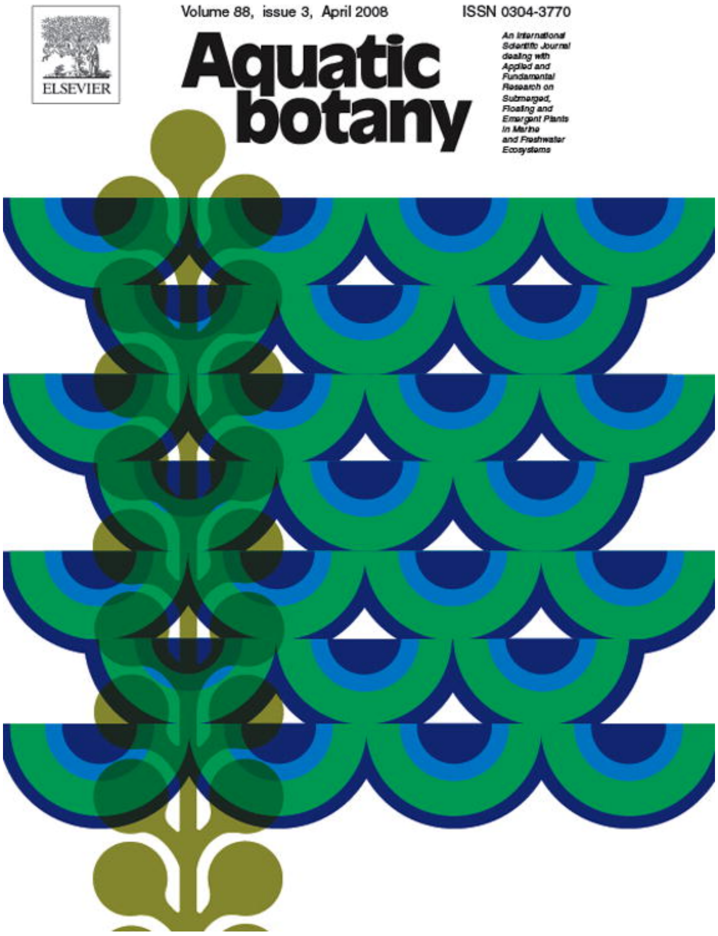
ELSEVIER
Volume 88, issue 3, April 2008
ISSN 0304-3770
Aquatic botany
An International Scientific Journal dealing with Applied and Fundamental Research on Submerged, Floating and Emergent Plants in Marine and Freshwater Ecosystems

Available online at www.sciencedirect.com

ScienceDirect

Aquatic Botany 88 (2008) 219–227

Aquatic botany

www.elsevier.com/locate/aquabot

Relationships between lake macrophyte cover and lake and landscape features

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Received 21 March 2007; received in revised form 10 August 2007; accepted 22 October 2007
Available online 26 October 2007

Abstract

We examined the ability of lake and landscape features to predict a variety of macrophyte cover metrics using 54 north temperate lakes. We quantified submersed cover, emergent cover, floating leaf cover, Eurasian watermilfoil cover and total macrophyte cover. Measured lake features included lake physio-chemical and morphometric variables and landscape features included hydrologic, catchment and land use/cover variables. Univariate regression analyses demonstrated that these macrophyte cover metrics are predicted by a wide range of predictor variables, most commonly by: Secchi disk depth, maximum or mean depth, catchment morphometry, road density and the proportion of urban or agricultural land use/cover in the riparian zone or catchment ($r^2 = 0.06–0.46$). Using a combination of lake and landscape features in multiple regressions, we were able to explain 29–55% of the variation in macrophyte cover metrics. Total macrophyte cover and submersed cover were related to Secchi disk depth and mean depth, whereas the remaining metrics were best predicted by including at least one land use/cover variable (road density, proportion local catchment agriculture land use/cover, proportion cumulative catchment urban land use/cover, or proportion riparian agriculture land use/cover). The two main conclusions from our research are: (1) that different macrophyte growth forms and species are predicted by a different suite of variables and thus should be examined separately, and (2) that anthropogenic landscape features may override patterns in natural landscape or local features and are important in predicting present-day macrophytes in lakes.

