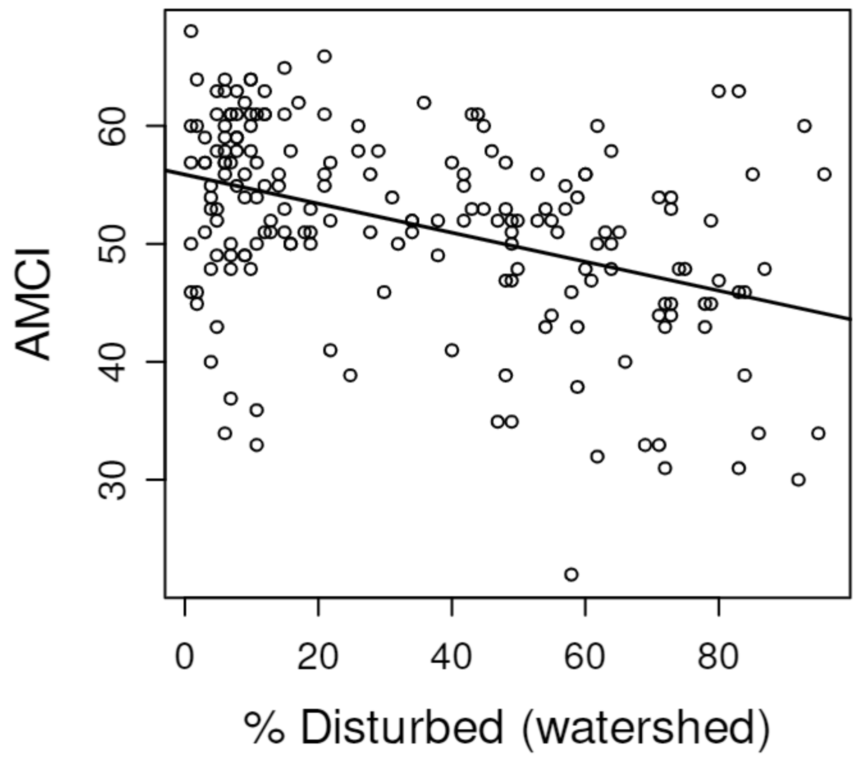

Figure 7. AMCI decreases with increasing watershed disturbance (adjusted $r^2 = 0.16$, $F = 37.95$, $df = 187$, $p = 4.35^{e-09}$).

We found that species richness increased with increasing littoral area. This species-area relationship is widely reported in terrestrial systems, but has been inconsistently reported for lakes, likely due to the inherent variability of lentic systems. Our study showed an effect of lake size, although the power of littoral area alone to explain macrophyte richness was limited. Nonetheless, lake littoral size remains an important predictive variable in a complex multivariate relationship. Additionally, species richness is an important component of both the FQI and AMCI scores, and thus, these parameters also tended to increase with increasing littoral area. Ecoregion was another important factor affecting macrophyte community characteristics. Lakes in the NLF region tended to have higher species richness, AMCI and FQI scores than lakes in the SWTP and NCHF regions. These trends may occur due to the following factors. First of all, the level of human disturbance is lower in the Northern region at both the buffer and watershed scales. Secondly, Northern lakes tend to be more oligotrophic, and they also tend to host communities of plants that prefer low alkalinity, which also generally have higher conservatism values (Canny, 2008). Finally, the lakes in the north tend more often to be seepage lakes, and seepage lakes statewide tend to have more species-rich macrophyte communities. Thus, species richness is likely influenced by the distinct, but at times correlated factors of landuse, ecoregion, type, and size.

The strongest regression relationships existed between watershed disturbance and FQI, followed closely by AMCI. Given that each of these metrics has a component that is directly related to landuse, our observations are in accordance with expectations. Both metrics use the conservatism value (C-value), which is a factor that reflects how often a particular species is thought to be associ-

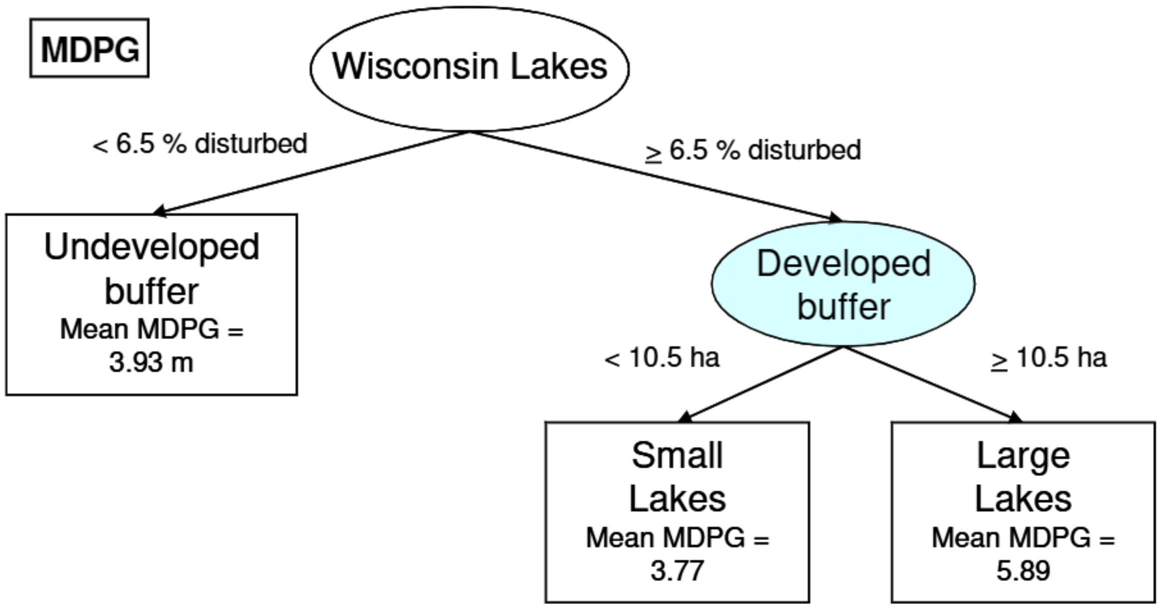

Figure 8. Pruned regression tree relating predictor variables to MDPG. Possible predictor variables are $\log_{10}$ littoral area, ecoregion (SWTP, NCHF, NLF), lake type (HW, LL, SE), lake class (1-6), buffer and watershed %disturbance, %agriculture, %urban, and buffer %canopy and % impervious surfaces.

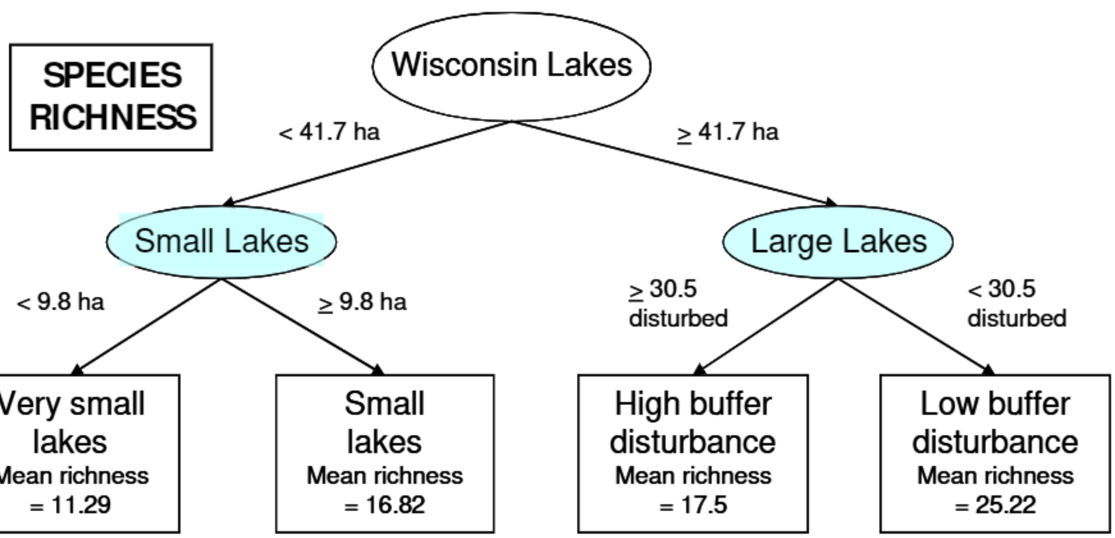

Figure 9. Pruned regression tree relating predictor variables to species richness.

