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Spatial and temporal variation in duckweed and filamentous algal levels in contiguous floodplain lakes of the Upper Mississippi River

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ABSTRACT

This study examined how free-floating macrophyte cover (principally composed of duckweeds [*Lemna* spp.]) and prevalence of floating filamentous algal mats (metaphyton) varied within and among lakes within three reaches of the Upper Mississippi River. Data were collected using standard sampling approaches over the period 1998 to 2008. Duckweed cover varied primarily within and among lakes; in comparison filamentous algae prevalence varied primarily among lakes and lake-years. Duckweed cover increased with submersed aquatic vegetation (SAV) abundance at within-lake and among-lake-year scales; in comparison, filamentous algae prevalence increased with SAV abundance at within-lake, among-lake and year scales. Given adjustment for SAV, filamentous algae prevalence decreased with increasing lake connectivity but was not statistically associated with annual changes in mean river discharge; duckweed cover was not associated with either connectivity or discharge. Documenting the relatively high levels of variation within lakes and of year-to-year variation in lake means improves our understanding of the dynamic nature of aquatic plant and algal communities in the Upper Mississippi River and will assist efforts to manage or control aquatic plants and nuisance algae in this region. In particular, this work explicitly characterizes sources of variability in free-floating macrophyte cover and filamentous algae prevalence, and highlights how this variation may complicate efforts to evaluate the short-term success of management and control efforts.

Key words: free-floating aquatic macrophytes, Lemnaceae, metaphyton, submersed aquatic vegetation, variance components

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INTRODUCTION

High levels of free-floating aquatic plants, including *Lemna* and *Azolla* species and filamentous algal mats, may have profound effects on aquatic ecosystems and may substantially influence food web structure, biogeochemical cycles, and the recreational use of freshwater systems (Janes et al. 1996, Scheffer et al. 2003, Pinto et al. 2007, Saunders 2009, Fontanarrosa et al. 2010).

Filamentous algae often form conspicuous mats attached to substrates or submersed aquatic vegetation (SAV) or float below or near the water surface. Algal mats that originate beneath the water surface, referred to as metaphyton (Howell et al. 1990, Wetzel 2001), may become suspended by wind-induced circulation (Wetzel 2001) or when trapped gases accumulate and float them to the surface (Saunders 2009). The establishment of metaphyton and its subsequent accumulation in littoral or pelagic regions is common in temperate eutrophic or acidic lakes (Howell et al. 1990, Makarewicz et al. 2007). Algal mats and free-floating macrophytes like duckweeds have been associated with thermal characteristics of water bodies, decreased SAV growth, and decreased dissolved oxygen concentrations (Dale and Gillespie 1977, Phillips et al. 1978, Jones et al. 2002, Morris et al. 2003, Parr and Mason 2004, Hilton et al. 2006).

The ability of free-floating plants and algae to absorb insolation and reduce incident light likely causes the most dramatic impact on other portions of the aquatic plant community (Giorgi et al. 2005). Specifically, low light availability may decrease SAV growth and photosynthetic rates, biomass, richness, and alter community composition (Phillips et al. 1978, Jones et al. 2002). Decreased SAV photosynthesis may, therefore, lead to changes in dissolved oxygen and pH. Because photosynthetically active SAV may substantially increase water pH (Spencer et al. 1994), reductions in photosynthetic activity may influence aquatic chemistry and the activity of epiphytic microorganisms (Eriksson and Weisner 1999). Finally, decreases in dissolved oxygen associated with

the decline of SAV can be detrimental to other aquatic life (Rooney and Kalff 2000, Morris et al. 2003) and may facilitate sediment phosphorus release (e.g., James et. al. 1995), promoting further epiphytic and metaphyton growth.

Despite their competitive interactions with and potential negative effects on SAV, the presence of filamentous algal mats in aquatic ecosystems is often dependent on SAV surfaces for establishment. Filamentous algae and SAV vary in composition and abundance in both space and time (Rooney and Kalff 2000, Ray et al. 2001), and these changes can be accelerated by cultural eutrophication (Cristofor et al. 2003, Rasmussen and Anderson 2005).

A natural choice for studying scales of variation of filamentous algae and duckweed at small to medium spatial scales is that of contiguous floodplain lakes (hereafter backwater lakes or lakes). Backwater lakes of large floodplain rivers often differ substantially in limnological properties, including in depth, water clarity, trophic status, and vegetation biomass. For example, comparative studies of backwater lakes have shown that these properties may be influenced by connectivity with channels and local morphometry (Heiler et al. 1995, Knowlton and Jones 1997, Van Geest et al. 2003). Roozen et al. (2003) studied associations between the dependent variables vertical light attenuation, inorganic suspended solids and chlorophyll *a* and the potential predictors of SAV cover, presence or absence of floating vegetation, and lake depth using data from 93 lakes from the lower Rhine River.

This study evaluated variation in duckweed cover (family Lemnaceae) and filamentous algae occurrence at multiple spatiotemporal scales in backwater lakes in three reaches of the Upper Mississippi River (UMR). We estimated variation for both taxa groups within lakes, among lakes and among lake-years. Associations between filamentous algae and SAV at multiple scales were also investigated.