Keywords: Lake morphometry; Physio-chemistry; Land use/cover; Catchment; Hydrology; Eurasian watermilfoil

1. Introduction

Macrophytes affect the physical, chemical and biological character of lakes, and are affected by a suite of factors such as lake morphometry, water chemistry, and biotic interactions (Carpenter and Lodge, 1986; Lacoul and Freedman, 2006). Although previous studies have documented that many lake physio-chemical and morphometric features are related to macrophyte biomass and species composition (e.g., Barko and Smart, 1986; Duarte and Kalff, 1990; Hudon et al., 2000), fewer studies have examined how these features are related to overall lake macrophyte cover. Traditionally, macrophyte density or biomass are measured in experiments and single-lake studies by counting the number of stems within a relatively small quadrat or measuring biomass along relatively few transects to estimate the number of stems per m^2 or g m^2. However, these metrics are not always practical or useful for multiple, whole-lake studies, because macrophyte density and biomass vary greatly within a lake, requiring a prohibitively large number of quadrats or transects to effectively capture whole-lake density, biomass or macrophyte spatial patterns. Percent macrophyte cover is an alternative, whole-lake approach. It is often assessed by measuring macrophyte presence along transects or a grid of points covering an entire lake, and represents the percent of a lake's surface area that supports macrophytes (Madsen, 1999; Cheruvelil et al., 2005). Whole-lake percent cover is an important way to quantify macrophytes because this measure of lake-wide macrophyte abundance is important for understanding ecosystem-level processes such as nutrient cycling and foodweb dynamics (e.g., Declerck et al., 2005; Cheruvelil et al., 2005). However, relatively few studies relating

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doi:10.1016/j.aquabot.2007.10.005

macrophytes to lake features have done so using percent lake macrophyte cover (but see Mäkelä et al., 2004; Madsen et al., 2006).

In addition to quantifying macrophytes at the whole-lake scale, we can improve our understanding of how and what variables predict lake macrophytes by including lakes across large geographic regions and including natural and anthropogenic landscape features in our studies. For example, the maximum depth of macrophyte growth is negatively related to the latitude of lakes across a very large geographic region (Duarte and Kalff, 1987; Rooney and Kalff, 2000). Duarte and Kalff (1990) postulated that the regulation of macrophyte biomass is hierarchically nested and that each level of the hierarchy is comprised of different environmental factors that constrain the potential macrophyte biomass: latitude, water chemistry, littoral morphometry, depth and finally sediment heterogeneity. However, we hypothesize that there is an intermediate spatial scale that should be included in this hierarchical framework that includes many potentially important landscape features.

The current framework includes within-lake variables such as nutrients, chlorophyll *a* (hereafter chl *a*), and alkalinity that affect macrophytes (Chambers and Kalff, 1985; Canfield et al., 1985; Duarte and Kalff, 1990) and are known to be driven by regional and local landscape features (e.g. Gibson et al., 1994; Riera et al., 2000; Soranno et al., 1999; Hakanson, 2005). An expanded hierarchical framework would also include landscape features such as landscape position (a measure of the hydrologic position of a lake within the landscape; Kratz et al., 1997) and land use/cover that likely have unique effects on macrophytes that have not yet bet quantified. One recent study examining Eurasian watermilfoil (*Myriophyllum spicatum* L., hereafter milfoil) invasions using landscape-level variables found that the amount of forest land cover in the catchment is consistently negatively related to milfoil presence (Buchan and Padilla, 2000). These results suggest that further research is needed to examine the relationships between natural and anthropogenic landscape features and macrophyte cover.

We performed a field study of 54 north temperate lakes to answer the question: what lake and landscape features are related to whole-lake macrophyte cover? We hypothesized that macrophyte cover, similar to biomass, is hierarchically nested and that this hierarchy can be improved upon by including local and regional features such as: land use/cover and density of roads around lakes, catchment morphometry and lake hydrology. Some combination of these variables was expected to best predict macrophyte cover because these variables are important for various aspects of macrophyte growth. However, because many of the relationships between macrophytes and physical, chemical, and biological lake characteristics also depend upon macrophyte growth form (emergent, floating-leaf, submersed) (e.g., Barko et al., 1982; Duarte et al., 1986; Middelboe and Markager, 1997), we expected that the particular variables related to macrophyte cover would differ depending on macrophyte growth form or species.

2. Methods

2.1. Study lakes and macrophyte sampling

Study lakes were chosen from a subset of 350 public inland lakes > 20 ha in the lower peninsula of Michigan USA for which we had existing data from STORET (U.S. Environmental Protection Agency's data storage and retrieval system). These lakes all had a mean depth > 2 m (signifying that the lake would be stratified), and a lake surface area < 140 ha (the maximum size we could sample within a single day). We then randomly chose 54 lakes (Table 1) stratified by water clarity (Secchi disk depth, three categories), mean lake depth (three categories), and lake area (two categories). Thirty-six lakes were sampled in 2001 and 18 lakes were sampled in 2002.