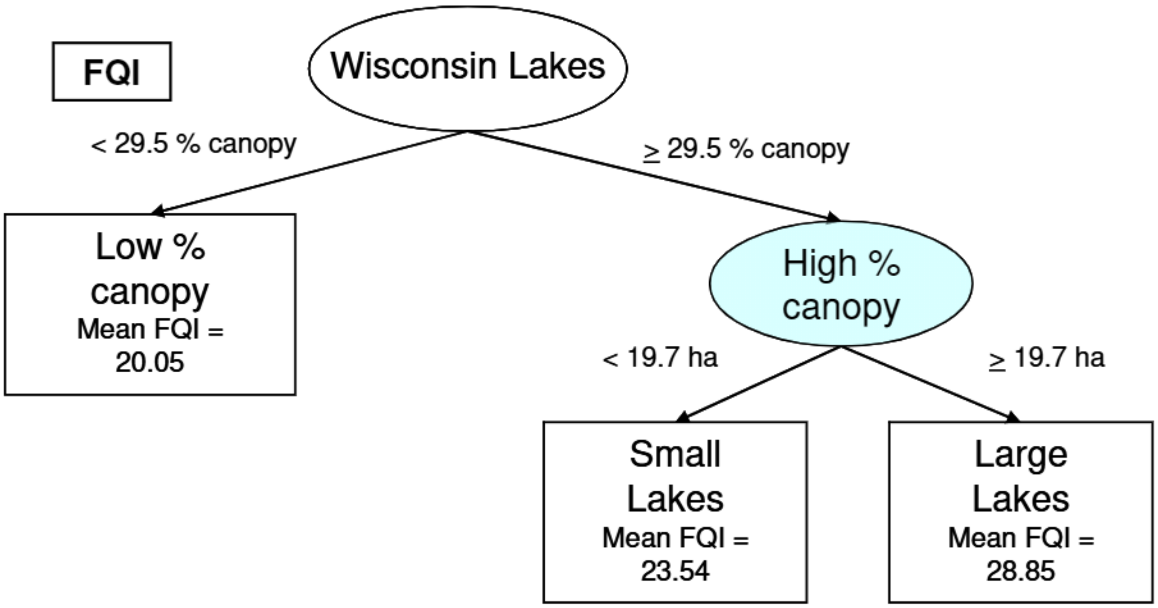

Figure 10. Pruned regression tree relating predictor variables to FQI.

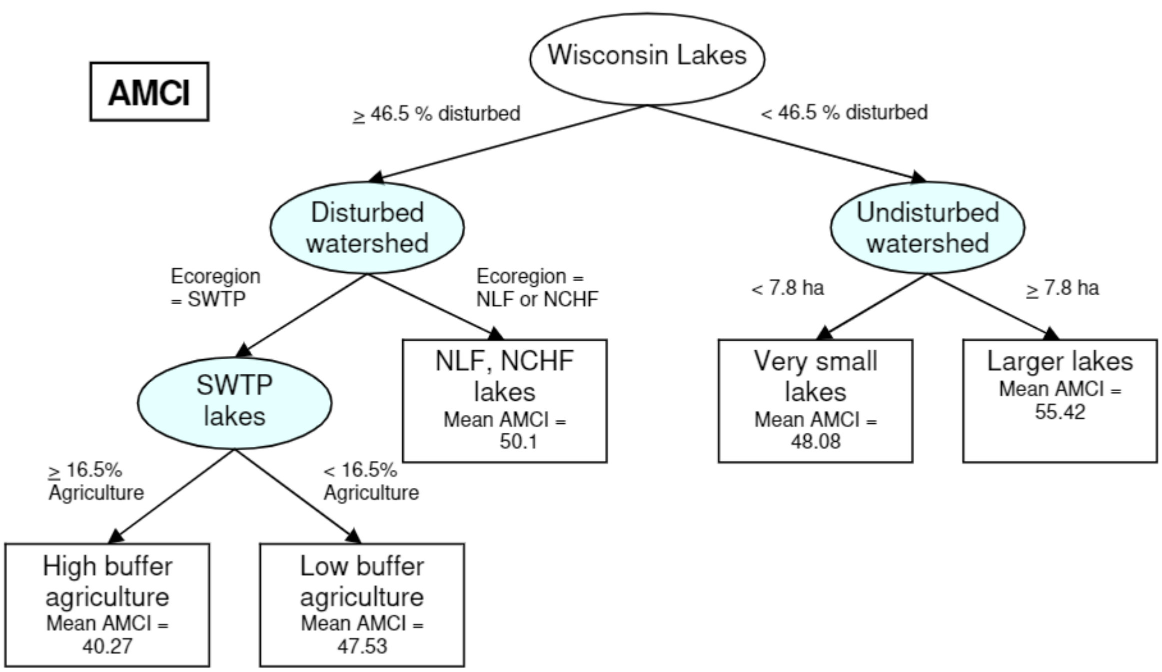

Figure 11. Pruned regression tree relating predictor variables to AMCI.

ated with least-disturbed conditions (Nichols 1999). The C-values were assigned on a species-by-species basis through a cooperative effort of leading Wisconsin botanists. Thus, the fact that our data show a negative relationship between landuse and AMCI and landuse and FQI is a valuable check on these metrics' worth and applicability while simultaneously supporting the ongoing use of macrophytes as bioindicators.

The relationship between species richness and watershed disturbance was negative, but not as strong. Although FQI and AMCI are designed to reflect community quality, the number of species does not relate to habitat quality in a simple linear fashion. Borman (2007) studied the relationship of species richness to habitat quality in northern Wisconsin lakes. Her conclusions show that oligotrophic lakes tend to support communities of isoetid plants that are less tolerant of high nutrient conditions, whereas meso-to-eutrophic lakes support communities of nutrient-tolerant elodeid species, which are in general more species-rich than isoetid communities. Increasing nutrient input to lakes tends to shift the lake towards a higher trophic state. This trophic shift has a concomitant effect on the plant community; as lakes become more mesotrophic, they tend to gain more nutrient-tolerant elodeid species. So, in this case, the degradation of the habitat is associated with increasing species richness (consistent with the intermediate disturbance hypothesis). Our analysis revealed a negative linear relationship between richness and disturbance, but the relationship was loose. Our data also showed

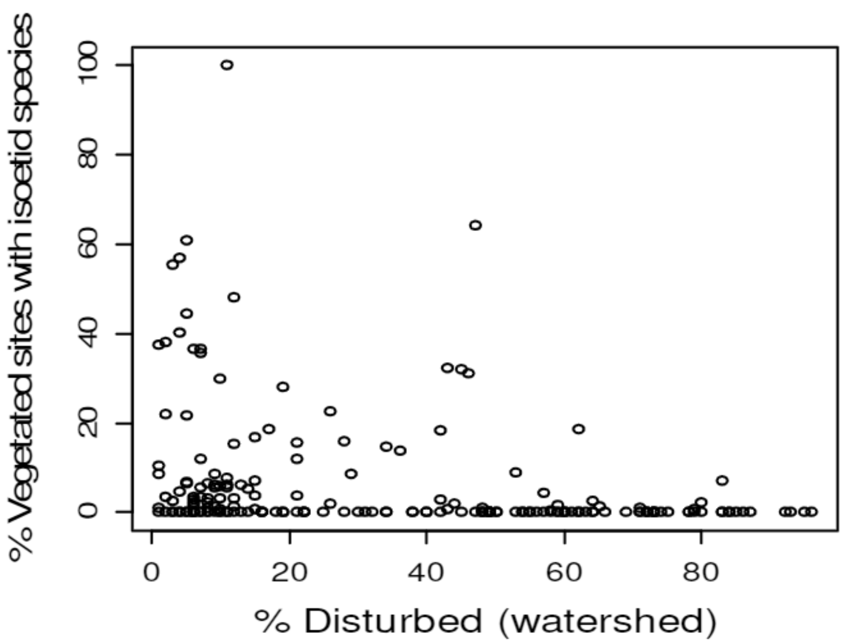

Figure 12. Percentage of aquatic plant community that is considered "isoetid" (small, low-nutrient adapted rosette species) decreases with increasing disturbance.

that the contribution of isoetid species to a lake's plant community decreased with increasing disturbance (Figure 12), but as a whole, these isoetid-community lakes aren't very well represented in our dataset. Thus, the relationship between disturbance and these low-diversity but high-quality communities likely contributed to the variation observed in the species richness factr, but was likely insufficient to influence statewide trends.

Despite the fact the ecoregion and type factors significantly influenced SAV in our exploratory models, these variables failed to show up on most of the regression trees we produced. Both type and ecoregion variables have three levels, and in general, the attributes measured differed among the levels. For example, species richness was lowest in the SWTP region, intermediate in the NCHF region, and high in the NLF region. Dichotomous splits may not provide a parsimonious method of modeling this variation. The trees did reveal that littoral area was among the strongest predictor variables in all models, and also pointed to the importance of several disturbance measures. In particular, the %urban land in the buffer zone was the most important variable influencing the maximum depth of plant growth. As this variable tends to decrease with decreasing water clarity and increasing algae levels, %urban likely reflects trends in nutrient input at the near-lake scale.