The scale-related focus of this study has implications for aquatic plant management. Artificial manipulation of filamentous algae (metaphyton) or free-floating macrophyte levels is logistically most efficient when applied at moderately large spatial scales (e.g., addressing loading and considering management considerations at the spatial scale of backwater individual lakes; Zohary et al. 1998, Makarewicz et al. 2007). However, selecting lakes with, for example, high and persistent metaphyton or free-floating macrophyte levels using data may be challenging when metaphyton or macrophyte levels vary substantially either within lakes or across years (for a given lake) or both. Further, evaluation of the success of any such intervention will need to acknowledge and address both sources of variation.

MATERIALS AND METHODS

Study regions. Vegetation data were collected by the Long Term Resource Monitoring Program (LTRMP; Johnson and Hagerty 2008) from backwater lakes in three reaches of the UMR. Backwater lakes were defined based on enduring geomorphic and physical features (Wilcox 1993) and quantified from 1989 aerial photography using a geographic information system (GIS). Lakes not connected to channels during typical summer water surface elevation were not sampled. The reaches represent Navigation Pool 4 below Lake Pepin, Minnesota (river mile 753 to 765); Navigation Pool 8 located

near La Crosse, Wisconsin (river mile 679 to 702.5); and Navigation Pool 13 located near Bellevue, Iowa (river mile 522.5 to 557; Figure 1). Lower Navigation Pool 4 and Navigation Pools 8 and 13 are hereafter denoted reaches 1, 2, and 3, respectively.

For this study, individual backwater lakes represent subregions within each backwater region of the three reaches, with lakes defined as units separated by channels and terrestrial areas (Figure 2) and delineated using Arc/Info Grid command "regiongroup" (ESRI 1991). Backwater lakes defined using this method may include very small bodies of water (e.g., 0.01 ha) that are well connected to channels. While such water bodies may be better described as bays or even channel edges, we use "lake" throughout to describe the full range of backwater units.

Sampling design. The sampling frame for each reach was defined by laying a square north-south and east-west grid over a reach-specific GIS coverage of backwater lakes; the grids had spacing of 50 m on each side. Each grid intersection represented a member of the population of possible sampling sites from which actual sampling sites were selected at random. The probability of sampling a given backwater was proportional to the area of the backwater. Sampling began in 1998 and continued through 2008. With the exception of years 2001 to 2004 in reach 2 (when sites were revisited), sampling sites were reselected each year. Sampling events were completed within 20 to 59 days, beginning as early as 15 June and ending as late as 31 July. Sampling plots were defined as a 2 m ring around the boat used for sampling (Figure 3); such plots represent the rectangular analogue of the square doughnut plot defined by Thompson (2002, p. 280).

Duckweed. Duckweed levels represented the estimated proportion of the above-mentioned 2 m ring that was covered by duckweed species. Cover assignments were categorical, with scores 0 through 5 denoting covers of 0%, 1 to 20%, 21 to 40%, 41 to 60%, 61 to 80%, and 81 to 100%, respectively. Duckweed is used here to generally describe the free-floating macrophyte community and included common duckweed (*Lemna minor*), star duckweed (*L. trisulca*), common duckmeat (*Spirodela polyrhiza*), and Columbian watermeal (*Wolffia columbiana*). Rare occurrences of Carolina mosquitofern (*Azolla caroliniana*) and slender liverwort (*Riccia fluitans*) were also included in this description of the free-floating assemblage of macrophytes we refer to as "duckweed." Taxonomic nomenclature used here follows that in the PLANTS database (USDA-NRCS 2011). Further vegetation sampling details are provided by Yin et al. (2000).