We sampled macrophytes in all lakes from mid-July to early September when these lakes are thermally stratified and macrophytes are at or near maximum growth. Macrophytes were sampled using the point intercept method (Madsen, 1999). The sample sites were located 40 m apart (for lakes with surface area < 49 ha) or 50 m apart (for lakes with a surface area of >50 ha), resulting in 132–378 sample sites visited per lake. At each sample site, we recorded water depth and macrophyte presence either by visual inspection (shallow sites) or by two-sided rake (deep sites). Because relationships between macrophytes and physical, chemical, and biological lake characteristics may depend upon macrophyte growth form (e.g. emergent, floating-leaf, submersed) and morphology (e.g. basal, medial) (e.g. Barko et al., 1982; Duarte et al., 1986; Middelboe and Markager, 1997), macrophyte presence at each site was assigned to four growth form/species categories that were not mutually exclusive: emergent macrophytes, floating leaf macrophytes, all submersed macrophytes and the alien nuisance milfoil. From these data, five whole-lake macrophyte cover metrics were calculated for each lake as the total number of sites with macrophytes present in each macrophyte category divided by the total number of sites in each lake.

2.2. Physio-chemical measurements and lake morphometry

We sampled water chemistry and clarity from the deepest part of each study lake on the same date that we sampled macrophytes. Secchi disk depth was averaged across two measurements taken over the shady side of the boat. An integrated epilimnetic water sample was taken with a tube sampler for total phosphorus, chl *a* and total alkalinity. Total alkalinity ($CaCO_3$) was determined on-site with a titration test kit (LaMotte). For chl *a* analysis, water was filtered on site through a glass fiber filter (Whatman GF-C) and stored on ice in the dark until being returned to the lab and frozen. Chl *a* concentrations were determined fluorometrically with phaeopigment correction following 24-h extraction in ethanol Nusch (1980). Total phosphorus was determined using a persulfate digestion (Menzel and Corwin, 1965) followed by standard colorimetry (Murphy and Riley, 1962).

Lake sediment type was assessed at the time of macrophyte sampling by visual inspection of approximately eight sites

Table 1
County, latitude and longitude of the 54 study lakes located in Michigan, USA

Lake	County	Latitude (m)	Longitude (m)
Gilead	Branch	569419	138732
Cary	Branch	573975	150852
Hemlock	Cass	515856	168161
Donnel	Cass	508865	150779
George	Clare	585500	378491
Cranberry	Clare	600516	390381
Section One	Crawford	609061	479044
Pratt	Gladwin	616246	387098
Duck	Allegan	507854	208437
Woodard	Ionia	576192	281649
Stevenson	Isabella	594590	357322
Vandercook	Jackson	631746	183504
Round	Jackson	654442	170760
Round	Jackson	626232	172077
Swains	Jackson	611495	178968
Eagle	Kalamazoo	555867	197504
Sugarloaf	Kalamazoo	530475	179016
Deep	Lenawee	645906	166352
Hackert	Mason	473820	381325
Pretty	Mecosta	561469	349694
Bergess	Mecosta	547830	353334
Townline	Mecosta	544794	352332
Clear	Mecosta	548731	347695
Round	Mecosta	555614	341329
Mecosta	Mecosta	556632	340076
Nevins	Montcalm	569742	303678
Dickerson	Montcalm	567340	305193
Clifford	Montcalm	565516	306708
Winfield	Montcalm	550956	315000
Cowden	Montcalm	551935	311704
Little Whitefish	Montcalm	537456	311888
Horseshoe	Montcalm	565931	317662
East Twin	Muskegon	485886	313021
Englewright	Newaygo	533674	307872
Baptist	Newaygo	533781	309240
Robinson	Newaygo	511623	331189
Nichols	Newaygo	507443	352789
Bills	Newaygo	527299	315892
Clear	Ogemaw	636470	429640
Todd	Osceola	543591	377725
Sunrise	Osceola	553739	386790
Fish	Barry	541115	222546
Carter	Barry	556475	235758
Rush	Van Buren	482816	188013
Van Auken	Van Buren	484704	189274
Maple	Van Buren	508875	186236
Threemile	Van Buren	503784	182475
Eagle	Van Buren	501965	179932
Huzzy	Van Buren	514783	175904
Brandywine	Van Buren	511851	199838
Cedar	Van Buren	513869	170910
Lake of the Woods	Van Buren	500220	173460
Saddle	Van Buren	495773	203445
Fourteen	Van Buren	498472	203530

Coordinates are from the GCS North American 1983 coordinate system.

randomly selected per lake. Each site was assigned one of four categories: sand, silt/muck/peat, marl, or gravel/cobble/rocks. Based on these site assessments, each lake was then given one dominant sediment type (note that because only one lake sampled had silt/muck/peat sediments, this type was not included in analyses). All lakes were examined for the exotic zebra mussel and nine lakes were confirmed as supporting populations (Michigan Sea Grant, 2003).