Multiple linear regression revealed a complex interaction between lake type, lake size, ecoregion, landuse, and plant community characteristics. For all macrophyte variables explored, littoral area, ecoregion type, and %urban (buffer) were included in the best models. Measurements of disturbance were also important in explaining the variation in plant communities. Of particular interest is that all the best models used disturbance variables at the watershed *as well as* the buffer scale. The way in which the disturbance factor was measured was variable, but as long as both local and watershed scales were considered, the linear models were notably improved over those that considered disturbance on only a single scale. The fact that disturbance on both scales is important in explaining decreases in aquatic plant community health might allow managers to strategically address how to minimize landuse impacts. For example, while it may not yet be in the purview of a community or a lake manager to halt agricultural activities that impact a lake's watershed, a coordinated effort on behalf of landowners to ameliorate disturbance on a local level has the potential to significantly impact plant communities.

The percentage of urban developed land in the buffer area was one of the most consistently strong factors in the linear models. While impervious surface is generally considered a more accurate way to express urban development as it relates to lake impacts, we have found that the category "%urban" is in fact more influential. The urban developed land category represents not only impervious surface, but also areas in which constructed materials combine with vegetation, and in this case the vegetation is usually in the form of planted lawns. While the impervious surface category will directly relate to run-off and nutrient influx, one of the most common types of disturbance at the lake shore level is the conversion of the natural wet-adapted vegetation to lawn grass. Lawn grass can contribute to high rates of runoff and is also associated with increased nutrient influx in the form of applied fertilizer (Graczyk et al. 2003). Thus, the urban category, as opposed to the impervious landuse category might more accurately capture local perturbations affecting SAV.

In summary, we have made significant steps toward proposing a lake classification scheme that will allow us to better understand the response of macrophyte communities to human perturbations. We know that we must account for the significant impacts of lake size, ecoregion and hydrological type. We also identified that lake plant communities respond to disturbance on at least two different scales. By designing studies that incorporate and account for the variables we have identified, Wisconsin ecologists will be better positioned to observe meaningful trends across gradients of both ecological and human-related factors. We have identified plant responses on a multi-lake scale; it is now of interest to ask whether and how plants are affected by disturbance on a smaller, in-lake scale. By examining the quality of the aquatic plant community on a site-by-site basis, we may be able to define the impact of local perturbations. Also of interest is the relationship between macrophytes and the lakeshore urban development factor. The amount of developed land in the buffer region of a lake may more strongly influence macrophyte communities, because unlike the %impervious category, the category "urban" captures an element of the cultural, relating not only nutrient impacts, but also human behavioural activities to ecological response variables. With the classification groundwork we have herein presented, we can now begin to efficiently address these intriguing and timely issues of human impact and environmental integrity.

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FISHERY

PART A: Moderate, Lowland Drainage Lakes

Development of a Fish IBI for Moderate Sized Drainage Lakes

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Efforts to construct a fish-based IBI were conducted along two tracks. One avenue explored the development of an IBI on small lakes although previous work (Hatzenbeler et al. 2004) had indicated that a fish-based IBI might not work well on small headwater lakes (Classes 1,2,5, and 6). Another approach attempted to develop a fish-based IBI on moderate sized lowland drainage lakes (Class 4). The effort to develop a fish-based IBI for Class 4 lakes is described below.

We used existing lake fish survey data to explore whether an effective fish-based IBI could be developed for moderate-sized lowland drainage lakes in Wisconsin. Findings described in the subsequent section (Jennings et al.) coupled with results of an earlier study (Hatzenbeler et al. 2004) indicated that a fish-based IBI would likely not work well in small (< 80 ha surface area) headwater Wisconsin lakes. However, other analyses from Wisconsin (Jennings et al. 1998) and Minnesota studies (Drake and Pereira 2002; Drake and Valley 2005) suggest more promising prospects for larger lakes with larger drainage areas. For this portion of the study, we considered only lakes that were moderate in size (80-800 ha surface area), relatively deep (> 5.6 m maximum depth), lowland drainage(> 4 mi^2 watershed area, class 4) lakes. These lakes are large enough and well enough connected to other waters to have an inherently more diverse and stable fish fauna than smaller headwater lakes, and consequently their fish assemblages should respond more consistently and predictably to human impacts in the riparian zone and watershed. They are also well-represented in the landscape, enough to allow for thorough and robust statistical analyses. We consider these moderately-sized class 4 lakes to have the best potential for development of a fish-based IBI in Wisconsin.

Our fish survey data had been collected by WDNR biologists between 1998-2005 as part of a systematic statewide lakes monitoring program. Sampled lakes had been chosen randomly within geographic strata that roughly corresponded to Level III ecoregions (Omernick et al. 2000). The number of lakes sampled in each stratum was directly proportional to the lake density within the entire stratum. Each lake was sampled once during the summer and fall. In summer, small-mesh mini-fyke nets (described in Fago 1998) were set overnight in the littoral zone to collect small-bodied fishes. In fall, portions of the shoreline were electrofished at night with a boom shocker to collect larger-bodied fishes. The amount of sampling by both methods was proportional to total shoreline length. All fish captured were identified and counted.

For analyses, we selected 164 lakes from the statewide data set that encompassed a wide range of shoreline and watershed development (i.e., agricultural and residential/urban land uses). However, not all combinations of geographic region, lake size, and development occurred in our dataset. In particular, we lacked sufficient lakes within our size range in southern Wisconsin with low levels of shoreline or watershed development, larger lakes statewide with low levels of shoreline development, and lakes of all sizes in northern Wisconsin with high levels of watershed development. Some of these combinations, particularly larger southern Wisconsin lakes with low levels of shoreline or riparian development, may no longer be found in Wisconsin, but other combinations, such as northern Wisconsin lakes with high levels of watershed development, were simply missed due to randomized sampling.

We considered a large number of possible relationships between lake fish assemblage characteristics and human land-use at both the riparian and watershed scale. We used general linear regression models (SAS 2007) to correlate 52 sampling-gear-specific measures of fish assemblage structure, composition, or function (hereafter, potential metrics, taken from Jennings et al. 1998 and Drake and Pereira 2002) with five measures of human impact. Using the National Land Cover Database, we calculated percent agricultural land, percent impervious surface, percent disturbed land [agricultural, urban, and other human land-uses combined], and percent forest in both the riparian area (within 100 m of the shoreline) and the entire watershed. We also used Radeloff et al.'s (2005) integrated NLCD and U.S. Census coverage to estimate house density. Because lake size and location influence many aspects of fish assemblages in Wisconsin lakes (Jennings et al. 1998), our regression models included geographic region (north vs south) as a blocking variable and lake surface area as a covariate. For each potential metric, we ran 10 separate models for each of the five impact variables for both the riparian buffer and the entire watershed, and we included interaction terms between the impact variable and lake surface area and geographic region. If the blocking variable, covariate, or an interaction term was not significant, it was dropped and the model rerun without it. The goal was to determine the simplest statistically significant model. If more than one impact variable or spatial scale (i.e., disturbance in the riparian buffer vs that in the watershed) yielded a significant model, we used Akaike's Information Criterion (AIC) (Akaike 1974) to rank relative model strength.

We found few promising relations between fish metrics and measures of human land-use impacts, in part because of limitations in our dataset. For many of the potential metrics there was a significant positive correlation with lake size, which was expected, but in most of these cases there was also a significant interaction between lake size and riparian buffer human impacts. This indicated that degree of human impact increased with lake size as well, and that buffer human impacts and lake size were largely confounded in our dataset. Consequently, for many potential metrics there was a positive relation with degree of riparian human impact, contrary to expectations. There was also a significant interaction effect between both riparian and watershed human impacts and geographic region, documenting the generally greater and more widespread human development of the southern Wisconsin landscape.

From our dataset, we could identify only three potential metrics that justified possible inclusion in a fish-based IBI. Each had a strong, consistent, and expected correlation with two or more measures of human impact across all lakes sizes in both northern and southern Wisconsin even after we accounted for variation due to lake size, geographic region, and human impacts. The number of intolerant species (certain minnows, sculpins, and darters) caught by mini-fyke nets was positively correlated with both buffer and watershed percent forest and negatively related to watershed housing density, watershed percent impervious surface, and watershed disturbed land. The catch-per-unit effort of intolerant fish by mini-fyke nets was positively correlated with watershed percent forest and negatively correlated with watershed impervious surface and disturbed land. Thus, species richness and abundance of small-bodied intolerant fishes was reduced in lakes with relatively low amounts of forest and high amounts of human impacts. Earlier analyses by Jennings et al. (1998) had also identified the richness and abundance of small-bodied intolerant species as good candidate metrics for a Wisconsin lake IBI. In contrast to intolerant fishes, the electroshocker catch-per-effort of sunfish (*Lepomis* species) was positively related to watershed percent disturbed land and watershed percent impervious surface. The abundance of sunfish was relatively high even in little-impacted lakes, but generally grew as watershed human impacts increased. The three potential metrics for inclusion in a fish-based IBI are shown in Table 1.