Filamentous algae. Filamentous algae were recorded using visual and rake methods at six approximately equidistant locations (subsites) located within the sample plot (Figure 3). The visual method was implemented prior to the use of the rake method and consisted of visual inspection from the boat of the intended rake location. Visual inspections were scored as either "present" or "not detected" (failure to detect algae may result from absence of algae or from a false negative). Rake surveys consisted of sweeping the substrate within an area of approximately 1.5 m by 0.36 m using a modified garden rake (Yin et al. 2000). The tines of the rake were marked to create five categories, with successive categories denoting increased proportions of rake teeth filled by biomass. These
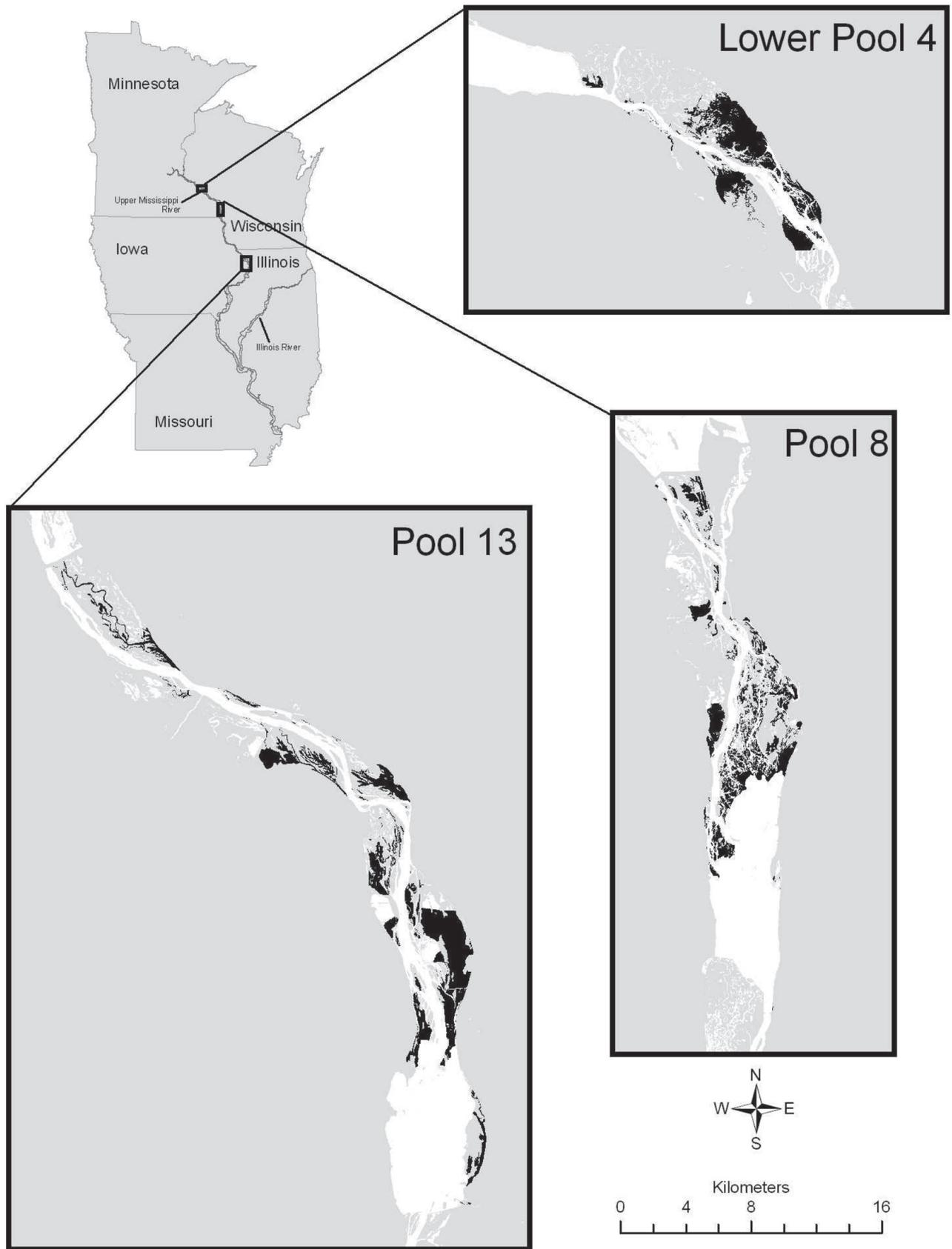
Figure 1. Location of study reaches for duckweed and filamentous algal levels in backwater lakes of the Upper Mississippi River, USA. Backwater lakes are depicted in black.

Figure 2. Illustration of typical backwater lakes (black) with respect to channels (gray) in the Upper Mississippi River floodplain.

proportions, along with their corresponding categorical scores, correspond to those listed above for duckweed cover (i.e., the "0" category corresponds to no algae observed on the rake). We analyzed filamentous algae as an indicator variable, with the indicator denoting present when algae was ob-
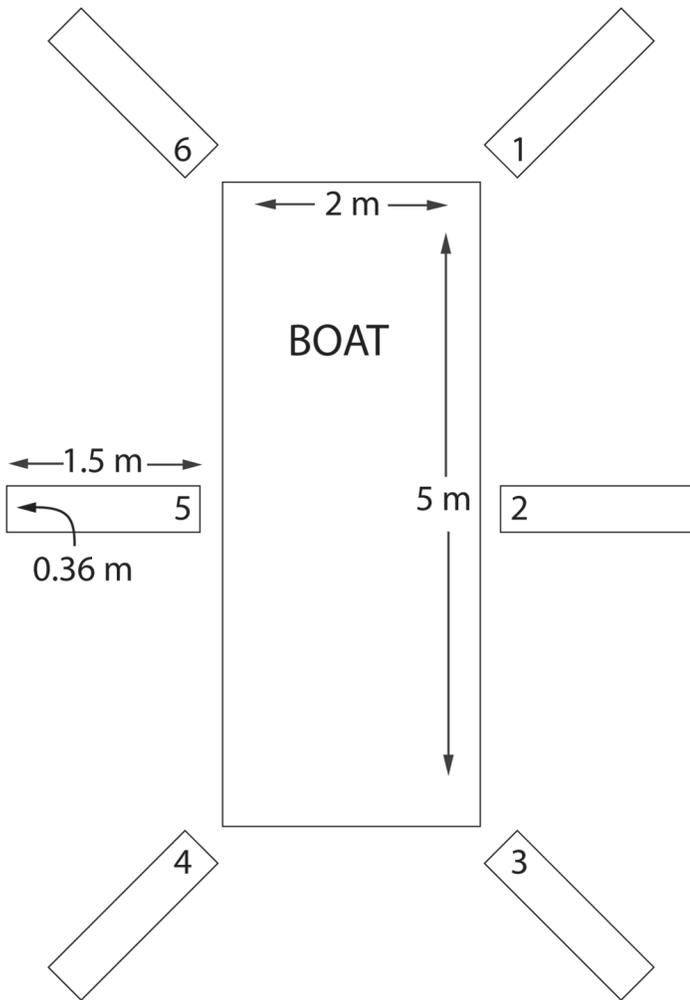