Lake morphometry was quantified from bathymetric maps, the STORET database, and a GIS lake polygon coverage. Shoreline complexity (shoreline development factor) was calculated as the ratio of lake perimeter to the circumference of a circle of area equal to that of the lake (Wetzel, 2001). Lake mean depth, maximum depth and surface area were obtained from bathymetric maps. Mean depth was determined by placing a grid of ~100 points over lake bathymetric maps and taking the arithmetic average of all points within the lake basin (Omernik and Kinney, 1983). Fetch was measured by measuring the longest distance across each lake that is uninterrupted by land (Wetzel, 2001) in ArcView (ESRI version 3.2). Lake basin slope was calculated using the equation: (lake surface area)$^{1/2}$/lake mean depth (Nurnberg, 1995).

2.3. Catchment and land use/cover variables

Surficial geology data were from a statewide database at a scale of 1:500,000 (Farrand, 1982). We aggregated similar geologic types into the following three categories: (1) outwash (postglacial alluvium, glacial outwash sand and gravel and postglacial alluvium, ice-contact outwash sand and gravel), (2) glacial till (fine, medium and coarse-textured glacial till), and (3) moraine (end moraine of fine, medium, and coarse-textured till). We quantified the soils surrounding each lake as the average surface soil texture from the State Soil Geographic database (STATSGO) (NRCS National Cartography and GIS Center, Fort Worth, Texas). Similar soil types were aggregated into the following four categories: (1) sand (fine sand, sand), (2) sand/silt loam (silt loam, sandy loam), (3) loam, and (4) loamy sand. Each lake was assigned a dominant (>50%) surficial geology and soil texture type within the 500 m equidistant buffer around each lake shoreline.

Local catchments (LOC, immediate drainage area surrounding lake) and cumulative catchments (CUM, the local catchment in addition to all upstream drainage from connected lakes and streams) for each lake were delineated by digitizing topographic boundaries using Digital Raster Graphic topographic maps (USGS). We calculated three catchment morphometric metrics in addition to catchment area for both LOC and CUM: relief ((maximum elevation − minimum elevation)/(area)$^{1/2}$), shape ((0.28 × perimeter)/(area)$^{1/2}$) and slope (mean of slope values within catchment).

Digital land use/cover data for the state of Michigan were obtained from the Michigan Resource Information Service (MIRIS, 2000, resolution of 2.5 ha) using aerial photographs taken during 1978–1985 and classified using the Level I Anderson Classification scheme (Anderson et al., 1976). Land use/cover types included in analyses were: urban, agriculture, forest and wetland. For the four land use/cover types, the proportion of each type was calculated for each lake in the local catchment, the cumulative catchment and in the riparian zone (the 100 m equidistant buffer around each lake shoreline). Road density was calculated as the length of all roads (from minor roads to major highways) in the 500 m buffer area around each lake, divided by the buffer area. Data were from Street Map USA data collected in 2000 (ESRI).

2.4. Hydrology

We had several measures of hydrology to reflect the overall hydrologic characteristics of the lakes. Each lake was assigned a landscape position of six possible types based on surface water connections to streams and other lakes using the National Hydrography Dataset (http://nhd.usgs.gov/) and the NHD ArcView Toolkit as described in Martin and Soranno (2006). We calculated mean base flow index (as a percent of total stream flow) of streams in the 500 m buffer around lakes to get an index of groundwater flow (USGS). Precipitation data were obtained from the U.S. average annual data from 1971 to 2000 averaged over the 500 m buffer around each lake (The Spatial Climate Analysis Service, Oregon State University). We calculated mean runoff in the 500 m buffer around lakes using the average annual runoff in the United States estimated from 1951 to 1980 (USGS).

2.5. Statistical analyses

We used Systat 9.0 (SPSS, Inc.) and SAS 9.1 (SAS Institute Inc.) to perform the following analyses. Non-normally distributed variables were $\log_{10}$, natural log, or square root arcsine-transformed and we generated descriptive statistics to examine each predictor variable for outliers. We performed correlation matrices to test for collinearity and multicollinearity among predictors, a common situation in ecological studies (Graham, 2003). Finally, we performed one-way ANOVAs of each macrophyte metric by year of sampling (2001, 2002) to test for year differences.

We explored relationships between macrophyte metrics and continuous lake and landscape features using univariate regression, and for categorical predictor variables (lake sediments, zebra mussels, landscape position, soils, surficial geology) we used one-way ANOVAs (significance level = alpha < 0.10). Then, we examined whether multiple lake and landscape predictor variables were related to the five macrophyte metrics using multiple regressions (stepwise, backward and forward; continuous variables only) or ANOVA models that included continuous covariates (categorical and continuous variables). Predictor variables included in these models were those that were not highly correlated ($r < 0.4$). If two variables were correlated, we chose which to include in models based on a combination of ecological understanding of the relationships between the response and predictors and the statistical criterion of which variable explained the most variation in the response in univariate regressions.