Table 1. Three significant fish metrics and their response to human disturbance.

Metric	Response
Number of intolerant species	Decrease with human disturbance
Abundance of intolerant species	Decrease with human disturbance
Abundance of sunfish	Increase with human disturbance

It is impossible to construct a viable lake IBI with only three potential metrics. However, this does not mean that a fish-based IBI can not be developed for moderate-sized class 4 Wisconsin lakes. Rather it points out the limitations of a dataset derived solely from random sampling for this purpose. Two key natural factors that influenced fish assemblage attributes, lake size and geographic location, were confounded with human riparian and watershed impacts, likely obscuring many relations between fish assemblages and impacts. To assess adequately the viability of an IBI, we need to supplement our existing dataset of randomly selected lakes with a group of carefully chosen lakes that represent gradients in lake size, location, and disturbance. Although not all possible missing combinations may actually exist (e.g., relatively large southern Wisconsin lakes with little riparian development), it is certain that many do. With a more balanced dataset, it should be possible to test more thoroughly and completely for relations between fish assemblage attributes and human impacts and to determine whether in fact a fish-based IBI will be practical for moderate-sized, relatively deep, lowland, drainage lakes in Wisconsin.

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PART B: Small Headwater Lakes

Natural and Human Influences on Fish Species Richness in Small North Temperate Lakes: Implications for Bioassessment

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Abstract

Understanding how natural and anthropogenic factors interact is important for assessing and predicting human impacts on aquatic communities. We developed analysis of covariance (ANCOVA) models predicting fish species richness as a function of two simple landscape-scale, binary variables, surface water connectivity to other aquatic systems, and human riparian development, with lake surface area as the covariate. All three variables were significantly related to species richness and explained 61 %of the variance in a data set from 55 limnologically similar lakes in northern Wisconsin. We developed additional ANCOVA models to assess the relative effects of these three variables on four functional species groups, including gamefish, riverine, tolerant, and intolerant species. The number of gamefish species was greater in lakes with riparian development than in undeveloped lakes; this is probably related to introductions by management agencies and anglers. Connectivity increased the number of riverine species and intolerant species. Intolerant species may be more abundant because connecting streams provide colonization routes and decrease time between periodic extirpation and recolonization events. In addition, flowing water connections may provide a refuge from winter hypoxia and decrease extirpation rates of intolerant species. Models predicting species richness of tolerant species were not significant. Tolerant fishes are ubiquitous on the landscape and unaffected by the measured variables. The use of fish as biological indicators for lake assessment requires adjusting expectations for connectivity and lake size. This study demonstrates that simple landscape variables can dominate assemblage dynamics of small lakes, and that human-mediated introductions increase species richness at low and moderate levels of disturbance.

Introduction

The need to assess and monitor water resource condition has led to development of numerous indices based on the resident biota, an approach termed "bioassessment". The index of biotic integrity, or IBI, is the best known bioassessment index in the United States and was originally developed with fish as indicators of condition in warmwater Midwestern streams (Karr et al. 1986). The IBI has been modified for application to other regions and stream types, and the concept has been expanded to other taxa (Karr and Chu 1997); however only a few studies have applied this concept to lakes (Jennings et al. 1998, Whitter and Hughes 1998, Drake and Periera 2002, Drake and Valley 2005). The application of the IBI concept to lakes requires some of the same steps involved with developing a stream index, such as determining reference conditions based on regional species pools and characteristics of the waterbody. Expectations for assemblage structure differ across a gradient of stream order; similar adjustments are required to account for differences expected among groups of lakes defined by characteristics such as size, depth, water chemistry, and landscape position (Emmons et al. 1999). One of the principal challenges to successful application of a lake IBI is documenting and accounting for the strong influence of these natural features on assemblage structure (Jennings et al. 1999, Whittier and Hughes 1998, Drake 2007). To successfully apply the IBI model to lakes requires a clear understanding of processes structuring lake assemblages, and specifically, an understanding of how natural processes and anthropogenic processes interact. A fundamental question is whether lake assemblage characteristics such as species richness provide a reliable indication of resource condition, or simply a validation of limnological lake class.

Assemblage structure can be evaluated with a variety of different metrics (Karr and Chu 1997); one of the simplest is total species richness. Species richness is determined by colonization and extirpation events that occur at frequencies modified by a combination of natural and anthropogenic influences. Natural colonization of lakes by fishes can be accomplished by immigration from connected waters. The rate of colonization is likely to be affected by the type of connection, which may be a permanent stream or an infrequent connection provided by episodic floods. The pool of species colonizing a lake is dependent on zoogeographic influences (Hocutt and Wiley 1986). In addition to these natural processes, fish can gain entry into lakes by anthropogenic processes including deliberate management action (Radomski and Goeman 1995), illegal but intentional transfers of sport fish, or inadvertent transfers from live wells or bait buckets (Ludwig and Leitch 1996).

Patterns of extirpation and colonization have been investigated in small lakes of Northern Wisconsin and Finland (Tonn and Magnuson 1982, Tonn et. al. 1995, and Magnuson et al 1998). In a finely detailed study of colonization and extinction incorporating many potential variables, Magnuson et al. (1998) concluded that extirpation variables dominated community dynamics in these lakes while colonization, though important, occurs relatively infrequently. Rahel (1986) concluded that colonization facilitated by connectivity was important in structuring fish communities in larger lakes but played little role in small, low alkalinity Wisconsin lakes. These studies provide a useful foundation by identifying lake characteristics that may play critical roles in colonization and extirpation processes, and are useful in structuring a conceptual framework for interpreting monitoring data.

In this study, we evaluate simple statistical models of fish species richness within a group of limnologically similar lakes in northern Wisconsin. Specifically, we address the issue of whether simple, easily determined variables related to colonization and extirpation potential can explain observed distributional patterns without more complex measurements of habitat and land use. We further examine how these variables differentially affect species groups to identify types of species that may be more or less sensitive to certain colonization and extirpation factors. These variables include two natural landscape features (presence or absence of a connection to other aquatic systems and lake surface area) and a binary indicator of overall human activity (presence or absence of riparian development).

Methods

Study Lakes

Fish assemblages in 55 northern Wisconsin lakes were sampled during a single summer from 1997 to 1999. These lakes were selected randomly from a class of lakes that were defined to be similar in limnology, morphology, and geologic origin (Emmons et al. 1999). The study lakes ranged from 8 to 80 ha in surface area, were slightly acidic to neutral (pH 5.1-6.9), had maximum depths greater than four meters, were located high in the landscape and were classed as oligotrophic to mesotrophic (Table 1). By sampling lakes from within a defined lake class, we reduced the expected variation in fish species composition related to differences in limnology. Therefore, the main differences among lakes are likely the result of small-scale colonization and extirpation processes rather than regional zoogeographic factors or differences in species habitat requirements or physiological tolerances.

Fish sampling

Fish sampling was conducted June through August. Each lake was sampled within a single week with multiple gears. The use of multiple gears overcomes sampling bias that may occur with a single gear, and more accurately describes the species composition of a lake (Weaver et al. 1993, Jackson and Harvey 1997). Fish assemblage was evaluated with 4 mini-fyke nets and ten 30m shoreline stations sampled with seines and dc-electrofishing (backpack or towed unit). Minifyke nets had two 0.91x0.91m frames, four 0.61 m hoops spaced 0.6 m apart, and a 0.76 m x 10m lead. Minifyke nets had 5.6 mm ace mesh, and the opening was covered with a 25mm bar mesh exclusion net. Bag seines with 5.6 mm ace mesh were pulled parallel to shore from the shore to the 1 m contour or 15 m. Several stations could not be efficiently seined because of bottom composition or obstructions, therefore, these sites were also sampled with DC-electrofishing. All sampling stations were randomly selected. The data approximate a presence/absence census of community composition for each

Table 1. Limnological, morphological, and colonization/extirpations attributes of the 55 northern Wisconsin lakes used in this study.