Figure 3. Diagram of sampling plot used by the Long Term Resource Monitoring Program for vegetation measurement. Six surveys were taken at roughly equal distances within a rectangular "doughnut," with "doughnut hole" defined by the boat.

served visually or by raking or as not detected, because only 0.3% of rake scores exceeded 1, and because visual scores were confined to present and not detected only. Filamentous algae were not identified at the species level during our surveys, but work in 2009 and 2010 from study reaches revealed filamentous algae assemblages composed of species from *Cladophora, Spirogyra, Oedogonium, Mougeotia, Lyngbya, Hydrodictyon, and Microspora* genera; *Cladophora* species were most common in both years (S. Giblin, Wisconsin Department of Natural Resources, 29 June 2010, pers. comm.). We use filamentous algae synonymously with metaphyton because some filamentous algal mats originate below the water surface on benthic or SAV substrates (Saunders 2009).

Submersed aquatic vegetation (SAV). SAV was surveyed using the same rake method and ordered rake scores as those described for algae. We estimated SAV species richness at each site from the SAV rake survey and visual measurements at each subsite.

While SAV should be presumed to be sampled by the rake method with classification errors, the effects of those errors on inferences from SAV rake data are not wholly clear. While vegetation rake score data have been treated using means of scores (e.g., Kenow et al. 2007), ordinal data in general are often presumed to best be modeled under ordinal multinomial assumptions (Fielding et al. 2003). Despite this, methods for elaborating multinomial models to accommodate classification errors (Royle and Link 2005, Holland and Gray 2010, Holland et al. 2010) make assumptions that the current study's data may not fulfill. These assumptions are that individual surveys represent replicates on site, that the highest rake score is observed without error, and that published methods for singly nested data may be extended for use with data from cross-classification (e.g., lake-year) designs. Hence, where a single rake value was required at a scale larger than that at which SAV was measured, we followed conventional methods by using mean rake scores.

Lake connectivity and discharge. Lake connectivity was defined as the percentage of each lake's perimeter (including channel connections) that was channel. This surface connectivity measure does not address actual discharges of water into and out of a lake but is expected to explain a substantial fraction of the variability in water exchange rates among lakes. Large values of this metric denote highly connected lakes.

Discharge represents the mean Mississippi River discharge prior to each annual sampling period at the gauging station closest to each study reach. For reaches 1, 2, and 3, these were Prescott, Wisconsin (US Geological Survey [USGS] 05344500); Winona, Minnesota (USGS 05378500); and Clinton, Iowa (USGS 05420500), respectively.

Statistical analyses. Binary algal data were modeled using logistic regression while the ordered duckweed cover and SAV rake data were modeled using cumulative logistic regression (Hosmer and Lemeshow 2000). For variance components and covariate analyses (but not for descriptive statistics), the 7% of SAV rake scores ≥2 were treated as 2s. SAV richness was modeled as a Poisson-distributed random variable with log link. Covariate associations with metaphyton were assessed using data from reach 2, with the forms of those associations (such as linear and quadratic) inferred from reach 1 data. Due to small sample sizes, the covariate associa-

tions at the lake and lake-year scales estimated for duckweed cover and possibly for filamentous algae may be too small in magnitude (Grilli and Rampichini 2011). Models were fitted using maximum likelihood (Vonesh 1996, Givens and Hoeting 2005), with random site, lake, year, and lake-year effects treated as normally distributed on the log (richness) or logit (else) scales. Lake-year variance estimates for duckweed cover incorporated not only lake-year variation but also site-year variation because sites were not typically revisited, duckweed cover was measured at the site but not subsite scale, and sampling variation of duckweed cover was assumed constrained to that of a standard logistic random variable. Estimates of "among-site variation" represented not only spatial variation among sites but also variation at spatial scales that were intermediate between site and lake scales. For brevity, however, we treated among-site variation and within-lake variation as synonymous. Variance components from logistic regression models were estimated under a latent logistic assumption (Snijder and Bosker 1999), while variance components for SAV species richness were estimated on the log scale. Spatial correlation within sites, lakes, and lake-years was broadly addressed by treating each as random. Dataset limitations precluded more extensive treatment of spatial correlation. Models were fitted using SAS' generalized linear mixed modeling procedure (GLIMMIX procedure; SAS 2009).

The nature of dependency is not always clear when estimating associations between metaphyton and SAV. As our models imply, filamentous algae and duckweed are dependent on SAV to provide substrate and protection from wind and current, respectively. However, the opposite may also be true; filamentous algae and duckweed compete with SAV for light and, for some SAV species, with nutrients, and such competition will increase with cover and density of filamentous algae and duckweed. For the study sampling periods of our study data, however, levels of filamentous algae and duckweed typically reached their maxima subsequent to LTRMP vegetation sampling. Hence, we treated SAV as a predictor of filamentous algae presence and duckweed cover.