3. Results

The 54 study lakes had wide ranges of lake and landscape features (Table 2). Macrophyte metrics also spanned a large range; most notably lake macrophyte cover ranged from 5% to 84% (Fig. 1). None of the five macrophyte metrics varied by year of sampling (2001, 2002; ANOVA $p > 0.05$). Some commonly observed emergent macrophyte species were *Typha latifolia* L., *Pontederia cordata* L., and *Scirpus subterminalis* Torr. Representative floating leaf species included *Nuphar advena* Ait., *Nymphaea odorata* Ait., and *Brasenia schreberi Gmel*. Examples of common submersed macrophytes included the macro-algae *Chara spp*., *Heteranthera dubia* (Jacq.) MacM., *Myriophyllum sibiricum* Komarov, *Najas flexilis* (Willd.) Rostk. and Schmidt and *guadalupensis* (Spreng.)

Table 2
Median, minimum and maximum for the continuous physio-chemical, morphometry, landscape and land use/cover predictor variables

Predictor	Units	Median	Minimum	Maximum
Physio-chemical				
Alkalinity	mg L^{-1} $CaCO_3$	164	44	280
Secchi disk depth	m	2.9	0.9	6.6
Total phosphorus[a]	µg L^{-1}	13.5	4.4	65.9
Chl *a*[a]	µg L^{-1}	2.7	0.1	20.7
Lake Morphometry				
Maximum depth[a]	m	13.1	2.7	27.4
Mean depth[a]	m	4.9	2.1	9.1
Surface area[a]	ha	50	20.9	117.3
Fetch[a]	m	1207	638	2178
Basin slope[a]	Unitless	153	57	444
Shoreline comp.[a]	Unitless	1.6	1.1	3.2
Catchment				
Elevation[a,b]	m	271	197	354
LOC area[b]	ha	408	59	23,309
LOC shape[b]	Unitless	1.58	1.22	2.15
LOC relief[a,b]	Unitless	0.014	0.004	0.014
LOC slope[a,b]	Unitless	1.8	0.6	4.5
CUM area[a,b]	ha	408	59	24,550
CUM shape[a,b]	Unitless	0.57	0.09	2.11
CUM relief[a,b]	Unitless	0.014	0.004	0.042
CUM slope[a,b]	Unitless	1.9	0.6	4.7
CUM CA:LK[a,b]		12	1	353
Hydrology				
Precipitation[a,b]	cm	88	78	100
Runoff[b]	cm $year^{-1}$	31	23	38
Baseflow[b]	%	72	61	88
Land use/cover				
RIP urban	%	51	0	84
LOC urban[c,b]	%	8	0	43
CUM urban[c,b]	%	8	0	55
RIP agriculture[c]	%	3	0	46
LOC agriculture[c,b]	%	33	0	74
CUM agriculture[b]	%	37	0	75
RIP forest[c]	%	24	1	82
LOC forest[c,b]	%	28	6	82
CUM forest[c,b]	%	32	3	87
RIP wetlands[c]	%	8	0	81
LOC wetlands[c,b]	%	5	0	15
CUM wetlands[b]	%	5	0	16
Road density[d,b]	m ha^{-1}	35	18	74

CA:LK is the ratio of catchment area to lake area. RIP = riparian, LOC = local catchment and CUM = cumulative catchment.
[a] Statistics performed on natural log (variable).
[b] Data not available for 5 of the 54 lakes.
[c] Statistics performed on square-root arcsine (variable).
[d] Statistics performed on $\log_{10}$(variable).