Lake	County	Area (ha)	Maximum Depth (m)	Connected	Developed	Species Richness
Cedar	Iron	77.3	6.1	Yes	Yes	28
Upper Clam	Ashland	67.2	6.1	Yes	Yes	26
Big Dardis	Price	58.3	7.0	Yes	Yes	21
Granite	Barron	62.3	10.4	Yes	Yes	19
Bass	Washburn	52.6	20.1	No	Yes	16
Cisco	Bayfield	38.4	32.0	No	Yes	16
Otter	Forest	32.8	5.8	Yes	Yes	15
Diamond	Oneida	50.2	5.2	No	Yes	15
Bass-Patterson	Washburn	76.1	10.7	Yes	Yes	15
Tahkodah	Bayfield	61.5	5.5	No	Yes	14
Waubee	Oconto	55.4	7.0	No	Yes	13
Spring	Oneida	36.4	4.0	Yes	Yes	13
Black	Sawyer	50.6	5.2	Yes	No	13
Poquette	Burnett	39.3	7.0	No	Yes	13
Crystal	Bayfield	44.9	8.8	Yes	Yes	13
Chain	Oconto	32.8	15.2	Yes	Yes	12
Dorothy	Oneida	38.9	10.7	No	Yes	12
Little Bear	Burnett	51.8	16.8	No	Yes	12
Anodanta	Bayfield	10.5	9.4	Yes	No	12
Arbutus	Forest	65.2	8.5	No	Yes	11
Flannery	Oneida	45.3	10.7	No	Yes	11
Pallette	Vilas	70.0	19.8	No	No	11
Loon	Barron	38.0	7.9	No	Yes	11
Atkins	Bayfield	71.2	24.4	No	Yes	11
Arrowhead	Bayfield	14.6	12.2	Yes	No	11
Little Long	Forest	41.3	9.1	No	Yes	10
John	Oconto	41.7	7.6	Yes	Yes	10
Bass	Oneida	29.9	9.4	No	Yes	10
Bird	Oneida	40.0	12.2	No	Yes	10

Townline	Oneida	24.7	7.6	No	Yes	10
Langley	Oneida	19.4	4.6	No	No	10
Warner	Burnett	71.2	22.9	No	Yes	10
Rose	Langlade	44.1	7.62	Yes	Yes	9
White Deer	Forest	25.1	13.4	No	No	9
Ellison	Bayfield	44.5	5.5	No	Yes	9
McLain	Washburn	60.7	9.1	No	Yes	9
Bass	Bayfield	29.5	10.7	No	No	9
Ruth	Bayfield	26.7	9.1	No	Yes	9
Leisure	Washburn	30.3	7.9	No	Yes	8
Woodbury	Forest	29.1	6.1	No	No	7
Ed's	Forest	12.5	5.5	No	Yes	6
Imogene	Vilas	26.7	12.5	No	Yes	6
Van Zile	Forest	31.6	5.2	No	Yes	6
Josie	Oneida	18.6	4.9	No	No	6
Luna	Forest	27.1	10.7	No	No	6
McLaren	Ashland	26.7	5.2	No	Yes	6
Little Star	Forest	8.1	5.4	No	No	5
Ludington	Forest	12.1	9.4	No	Yes	5
Dewey	Vilas	19.4	5.5	No	No	5
Crystal	Oneida	22.3	9.1	No	Yes	5
Wolf	Forest	13.3	4.6	No	No	5
Bastile	Forest	19.0	7.0	No	No	4
Nebish	Vilas	36.8	15.8	No	No	3
Flynn	Bayfield	25.9	12.8	No	No	3
Bailey	Forest	32.4	5.5	No	No	2

lake (Jennings et. al. 1999).

Predicting assemblage species richness

To examine the importance of natural and anthropogenic landscape features in altering colonization and extirpation processes, we used two simple landscape-scale, binary variables. Development described the presence or absence of homes or cabins within the riparian zone, defined as the land within 100 m of the shore. Connectedness (Rahel 1984) described the presence or absence of a permanent surface water connection to the lake. Because species-area relationships have been previously identified as important for predicting species richness in northern Wisconsin lakes (Jennings et.

al ,1998; Magnuson et. al., 1998), lake area was included as a continuous covariate in the analyses.

We used an Analysis of Covariance (ANCOVA; Yandell, 1997) to examine the overall relationship between total lake species richness and the landscape variables. Species richness was modeled as a function of development and connectivity, with lake area used as a covariate. Least square means were used for post-hoc comparisons of treatment means. Tests for separate slopes (main-effect interactions) were used to determine if the response of lake area with respect to species richness was the same across the extirpation and colonization variables. A nonsignificant effect implies that the effect (if any) of lake area on species richness was constant across the extirpation and colonization terms. All nonsignificant interactions effects were removed from the final models. Alpha was set at 0.05.

Components of species richness

Total species richness includes individual species or groups of species that may respond differently to the three landscape variables. Assigning species to functional groups based on ecological similarities or their value to humans allow tests of hypotheses regarding landscape features affecting extirpation and colonization rates. Game species were defined as species that are commonly targeted for recreational catch and/or harvest by anglers; we hypothesize that these species will be moved to lakes with more human activity, and thus will be more numerous in developed lakes. The riverine species group consisted of those species found primarily in lotic habitats, as described in Becker (1983). We expect these species to be more numerous in lakes with permanent stream inlets or outlets. The concept of tolerance is usually applied to functional group designations in IBI development (Karr and Chu 1997). Intolerant and tolerant species are groupings that are expected to be sensitive (intolerant) or resilient (tolerant) to anthropogenic degradation, usually thought of as a complex of effects including diminished water quality, sedimentation, and other forms of habitat degradation. These groups are of particular interest because water quality can vary as a result of both natural and anthropogenic influences. Whereas intolerant species can provide useful insight regarding relative importance of human influence and natural processes, tolerant species are ubiquitous, and no relation is expected between tolerant species richness and development or connectivity. Tolerance designations are based on Whittier and Hughes (1998), Drake and Pereira (2002), and Jennings et al. (1998).

Membership of species within groups is not exclusive; assignment is based on ecological relevance and results in some species belonging to more than one group (Table 2). The issue of redundancy among metrics and other statistical issues with IBI are addressed by Karr and Chu (1997). Because biological assessment methods typically contain overlapping groups to maximize biological relevance, their use is appropriate here.

To examine the relationships between colonization/extirpation factors and richness of species groups, we used ANCOVA. In these analyses group species richness was modeled as a function of development and connectivity, with lake area as a covariate.

Species richness was square root transformed for all ANCOVAs, and only main effects were tested without interactions. All analyses were performed with the GLM procedure in SAS (version 9.1, 2004).

Table 2. Species list of fish collected from 55 northern Wisconsin lakes along with group designation and frequency of occurrence. For group designation, 12 were game species (G), nine were intolerant (I), six were tolerant (T), four were riverine (R), and 12 of 42 species were not used in a group (-).

Scientific Name	**Common Name**	**Occurrence**	**Group Designation**
Amia calva	Bowfin	2	-
Cyprinus carpio	Common carp	1	T
Luxilus cornutus	Common shiner	11	-
Nocomis biguttatus	Hornyhead chub	4	R
Notemigomus crysoleucas	Golden shiner	18	T
Notropis atherinoides	Emerald shiner	1	-
Notropis heterodon	Blackchin shiner	3	I
Notropis heterolepis	Blacknose shiner	3	I
Notropis volucellus	Mimic shiner	2	-
Phoxinus eos	Northern redbelly dace	4	R
Phoxinus neogaeus	Finescale dace	1	-
Pimephales notatus	Bluntnose minnow	22	-
Pimephales promelas	Fathead minnow	4	-
Semotilus atromaculatus	Creek chub	6	R
Catostomus commersonii	White sucker	16	-
Moxostoma erythrurum	Golden redhorse	1	R
Moxostoma macrolepido-	Shorthead redhorse	2	R
Ameiurus melas	Black bullhead	20	T
Ameiurus natalis	Yellow bullhead	27	T
Ameiurus nebulosus	Brown bullhead	1	-
Noturus gyrinus	Tadpole madtom	10	I
Esox lucius	Northern pike	35	G
Esox masquinongy	Muskellunge	12	G
Umbra limi	Central mudminnow	30	T

Oncorhynchus mykiss	Rainbow trout	1	G
Salmo trutta	Brown trout	1	G
Cottus bairdii	Mottled sculpin	2	I
Ambloplites rupestris	Rock bass	25	G
Lepomis cyanellus	Green sunfish	10	-
Lepomis gibbosus	Pumpkinseed	37	G
Lepomis macrochirus	Bluegill	47	G, T
Micropterus dolomieu	Smallmouth bass	17	G
Micropterus salmoides	Largemouth bass	51	G, T
Pomoxis nigromaculatus	Black crappie	34	G
Etheostoma exile	Iowa darter	17	I
Etheostoma flabellare	Fantail darter	3	I
Etheostoma microperca	Least darter	1	I
Etheostoma nigrum	Johnny darter	19	I
Perca flavescens	Yellow perch	51	G
Percina caprodes	Logperch	2	-
Percina maculate	Blackside darter	2	I
Sander vitreus	Walleye	19	G

Results

A total of 42 species was collected from the 55 lakes sampled (Table 2). Species richness in lakes varied from 2 to 28 species with a median of 10.