RESULTS AND DISCUSSION

Descriptive statistics. Study data contained relatively large numbers of lakes and lake-year combinations, and for reaches 1 and 3, mean numbers of sites sampled per lake (Table 1). However, median numbers of sites per lake and mean and median numbers of sites per lake-year were low (<8) in all reaches. Fewer sampling sites per lake in reach 2 reflect, in part, smaller lakes in that reach. Correlations between number of sites per lake and lake area were high for all reaches (r = 0.96, 0.81, and 0.93; n = 39, 150, and 46; and p < 0.0001 for reaches 1, 2 and 3, respectively).

Mean duckweed cover, filamentous algae, SAV rake cover score, and SAV species richness values were typically low (Table 2). For example, mean and median duckweed cover proportions fell in the 1 to 20% category and the 0% category, respectively.

As may be expected from the subsite statistics (Table 2), the proportion of sites without algal detections was high. When filamentous algae was detected at a site, however, it was more

TABLE 1. SAMPLE SIZES BY SPATIAL UNIT AND STUDY REACH FOR A STUDY OF DUCKWEED AND FILAMENTOUS ALGAL LEVELS IN BACKWATER LAKES OF THE UPPER MISSISSIPPI RIVER.

Number of	Reach 1	Reach 2	Reach 3
Lakes sampled	39	150	46
Lakes sampled per year (range)	13-23	44-62	18-30
Unique lake × year combinations	182	567	249
Sites per lake (all years; mean/median)	37.1/4	10.3/3	37.4/5.5
Sites per lake per year (mean/median)	7.9/2	2.7/1	6.9/3
Total sites	1446	1544	1722
Area (mean [SE[a]]/median) (ha)	46 [24]/4.8	12 [3]/2.6	60 [22]/8.2

[a]Standard error.

frequently detected at all rather than only some subsites (Table 3), suggesting clustering of filamentous algae within sites. An example of clustering is when the probability of algal presence at a site is low, but if present has a higher than expected probability of being present at most or all locations within that site. This topic may be addressed by comparing observed probabilities of algal detection at sites with those calculated from subsite probability estimates. The site-level estimates were 0.24, 0.32, and 0.28 for reaches 1, 2, and 3, respectively; however, the corresponding estimates from the subsite estimates (Table 2) are much larger: 0.60, 0.74, and 0.67, respectively (obtained under assumptions of independence and identical distribution by $1 - (1 - \hat{p})^6$, where $\hat{p}$ denotes the subsite scale probability estimate from Table 2 and "6" the number of subplots per site). The differences among these sets of values seems to be explained by mismatches between observed and expected relative count frequencies. Given the relatively small subsite-level probability estimates and properties of the binomial distribution, we would expect roughly equal proportions (~35%) of 0s and 1s, roughly 20% 2s, fewer than 2% 4s, and <0.2% of counts of 5 or 6. However, the proportions of sites where algae was detected 1, 2, or 3 times were considerably lower than these expected proportions while the proportions of sites where algae was detected more than 3 times was considerably higher than expected (Table 3). These findings may reflect a conditional process. Filamentous algae is rarely found at sites but, when present it is often found at a majority of locations within that site. We did not model this conditional process and suspect that not doing so accounted for our failure to successfully model unexplained variation in algae at the site scale (see next section).

Mean lake connectivity was highest in reach 2 whereas discharge increased downriver and, hence, with reach number (Table 2). The finding of higher connectivity in reach 2 is related to the finding that lakes in that reach are typically smaller (Table 1) and that many of these small lakes are channel border-like or bay-like.

Variance component estimates. Duckweed cover varied most among sites in reaches 1 and 2 and among lakes and sites in reach 3 (Table 4). Contributions of year, lake-year, and lake (reaches 1 and 2 only) effects to variation in duckweed cover levels were modest. From an across-reach perspective, duckweed cover varied most among lakes in reach 3, while lake levels of duckweed cover were most stable among years in reach 1.

TABLE 2. DESCRIPTIVE STATISTICS FOR VEGETATION VARIABLES AND THEIR POTENTIAL COVARIATES BY REACH FROM A STUDY OF DUCKWEED AND FILAMENTOUS ALGAL LEVELS IN BACKWATER LAKES OF THE UPPER MISSISSIPPI RIVER.[a]

Variable	Unit	Scale of variation	Reach 1		Reach 2		Reach 3	
			Mean (SE[b])	Median	Mean (SE)	Median	Mean (SE)	Median
Duckweed	Mean percent cover[c]	Site	13 (0.7)	0	15 (0.7)	0	6 (0.4)	0
Filamentous algae	Mean probability of detection	Subsite	0.14 (0.004)	0	0.20 (0.004)	0	0.17 (0.004)	0
Submersed aquatic vegetation (SAV)	Mean percent rake teeth filled[c]	Subsite	10 (0.2)	10	13 (0.2)	10	10 (0.2)	0
		Site	10 (14[d])	8	13 (16[c])	10	10 (15[c])	5
		Lake	13 (15[d])	9	9 (8[c])	8	5 (8[c])	2
		Year	11 (7[d])	9	14 (4[c])	13	10 (3[c])	10
		Lake-year	11 (13[d])	8	11 (11[c])	8	7 (12[c])	2
SAV species richness	Number species detected	Subsite	1.55 (0.02)	1	1.74 (0.02)	1	1.08 (0.01)	0
Connectivity	% channel	Lake	17.6 (3.1)	6.8	29.7 (2.1)	25.0	14.4 (2.8)	5.0
Discharge	1000 cfs	Year	21.1 (3.2)	18.4	35.4 (6.3)	29.4	54.2 (6.9)	48.4

[a]Not adjusted for group effects. [b]Standard error. [c]Means of midpoints of cover classes or rake score classes. [d]Standard deviation.