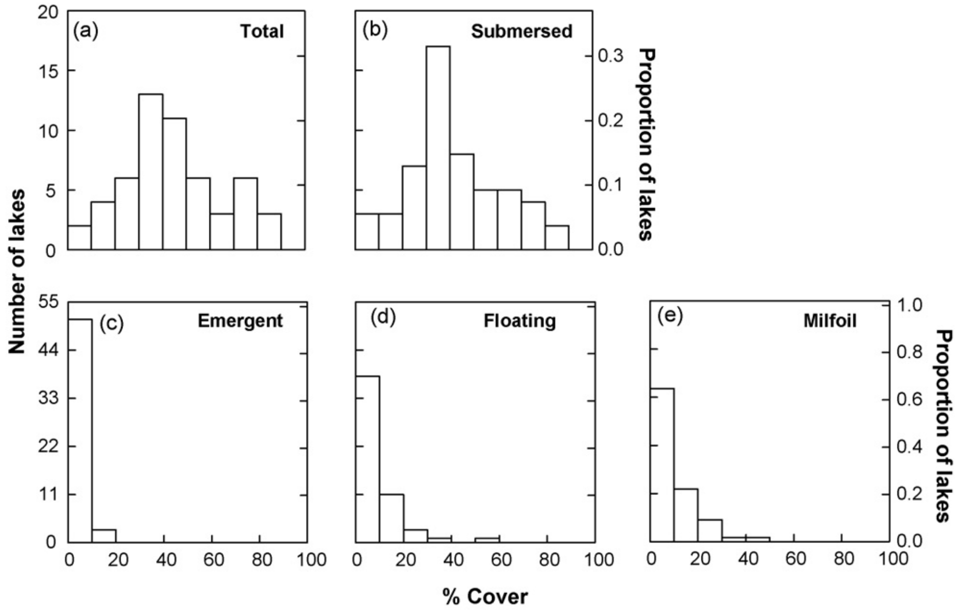

Fig. 1. Frequency distributions of lake (a) total macrophyte% cover, (b) submersed % cover (c) emergent % cover, (d) floating % cover and (e) lake milfoil % cover. Statistics were performed on these variables as described in Table 2.

Magnus, *Potamogeton spp*. (including *P. amplifolius* Tuckerm., *crispus* L., *foliosus* Raf., *gramineus* L., *illinoensis* Morong., *natans* L., *nodosus* Poir., *pectinatus* L., *praelongus Wulf*., *richardsonii* (A.Benn.) Rydb., *robbinsii* Oakes., and *zosteriformis* Fern.), *Utricularia vulgaris* L. and *Vallisneria Americana* Michx., as well as *M. spicatum* L.

Univariate analyses demonstrated that all five macrophyte metrics could be predicted by eight to ten lake or landscape features with varying success (r^2 range = 0.06–0.46; Table 3). The predictor variables that consistently were most important in predicting macrophytes ($r^2 \geq 0.15$) were: physio-chemical (chl *a* and lake sediments), lake morphometry (mean or maximum depth and lake basin slope), and land use/cover (road density, proportion riparian urban land use/cover, proportion riparian forest land cover and proportion local catchment agriculture land use/cover). All macrophyte metrics, with the exception of milfoil cover, had a moderate amount of variation explained by a single predictor variable (r^2 = 0.36–0.46).

Multivariate analyses demonstrated that multiple lake and landscape variables could explain on average approximately 46% of the variation in the five macrophyte metrics after removing predictor variables that were highly correlated ($r > 0.40$) (Table 4). Stepwise, backward, and forward multiple regressions provided the same results for each macrophyte metric. All metrics were statistically significantly predicted by two to three physio-chemical, lake morphometry or land use/cover predictors (r^2 range = 0.29–0.55; Table 4). Overall, two of the metrics were predicted best with just one physio-chemical (chl *a* or Secchi disk depth) and one morphometry variable (mean depth), whereas the remaining metrics were best predicted using at least one land use/cover variable (road density, proportion local catchment agriculture land use/cover, proportion cumulative catchment urban land use/cover, or proportion riparian agriculture land use/cover; Table 4). All macrophyte metrics, with the exception of milfoil cover, had a moderate amount of variation explained by multiple predictor variables ($r^2 \geq 0.44$).

4. Discussion

We found that all macrophyte cover metrics could be predicted by some combination of lake and landscape predictor variables, most often lake physio-chemistry, lake morphometry or land use/cover. Thus, our research supports the idea that there exists an intermediate spatial scale in the hierarchical framework predicting macrophytes cover: global landscape features, regional and local landscape features, and within-lake features. Our results for predicting total and submersed macrophyte cover corroborate other research documenting that water clarity, and thus the amount of light reaching macrophytes, and overall lake depth are important for predicting macrophyte cover (Hakanson and Boulion, 2002). However, our results for the other macrophyte metrics diverged from these expected patterns. The two main conclusions from our research are: (1) that different macrophyte growth forms and species are predicted by a different suite of variables and thus should be examined separately, and (2) that anthropogenic landscape features may override patterns in natural landscape or local features and are important for predicting present-day macrophytes in lakes.