Predicting Assemblage Species Richness

Total species richness of sampled lakes was strongly related to the connectivity and development status of lakes (Table 3), with 61%of the variation in species richness explained by the additive effects of the two variables and the covariate, lake area. Tests of separate slopes (area with main-effect interactions) indicated that none of the covariate-main effect interactions were significant (all $p > 0.05$). This implies that the effect of lake area on species richness was constant between the two development and the two connectivity levels.

Analysis of least square means for each main effect indicated that connected lakes contained more species than did landlocked seepage lakes and developed lakes had higher species richness than did undeveloped lakes (Figure 1). Species richness increased with lake size (Figure 2).

Components of Species Richness

Tests of species richness within functional groups produced significant models for all groups except tolerant species (Table 4). Among groupings with significant models, the importance of the landscape variables differed. The number of game species in lakes was strongly related to the riparian development status of the lake, with developed lakes having a higher incidence of game species than undeveloped lakes (Figure 3). As expected, the number of river species was strongly related to the connectivity of the system, with more species found in connected lakes (Figure 4). The number of intolerant species was positively related to connectivity and lake area, but unrelated to development. Lake area was not a significant covariate in predicting species richness of either riverine species or game species.

Table 3. Analysis of covariance of total species richness versus colonization and extirpation variables. Lake area is used as covariate.

Effect	F	P	Model P
Connectivity	23.15	<0.001	<0.001
Development	5.78	0.020	
Lake Area	20.85	<0.001	

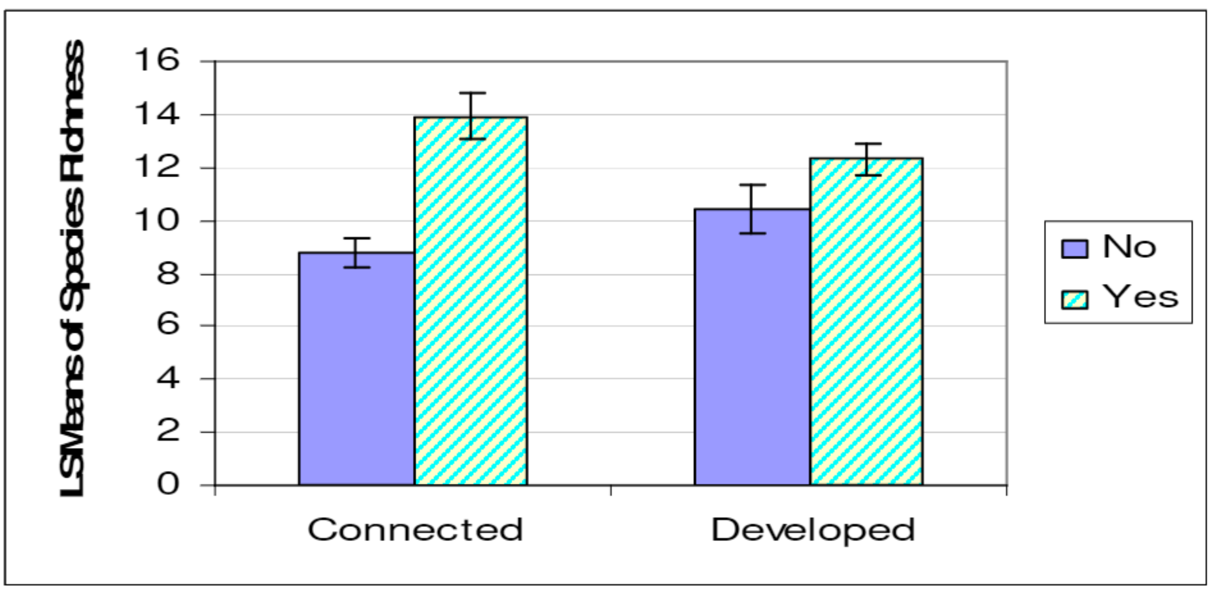

Figure 1. Results of least square mean comparisons of extirpation-colonization variables versus species richness. Results are non-transformed least square means adjusted for area and the other effects in the model along with standard errors. All pairwise comparisons were significantly different.

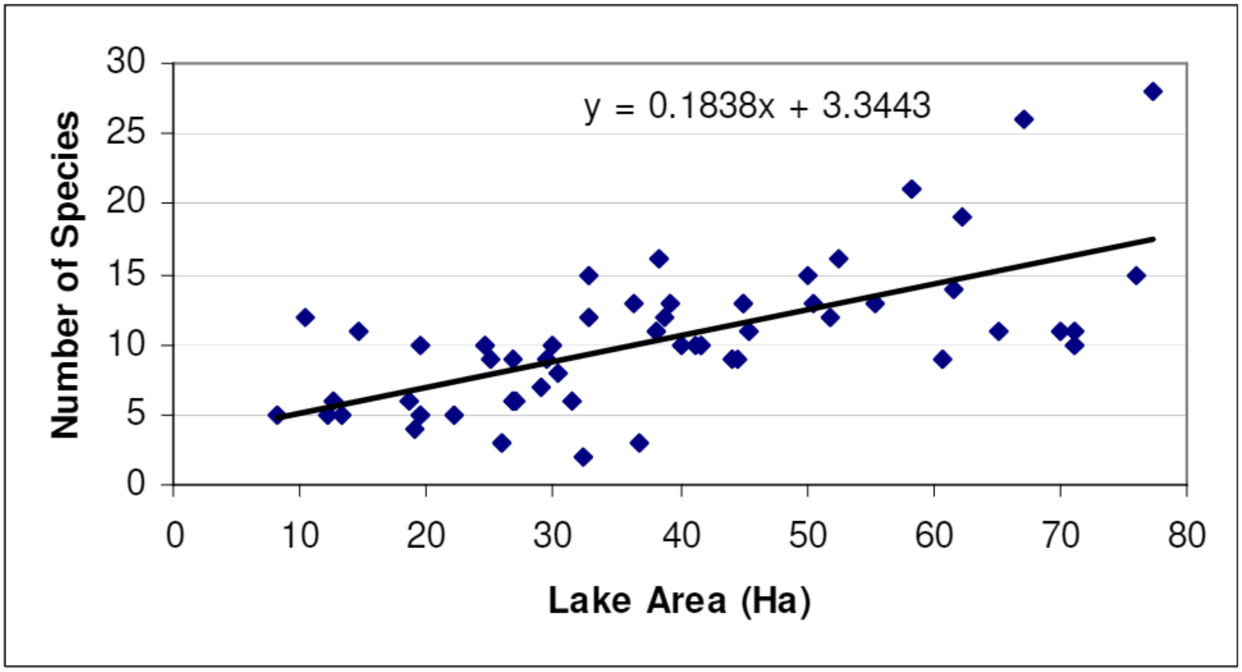

Figure 2. Linear relationship between the observed number of fish species per lake and lake area for 55 northern Wisconsin study lakes.

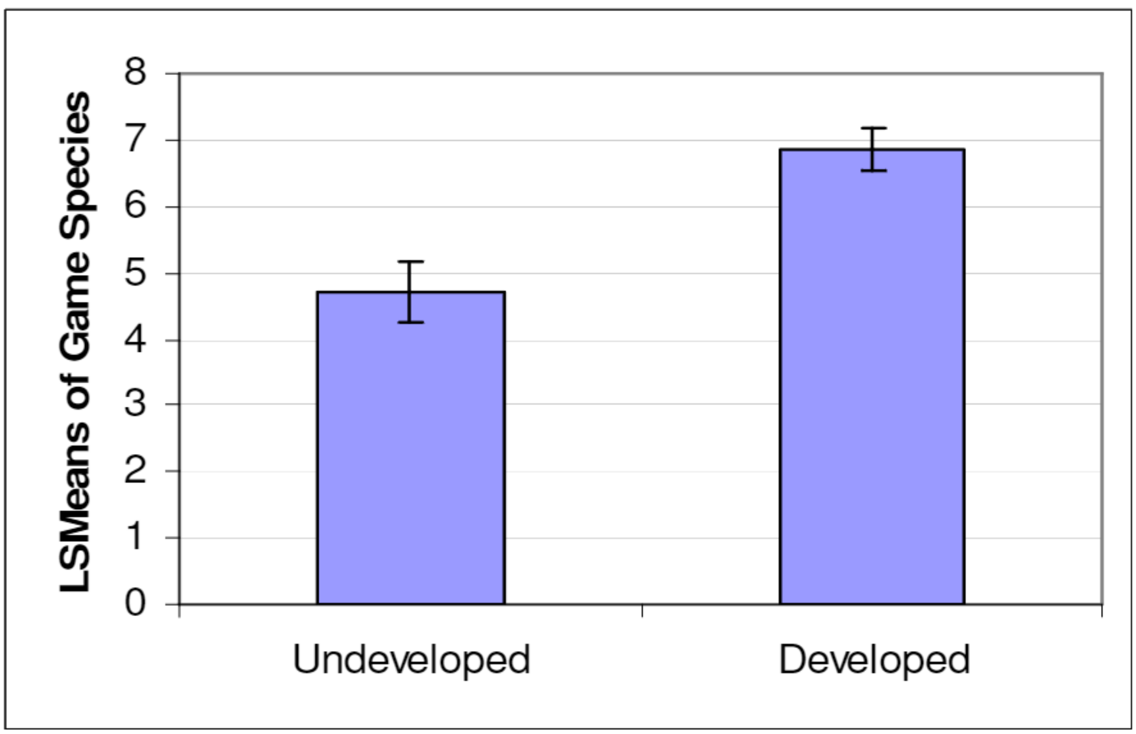

Figure 3. Results of least square mean comparisons of game species in developed vs. undeveloped lakes. Results are non-transformed least square means of number of game species ± SE ($p<.05$).