Filamentous algae varied most among lake-years, subsites, and possibly sites in reaches 1 and 2 and most among lakes and subsites in reach 3. Failure to adequately model variation among sites for filamentous algae (Table 4, footnote "d") ensured that a fraction of the estimates of among lake-year variation for filamentous algae arose from the site scale. As with duckweed cover, contributions from year effects to variation in algae detection were modest for all reaches.

Patterns in relative variance components of SAV rake scores were qualitatively similar to those seen for duckweed cover: highest at the site scale in reaches 1 and 2 and highest at the lake scale in reach 3 (Table 4). Patterns for SAV species richness were broadly similar to those seen with SAV rake scores.

Covariate associations (reach 2). Duckweed cover was positively associated with SAV levels and, specifically, with mean SAV rake score at the site and lake-year scales, based on comparison of -2 log likelihood and Akaike Information Criterion (AIC) values (Table 5) and inspection of point estimates with confidence intervals (Table 6). For example, the odds of a higher observed duckweed cover class at a typical site increased by approximately 300% for each 1-unit increase in mean SAV rake score. This value may be derived by subtracting 1 from the odds ratio point estimate of 4.18 and multiplying by 100% [i.e., $100 \times (4.18 - 1)$]. The corresponding estimate for a unit increase in mean lake-year rake score was 73%. In contrast, duckweed cover was not clearly associated with connectivity or discharge (Table 4 and 5).

The odds of detecting filamentous algae at the subsite scale increased when SAV was present at that same scale (Table 6). Specifically, the odds of detecting filamentous algae at the subsite scale given failure to detect SAV at that scale (i.e., of rake score = 0) was 73% lower than the corresponding odds given SAV rake score = 2 [i.e., $100 \times (0.27 - 1)$]. The odds of detecting algae appeared similar at rake score = 1 and at rake score ≥ 2.

The odds of detecting filamentous algae also increased substantially as mean SAV rake score increased at site, lake and year scales. Confidence intervals for the algae-SAV site-scale association were probably too narrow, owing to our failure to adequately model variation in algae at that scale (Table 4). The odds of algal presence decreased with lake connectivity but were not clearly associated with discharge (Table 5 and 6). SAV rake score was not clearly associated with either lake connectivity or discharge.

Duckweed cover considerations. The relatively high levels of unexplained variation in duckweed cover among sites in reaches 1, 2, and, to lesser extent, reach 3 suggest efforts to identify sources of that variation (Table 4). Given important associations between duckweed cover and SAV (Table 5 and 6), factors contributing to the abundance of SAV (e.g., sediment organic matter content; Makkay et al. 2008) may represent useful predictors of duckweed cover. Other factors associated with variation in duckweed cover include water velocity, local wind patterns, and recreational water use (Portielje and Roijackers 1995, Mumma et al. 1996, Rooney and Kalff 2000, Makarewicz et al. 2007, Makkay et al. 2008).

Efforts designed to manage nuisance levels of duckweed must consider the range and scale of factors that contribute to the distribution and abundance of plants within lakes.

	Proportion of sites with given number of detections per subsite (maximum = 6)						
Reach	0	1	2	3	4	5	6
1	0.761	0.057	0.036	0.025	0.021	0.018	0.082
2	0.676	0.076	0.042	0.034	0.029	0.037	0.105
3	0.725	0.060	0.038	0.034	0.023	0.036	0.084

While our results do not preclude the possibility of successful whole-lake interventions to control duckweed cover in reaches 1 and 2 in lakes with high cover levels, our results do suggest that efforts to document that success in typical lakes may be hampered by relatively high levels of within-lake variability and, for reach 2, of among-year variability (Table 4). The relatively high among-lake variance estimate for duckweed cover in reach 3 suggests that efforts to document the effects of duckweed management in typical lakes in that reach will, on average, be more successful than will similar efforts in reaches 1 and 2.

Duckweed cover in reach 2 was associated with mean SAV rake score not only at the site scale but also at the lake-year scale (Table 6). The latter association, given failure to observe a duckweed cover-SAV association at the lake scale, may have arisen from annual fluctuations in the lake-specific importance of SAV levels (which might occur, for example, if the prevalence of strong winds varied among study years and fetch varied among lakes) or by annual fluctuations in lake-specific nutrient and other limnological characteristics that might affect both duckweed cover and SAV. Another plausible explanation is related to the sampling design; sites were revisited in only a minority of years (2000-2003) and in only reach 2. Consequently, the observation of lake-year effects will reflect to at least some degree the selection of different sites within lakes in different years.