Although there have not been many studies of land use/cover effects on lake macrophytes, one Minnesota study found a 20–28% decrease in emergent and floating-leaf cover along developed shorelines as compared to undeveloped shorelines (Radomski and Goeman, 2001). Our study corroborates these findings by quantifying the relationship between multiple anthropogenic landscape features and emergent and floating leaf macrophytes. Interestingly, we found that road density in

Table 3
Univariate regression and ANOVA results for each predictor variable versus each macrophyte metric

Predictor	Lake cover	Lake emergent cover	Lake floating cover[a]	Lake submersed cover[a]	Lake milfoil cover[a]
Physio-chemical					
Alkalinity	0.06−	0.07+			
Secchi disk depth	0.11+			0.12+	
Total phosphorus					0.08+
Chl *a*					**0.20+**
Lake sediments[b]					**0.17**
Zebra mussels[b]					
Lake Morphometry					
Maximum depth	**0.19**−		0.05−	0.14−	0.09−
Mean depth	**0.46−**		0.07−	**0.39−**	
Surface area			0.11−		
Fetch			0.06−		
Basin slope	**0.35+**			**0.31+**	
Shoreline complexity					
Catchment					
Elevation[c]					
LOC area[c]					0.06+
LOC shape[c]					0.08+
LOC relief[c]					
LOC slope[c]					
CUM area[c]					0.08+
CUM shape[c]	0.08+			0.06+	0.09−
CUM relief[c]					
CUM slope[c]					
CUM CA:LK[c]					0.08+
BUF surficial geology[b]					
BUF soils[b]					
Hydrology					
Precipitation[c]			0.06+		
Runoff[c]					
Baseflow[c]					
Landscape position[b]					
Land use/cover					
RIP urban		**0.18**−	**0.17−**		
LOC urban[c]		0.14−	0.09−		
CUM urban[c]		0.13−	0.10−		
RIP agriculture		0.07+			0.08−
LOC agriculture[c]		**0.17+**			
CUM agriculture[c]		0.14+			
RIP forest			**0.19+**		
LOC forest[c]					
CUM forest[c]					
RIP wetlands					
LOC wetlands[c]	0.08−			0.08−	
CUM wetlands[c]	0.12−			0.12−	
Road density[c]		**0.39−**	**0.36−**		

Numbers are r^2, and ± indicates the sign of the coefficient for the regressions. All values are significant at alpha < 0.10. Bolded values are those with $r^2 \geq 0.15$. Predictor variable transformations, abbreviations and units are the same as in Table 1, except BUF = the 500 m buffer around each lake.
[a] Statistics performed on square-root arcsine (variable).
[b] Indicates categorical variables.
[c] Data not available for 5 of the 54 lakes.

the 500 m surrounding a lake was the single best predictor of emergent and floating leaf macrophytes ($r^2 = 0.39$ and 0.36, respectively). The negative relationship between road density and these two types of macrophytes may be indicating that as people are afforded more access to lakes, or as overall development increases (road density as a surrogate for overall development of land), human removal of these very visible macrophytes increases.

In addition to road density, land use/cover was related to emergent and floating leaf macrophyte cover. We found a positive relationship between the proportion local catchment agricultural land use/cover and emergent macrophytes, which may come about as a result of two different mechanisms. First, it may be that people tend not to use lakes in an agricultural landscape, and thus emergent vegetation is not actively removed. A second mechanism is that agricultural land use

Table 4
Results of multiple regressions for each of the macrophyte metrics showing the significant (alpha < 0.05), but not highly correlated ($r < 0.4$), physio-chemical, morphometry, landscape and land use/cover predictor variables

Macrophyte metric	Predictors	n, d.f.	F	r^2	p
Lake cover	Secchi disk depth, mean depth	54, 51	31.2	0.55	<0.0001
Lake emergent cover	Road density, LOC agriculture	49, 46	30.6	0.44	<0.0001
Lake floating cover	Mean depth, road density, CUM urban	49, 45	16.8	0.52	<0.0001
Lake submersed cover	Secchi disk depth, mean depth	54, 51	24.4	0.49	<0.0001
Lake milfoil cover	chl a, RIP agriculture	54, 51	10.4	0.29	0.0002

Abbreviations and units are the same as in Table 1 and statistics were performed on transformed variables as in Tables 2 and 3.

leads to increased nonpoint source nutrient inputs to lakes directly to the littoral zone, thus increasing emergent vegetation in this zone. Because we only measured nutrients in pelagic water samples, we are not able to tease apart these two possible mechanisms with our data. Although road density and proportion local catchment agricultural land use/cover are correlated ($r = -0.34$, $p = 0.02$), these two variables likely can have unique direct and indirect effects on macrophytes. We also found a negative relationship between proportion cumulative catchment urban land use/cover and floating leaf macrophytes. Again, road density and proportion cumulative catchment urban land use/cover are moderately correlated ($r = -0.39$, $p = 0.005$), however, urban land use/cover will have additional direct and indirect effects on macrophytes beyond those associated with roads. We suspect that the relationships between anthropogenic landscape features and emergent and floating leaf macrophytes are due to either the direct human removal of these macrophytes or these growth forms being more sensitive to human degradation of lakes. We were not able to tease apart these potential mechanisms in this study, but the issue warrants further study.