Table 4. Analysis of covariance of within group species richness versus colonization-extirpation variables. Lake area is used as a covariate. NS indicates that the overall model was not significant.

Species Group	**Effect**	**F**	**P**	**Model P**
Riverine Species	Connectivity	7.95	0.007	0.003
	Development	1.40	0.242	
	Lake Area	0.99	0.325	
Tolerant				NS
Game Species	Connectivity	2.28	0.138	<0.001
	Development	15.01	<0.001	
	Lake Area	2.67	0.109	
Intolerant	Connectivity	22.47	<0.001	<0.001
	Development	0.15	0.697	
	Lake Area	18.68	<0.001	

Discussion

Much of the variance in species richness among the 55 lakes can be explained by 3 simple variables that describe overall human activity (development) or simple, natural landscape features (connectivity and lake area). Thus, assemblages were influenced strongly by both natural and anthropogenic processes. A predictable response to human activity suggests that fish indicators may have utility in a lake monitoring program; however, the strong influence of natural factors suggests that reference conditions would need to be finely tuned to variables affecting natural rates of colonization and extirpation.

The analyses of species richness within functional groups provide further insight regarding the relative importance of natural and anthropogenic factors in structuring fish assemblages. We hypothesized that simple landscape variables are related to the rate at which new species colonize lakes, and the rate at which species are extirpated. Although mechanisms such as competition and predation are obviously important to understanding how species pairs might interact (Tonn and Paszkowski 1986), or even which species might be extirpated, landscape variables are more useful to understanding simple assemblage metrics such as species richness.

Perhaps the most interesting of the groups is the intolerant species, because their distribution is potentially affected by different landscape-scale processes. We hypothesize that intolerant species are prone to extirpation in the face of anthropogenic degradation, and thus would be less numerous in developed lakes. Alternatively, their distribution may be affected more strongly by natural features of the landscape. Specifically, many small seepage lakes in the region are subject to winter hypoxia, whereas inflows can provide refuge (Rahel 1986); therefore, intolerant species may be more abundant

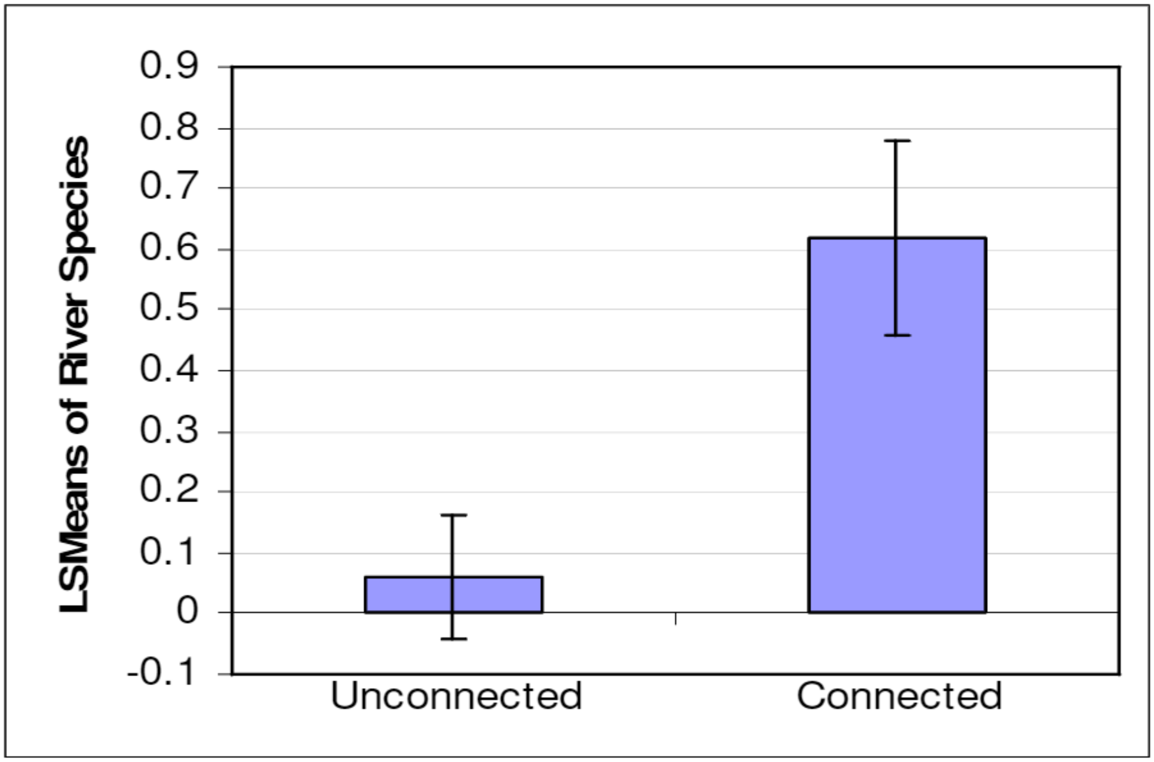

Figure 4. Results of least square mean comparisons of riverine species in connected vs. unconnected lakes. Results are non-transformed least square means of number of river species ± SE ($p<.05$).

in connected lakes. Connectivity also increases opportunity for colonization from other water bodies. The results indicated that intolerant species were more numerous in systems with connectivity and in larger lakes, but species richness of this group was unrelated to development (Table 4). This result does not help resolve whether colonization through the connection or refuge from hypoxia is the principal mechanism, but does suggest that at the level of human impact present in these lakes, human influence is not the primary driver of intolerant species richness. This contrasts with the situation in streams, where intolerant species are very sensitive to anthropogenic degradation and a critically important component of IBI (Karr et al. 1986).

Tolerant species would be expected to be resistant to extirpation from either natural events, such as low winter dissolved oxygen, or anthropogenic impact. In fact, they are ubiquitous in their distribution, and the model of tolerant species richness was not significant, explaining less than 10% of the variance.

Riverine species were associated with connectivity (Figure 4). This is not surprising, and suggests that the presence of these species is the result of colonization, or perhaps temporary movement from streams with connections to the study lakes. While not a surprising result, it does highlight the importance of scaling reference conditions for species richness to account for colonization processes.

Finally, gamefish species were positively related to development (Figure 3), suggesting a role of human-mediated introductions by management agencies and/or anglers. This phenomenon has been documented within Minnesota lakes (Radomski and Goeman 1995), as well as in a more broad analysis of lakes in the USA (Rahel 2000). While not unexpected, the result is highly relevant to implementation of biological monitoring based on fish. In most IBI's, the typical response of native species to degradation is a reduction in species richness (coldwater stream IBI provides a notable exception (Lyons et al. 1996)). However, the game fishes in this study are native, and undergo an increase in richness at low to moderate levels of human impact. We can hypothesize that at extreme levels of degradation, conditions would be unsuitable for some of these and other species, and a reduction in total species would be observed. This results in a distribution that is not monotonic; therefore sampling can produce results that are ambiguous if the goal to use fish species richness to indicate water resource condition.

Species-area relations (MacArthur and Wilson 1967) are often demonstrated in ecological studies (Matthews and Robison 1998, Pfister 1998, Kodric-Brown and Brown 1993). These relations were also evident within our data set but were not as important as colonization-extirpation variables when all were included in the model. The role of lake area may become more apparent in data sets that contain a larger range of lake areas than our data set, which contained a relatively homogeneous group of lakes. Tests for common slopes within the covariance analyses showed no interactions between lake area and other variables, suggesting that colonization effects were independent of lake area. Since larger lakes tend to have more species and the effect of lake area and colonization variables appear to operate independently, large lakes would be expected to have reduced extirpation rates, possibly related to increased within-species population size (Bolger et al. 1991, Pimm et al. 1988, Diamond 1975). Lake area can therefore be considered an extirpation variable, in contrast to connectivity, which is related to colonization rates. Development is also related to colonization, although it may hypothetically lead to extirpation of intolerant species. As discussed above, connectivity may mediate extirpation rates by reducing winter hypoxia but connectivity may also increase natural rates of colonization.