A final comment about duckweed addresses commonality among patterns of variation. Correlation between variance components for duckweed and SAV rake scores among reaches, as seen with duckweed cover and SAV rake scores, for example, does not necessarily imply correlation at smaller scales (Table 4). If duckweed coverage, for example, increased with SAV levels at the within-lake scale but SAV levels varied more among than within lakes (perhaps because nutrient levels were broadly constant within lakes), then duckweed levels will be observed to vary primarily among lakes, even if dependence primarily occurred at the within-lake scale (Table 4 and 6).

Filamentous algae considerations. Filamentous algae was seen to vary most at the lake-year scale in reaches 1 and 2 and at the lake scale in reach 3 (Table 4). As with duckweed cover, variation among lake-year means probably reflected some contribution of site selection. The patterns in variance components in algae did not mirror those seen with duckweed, possibly because filamentous algae mats may have been adhered to SAV and were submersed during sampling and/or there were low levels of internal gases inside the mats (Saunders 2009).

TABLE 4. VARIANCE COMPONENT PERCENTAGES FROM INTERCEPT-ONLY MODELS OF VEGETATION VARIABLES AS MEASURED IN BACKWATER LAKES OF THE UPPER MISSISSIPPI RIVER.

	Variance percentages by scale [point estimate (standard error[a])]				
Reach	Subsite	Site	Lake	Year	Lake-year
			Duckweek cover		
Reach 1	na[b]	59% [3.29[c]]	25% [1.37 (0.66)]	15% [0.82 (0.40)]	1% [0.06 (0.06)]
Reach 2	na[b]	53% [3.29]	13% [0.77 (0.22)]	21% [1.31 (0.60)]	13% [0.79 (0.20)]
Reach 3	na[b]	32% [3.29]	42% [4.27 (1.70)]	14% [1.40 (0.71)]	12% [1.20 (0.36)]
			Filamentous algae		
Reach 1	32% [3.29]	na[d]	17% [1.74 (1.14)]	9% [0.97 (0.61)]	41% [4.25 (1.11)]
Reach 2	24% [3.29]	na[d]	20% [2.70 (0.88)]	14% [1.94 (0.90)]	42% [5.83 (0.82)]
Reach 3	25% [3.29]	na[d]	47% [6.29 (2.77)]	7% [0.87 (0.50)]	21% [2.86 (0.71)]
			SAV rake score		
Reach 1	9% [3.29]	50% [18.37 (1.27)]	28% [10.38 (4.24)]	10% [3.65 (1.83)]	4% [1.37 (0.66)]
Reach 2	16% [3.29]	53% [10.71 (0.65)]	20% [4.10 (0.94)]	7% [1.33 (0.62)]	4% [0.79 (0.32)]
Reach 3	8% [3.29]	25% [10.72 (0.67)]	54% [23.06 (7.60)]	na[d]	13% [5.62 (1.15)]
			SAV species richness[e]		
Reach 1	[0.24]	[1.63 (0.10)]	[0.99 (0.40)]	[0.13 (0.09)]	[0.26 (0.10)]
Reach 2	[0.23]	[0.83 (0.05)]	[0.53 (0.13)]	[0.12 (0.06)]	[0.10 (0.04)]
Reach 3	[0.29]	[0.91 (0.06)]	[4.96 (1.60)]	[0.30 (0.15)]	[0.40 (0.10)]

[a]Asymptotic or large sample estimates. [b]Duckweed cover not measured at the subsite scale. [c]Variance of a logistic random variable (i.e.,$\pi^2/3$). [d]Models containing this term did not converge or yielded invalid estimates. [e]Log scale; sampling variance estimate derived after Gray and Burlew (2007), with multiplicative adjustment for under-dispersion with respect to a Poisson distributional assumption.

TABLE 5. Vegetation-covariate model statistics by vegetation type from a study of duckweed and filamentous algal levels in backwater lakes of the Upper Mississippi River. Smaller Akaike Information Criterion (AIC) values indicate models with greater support from the data; −2 log LL and AIC values cannot be compared across vegetation types.

Covariate(s)	Scale at which covariate(s) vary	Number of parameters	−2 log LL	AIC
Duckweed cover				
None	na	4	3608.0	3624.0
SAV	All (site, lake, year, lake-year)	10	3396.6	3420.6
Connectivity	Lake	5	3606.6	3624.6
SAV, connectivity	All, lake	11	3396.3	3422.3
Discharge	Year	5	3605.6	3623.6
SAV, discharge	All, year	11	3394.8	3420.8
Connectivity, discharge	Lake, year	6	3604.2	3624.2
SAV, connectivity, discharge	All, lake, year	12	3394.5	3422.5
Filamentous algae[a]				
None	na	4	6822.3	6830.3
SAV	All (subsite, site, lake, year, lake-year)	10	5915.2	5935.2
Connectivity	Lake	5	6814.8	6824.8
SAV, connectivity	All, lake	11	5906.9	5928.9
Discharge	Year	5	6821.9	6831.9
SAV, discharge	All, year	11	5915.0	5937.0
Connectivity, discharge	Lake, year	6	6814.3	6826.3
SAV, connectivity, discharge	All, lake, year	12	5906.7	5930.7
Submersed aquatic vegetation rake score[a]				
None	na	8	15608.6	15618.6
Connectivity	Lake		15608.1	15620.1
Discharge	Year		15608.3	15620.3
Connectivity, discharge	Lake, year		15607.8	15621.8
Species richness (SAV)				
None	na	5	26073.6	26083.6
Connectivity	Lake	6	26073.5	26085.5
Connectivity×yr	Lake, lake×yr	7	26067.6	26081.6
Discharge	Year	6	26073.1	26085.1
Connectivity, discharge	Lake, year	7	26073.0	26087.0

[a]Excludes an among-site variation in intercept term (cf., model presented in Table 4).