Of the macrophyte metrics quantified, we were least able to explain variation in milfoil percent cover. A study of Wisconsin lakes found that milfoil presence (percent cover not measured) was more likely in lakes with higher alkalinity and either more agriculture in the catchment or a high number of residences around the lake, and less likely in forested catchments (Buchan and Padilla, 2000). In our study, milfoil cover was best predicted by chl a and proportion riparian agricultural land use/cover. However, contrary to the Wisconsin study, we found that milfoil was less likely in areas of high agriculture. This difference and our low ability to explain variation in milfoil cover may be due in part to the relatively narrow range of milfoil found in our study lakes (0–44% cover) and the preponderance of lakes with milfoil cover less than 10% (63% of lakes). Additionally, we were unable to include in our study some key predictor variables for understanding variation in lake milfoil cover. Such variables include measures of milfoil introduction (human activity levels on the lake and some measure of distance to nearest milfoil infestation), spread (fragmentation accounts for the majority of milfoil reproduction within and among lakes; Smith and Barko, 1990; Madsen and Smith, 1997), and management (mainly whole-lake chemical control). It is likely that these data would improve our ability to explain variation in milfoil cover among lakes.

Three variables that we had expected to predict macrophyte cover, and did not, were total alkalinity, fetch and lake sediments. We attribute the absence of a moderate to strong positive relationship between alkalinity and macrophyte cover to the relatively high alkalinity in our study lakes (median = 164, range = 44–280 mg L^{-1} $CaCO_3$). Previous studies documenting a relationship between alkalinity and macrophytes biomass had overall lower alkalinity, (e.g., median = 28, range = 7–78 mg L^{-1} $CaCO_3$ in Duarte and Kalff (1990) and median = 16, range = 1–52 mg L^{-1} $CaCO_3$ in Mäkelä et al. (2004)). Therefore, we may have failed to detect a threshold effect of low carbon levels in our relatively high alkalinity lakes. We also anticipated fetch, one way to estimate wave exposure, to play a more important role in predicting macrophyte cover. However, we did not take into account prevailing winds when calculating fetch for our study lakes, which may have reduced our ability to detect this effect. Additionally, fetch may not play a large role in predicting macrophyte cover in our study because we included only small lakes (range 20.9–117.3 ha as compared to 0.4–4270 ha in Mäkelä et al. (2004)). In small lakes, wind energy is less important for determining epilimnion depth than light transmission (Fee et al., 1996), and thus it is likely that wind exposure (the primary mechanism behind the importance of fetch for macrophyte growth) also does not vary significantly with fetch in such small lakes. Finally, we may have failed to detect an effect of sediment type because of the coarseness of our sediment data, or because there was little variation in sediment type across our lakes. In fact, 44 of the 54 lakes were predominantly sand or gravel/cobble/rocks.

Using a combination of lake and landscape features, we were able to explain 29–55% of the variation in macrophyte cover metrics. We were least able to predict milfoil cover, and best able to predict total macrophyte cover. This latter result is encouraging because we often attempt to manage whole-lake macrophyte cover, and thus a better understanding of how this whole-lake metric is related to natural and anthropogenic lake and landscape features can lead to more effective management and realistic expectations. Our research also lends credence to the idea that there exists an intermediate spatial scale in the hierarchical framework predicting macrophytes cover: global landscape features, regional and local landscape features, and within-lake features, but that we must take into account anthropogenic drivers that likely impact all spatial scales.

Acknowledgements

Financial Support was provided by EPA Star Fellowship number U-91595801-2 to K. Spence Cheruvelil and a Michigan State University Agricultural Experiment Station Disciplinary Grant to P.A. Soranno. We thank two anonymous reviewers and Dr. Bowes for their thoughtful reviews and Matt Baker, Mike Belligan, Jim Breck, Sherry Martin, Lidia Szabo Kraft, and Kevin Wehrly for their contributions to and creation of the landscape and lake GIS databases. Additionally, Laura Barrett, Stephen Bowman, Tyler Rosa, Remi Brim, Cassie Meier, Dave Meyers, and Sarah Wills helped with data entry and quality control of the databases. Catchment-level spatial data acquisition, lakeshed deliniation, and geospatial analysis were performed by Remote Sensing and GIS Research and Outreach Services, Michigan State University. We thank Dr. Gary Weissmann for help interpreting the geology data and Dr. Dan Hayes for statistical guidance. Finally, we thank Jubin Cheruvelil, Kevin Hoffman, Pete Hrodey, Aaron Jubar, Tamara Brunger Lipsey, Sherry Martin, Stacy Nelson, and John Whitlock for help with field sampling.

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