Previous work in northern Wisconsin lakes suggested that extirpation events dominate the dynamics of fish species assemblages (e.g., Magnuson et al. 1998). The lake set used in the Magnuson et al. study differed from ours in some important attributes, such as inclusion of lakes with low pH (acid bog lakes), and shallow depth. Extirpation is more frequent in these systems with severe winter conditions, low pH, and small area (Rahel 1984) all of which are natural features of the landscape.

Our results suggest that as human activity increases, an increase in the importance of colonization as the driving process would be expected. As species are periodically extirpated from a system, they, or a species like them can be reintroduced by humans at some probability higher than the natural colonization rate, leading to an increase in observed species richness. This general pattern is likely to hold over a wide range of conditions, up to a point where human impacts on water quality or habitat would lead to an increase in extirpation events. As a result of the relations between human activity and colonization or extirpation events, a moderate degree of degradation increases species richness but more severe degradation would be expected to reduce species richness.

The non-monotonic response of species richness to human activity complicates interpretation of simple measures of species richness as indicators of ecological integrity, and is a significant issue to consider in structuring a biological monitoring index. Systems that contain a larger pool of species also have greater potential for developing useful monitoring indices. For lakes similar to those evaluated in this study, water quality monitoring or biotic indices based on alternative taxa such as macrophytes (Hatzenbeler et al. 2004) are likely to provide more reliable and precise indicators of resource condition. However, fish-based indices may be more useful in larger systems (Drake and Pereira 2002) that contain a more diverse assemblage, and their use should not be ruled out based on results from small lakes.

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SYNTHESIS

Development of Assessment Metrics to Assess Lakes in the Upper Midwest.

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The desire to assess and monitor water resources has resulted in the development of numerous indices based upon biota present in the water body. Some of the most widely used indices were developed for biota in rivers and streams. Two examples that are widely used are the Index of Biotic Integrity (IBI) (Karr et al. 1986) and the Hilsenoff Biotic Index (HBI). The IBI is based upon fish species while the HBI relies on the macroinvertebrate community. Indices to assess lakes are less common but they do exist. Indices based upon the fish community have been developed in Minnesota (Drake and Pereira 2002; Drake and Valley 2005), and a preliminary assessment of potential fish metrics has been published for Wisconsin (Jennings et al. 1998) Indices based upon the composition of the macrophyte community have also been developed for Wisconsin lakes. Examples are the Floristic Quality Index (FQI) (Nichols 1999) and the Aquatic Macrophyte Community Index (AMCI) (Nichols et al. 2000).

Indices for the assessment of water quality have been in use longer than those for fish or macrophytes. One of the most widely used is Carlson's Trophic State Index (TSI) (Carlson 1977). This index was developed from the interrelationships of summer Secchi transparency, and epilimnetic concentrations of chlorophyll-a and total phosphorus. This index primarily relies on the amount of planktonic algae in the lake to assess the water quality. The TSI assesses eutrophication but not other stressors, e.g., acid precipitation.

The purpose of this study was to develop a family of indices that incorporate diverse parts of the lake ecosystem to assess the overall health of the lake. An assessment of lake health must include water quality as well as other aspects of ecosystem structure and function such as habitat condition, energy flow between trophic levels, and species interactions. While eutrophication can be determined using the TSI, indices based on the macrophyte community or the fish community or both are also necessary to assess these other aspects of the lake ecosystem. The macrophyte community provides both habitat and a pathway for energy and nutrient flow to higher trophic levels and has complex competitive species interactions, particularly involving exotic invasive species. The fish community comprises the highest trophic levels and is particularly sensitive to changes in energy and nutrient pathways, shifts in habitat, and alterations in species compostion.

An existing lake classification system for Wisconsin was used that grouped lakes based upon their hydrology, watershed area and depth. All lakes were separated based upon their maximum depth with the divide between deep and shallow lakes being about 18 feet. This separation roughly divides lakes that stratify from those that are polymictic. Seepage lakes were separated from drainage lakes and drainage lakes were further divided based upon the size of their watersheds. Drainage lakes with a watershed less than 4 square miles were considered headwater lakes and those with larger watersheds were lowland lakes. This classification system resulted in 6 lake classes:

1. Headwater, shallow drainage
2. Headwater, deep drainage
3. Lowland, shallow drainage

4. Lowland, deep drainage
5. Shallow seepage
6. Deep seepage

Historical reference conditions were determined for each lake class using the historical diatom community in cores extracted from 134 lakes. This analysis showed that without anthropogenic influences in the watershed, the number of classes could be reduced to 4. While the hydrology and maximum depth are important factors in determining the trophic status of the lake, the size of the watershed was not an important determinant.

An analysis of landuse in the riparian area around the lake as well as in the watershed indicated that the single anthropogenic activity most important in determining the phosphorus concentration in a lake was agriculture. The amount of agriculture in the riparian area was not as important as the amount in the watershed. The lack of influence of agriculture in the riparian area may have been due to the low number of lakes with significant agriculture in their riparian area. Most lakes in Wisconsin have little agricultural activity immediately adjacent to the lake shore because residential development of this area makes more economic sense. It is interesting to note that the amount of urbanization in the riparian area was not an important determinant of the lake's phosphorus concentration.

Morphometry and hydrology were also important factors in determining the phosphorus concentration of a lake. Seepage lakes tended to have lower background phosphorus levels and shallow lakes naturally had higher phosphorus levels.

These results support the division of lakes into 6 classes. Morphometry and hydrology are important determinants of a lake's trophic status, both historically and at the present time. With the significant anthropogenic impact during the last century the size of the watershed also became an important determinant. The size of the watershed is important because of varying landuses. When the landscape was natural the size of a lake's watershed was not very important.

Four metrics were used to describe the macrophyte community. These metrics were species richness, maximum depth of plant growth (MDPG), Floristic Quality Index (FQI), and Aquatic Macrophyte Condition Index (AMCI). All of these metrics show promise in assessing the health of a lake. The size of the littoral area has a significant impact on the species richness in a lake. As the lake size increases so does the number of species. In larger lakes the amount of disturbance in the riparian area also impacts species richness with the number of species declining with increased disturbance. Since species richness is an important part of FQI and AMCI these indices also increase with littoral surface area. However even when accounting for lake size the amount of disturbance in the watershed and riparian zone is important. As the amount of disturbance increases both FQI and AMCI decline. The percentage of urbanization in the riparian zone strongly influences the MDPG. As the percentage of urban development increases, the MDPG declines indicating the adverse impact of cottage development upon the lakes' water clarity and thus the depth maximum plant growth.

The macrophyte community may be useful for developing an index to assess the impact of riparian development. This study found that unlike water quality variables, the plant community reflects human disturbance in the watershed as well as the riparian area. It is especially sensitive to the percentage of urban development in the riparian zone. Other studies have shown that development significantly alters the riparian habitat. Examples of alteration are removal of course woody habitat (Christiansen et al., 1996) as well as alteration of nearshore habitat which affects amphibians and birds (Meyer et al. 1997; Woodford and Meyer 2003). Studies by Garrison and Wakeman (2000) and Borman (2007) show that shoreland development often alters the architecture of the macrophyte community resulting in larger species which fill more of the water column. This provides a different type of habitat for fish and other aquatic fauna.

Our study indicates that the effective use of the fish community for bioassessment may be limited to larger lakes. Species richness is highly dependent on lake size with larger lakes containing more taxa. The relatively low number of fish species in small lakes coupled with the relatively large number of human introductions of non-indigenous fishes (intentional stocking for fisheries and accidental escapes of bait minnows) even in remote and lightly developed waters makes it nearly impossible to define a "least-disturbed" fish community in smaller lakes, hindering index development. We conclude that it is not worthwhile to pursue developing a fish index for headwater drainage lakes and seepage lakes (classes 1, 2, 5, and 6), confirming the findings of Hatzenbeler et al (2004).

In the larger lakes there was a significant impact of riparian disturbance upon the fish community. After accounting for the influence of lake surface area, the number and abundance of intolerant species, which are usually habitat specialists, declined with increased disturbance, whereas the number of sunfish species, which tend to be relatively tolerant generalists, increased. This result has been found in a wider context in both Minnesota lakes (Radomski and Goeman 1995) and in a broader analysis of lakes across the USA (Rahel 2000).

Although this study was unable to fully develop bioassessment indices to evaluate lake ecosystem health using either macrophyte or fish communities, some macrophyte and fish metrics show promise. Both the plants and the fishes appear to experience a loss of sensitive specialist species and an increase in more tolerant generalist species as a result of riparian development. The macrophyte community also seems to be impacted by human disturbance in the watershed as are other lake health indicators such as water clarity.

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