Associations in reach 2 between filamentous algae at the subsite scale and SAV rake score were seen at all study scales, other than possibly that of lake-year (Table 6). Associations at scales other than the subsite scale imply contextual effects, suggesting that algal levels would depend not only on SAV at the measured or subsite scale but also at larger or "context" scales. The implication is that the probability of the presence of algae increased not just when SAV was present at the scale at which algae was measured but also when SAV was present at other locations: other subsites within the same site and other sites within lakes, years, or lake-years. SAV at other locations within a site and at nearby sites may affect hydraulics (principally water velocities; Gregg and Rose 1982, Wilcock et al. 1999) and nutrient levels (Scheffer et al. 2003) at the measurement or subsite scale.

Contextual effects may be better understood by considering year and lake effects. Previous investigations have noted associations between variation in SAV and among-year variation in growing season temperature, hydrologic condition, nutrient loading and, to lesser extent, recreational use (Mumma et al. 1996, Rooney and Kalff 2000, Biggs et al. 2005, Makarewicz et al. 2007). Similar associations have been seen for lake-scale potential predictors, including lake morphometry, connectivity, and size (Rooney and Kalff 2000, Ray et al. 2001). However, absent contextual effects, we would expect these reported year and lake associations to be primarily expressed at the spatial scale at which filamentous algae attaches to SAV because filamentous algae often uses SAV surfaces for establishment (Wetzel 2001). However, the lake- and year-scale effects found in the current study (Table 6) reflect associations that were adjusted for such local-scale effects (at subsite and site scales). Hence, metaphyton levels appear to have changed not only locally with SAV but also when SAV changed at larger scales. As mentioned earlier, such changes might be associated with changes in hydrology that were associated with changes in SAV abundance at those larger scales.

Filamentous algae decreased with increasing connectivity but was not clearly associated with discharge (both adjusted for SAV rake score levels; Table 6). Understanding how connectivity affects the different growth forms of the aquatic plant community may be important when devising management options for nuisance levels of filamentous algae or free-floating macrophytes (Barko et al. 1986). For example, artificially manipulating connectivity between lakes and channels

TABLE 6. ESTIMATED COVARIATE ASSOCIATIONS BY VEGETATION OUTCOME (FROM FULL OR LARGEST MODEL DEFINED IN TABLE 5) FROM A STUDY OF DUCKWEED AND FILAMENTOUS ALGAL LEVELS IN BACKWATER LAKES OF THE UPPER MISSISSIPPI RIVER.

Covariate(s)	Scale at which covariate varies	Units	Odds ratio estimate (95% CI[b])
	Duckweed cover		
SAV	Site	Mean rake	4.18 (3.17, 5.51)
	Lake	Mean rake	0.73 (0.34, 1.59)
	Year	0.25 mean rake	2.07 (0.89, 4.84)
	Lake-year	Mean rake	1.73 (1.01, 2.96)
Connectivity	Lake	10 points	0.97 (0.87, 1.08)
Discharge	Year	1000 cfs	0.99 (0.97, 1.01)
	Filamentous algae		
SAV	Subsite (rake = 0)	Rake	0.27 (0.17, 0.41)
	Subsite (rake = 1)	rake	0.93 (0.74, 1.17)
	Subsite (rake > 2)	na	Reference
	Site	Mean rake	5.26 (4.03, 6.85)
	Lake	Mean rake	4.48 (1.36, 14.76)
	Year	0.25 mean rake	5.44 (2.44, 12.12)
	Lake-year	Mean rake	1.58 (0.72, 3.47)
Connectivity	Lake	10 points	0.79 (0.67, 0.93)
Discharge	Year	1000 cfs	1.004 (0.986, 1.022)
	Submersed aquatic vegetation rake score		
Connectivity	Lake	10 points	0.958 (0.850, 1.081)
Discharge	Year	1000 cfs	0.996 (0.979, 1.013)
	Species richness (SAV)		
Connectivity	Lake	10 points	1.005 (0.940, 1.075)
Discharge	Year	1000 cfs	0.997 (0.988, 1.006)

[b]95% confidence interval; degrees of freedom estimated as number of units at which covariate varied (from Table 1) less the number of covariates that varied at that scale.

may lead to decreases in metaphyton prevalence without detrimentally affecting SAV levels.

Conclusions. The study data and methods seem broadly suitable for identifying lakes with free-floating macrophyte (e.g., duckweed) and metaphyton levels that are typically high. We recognize that managers interested in implementing duckweed or algae control strategies may be interested in identifying lakes that attain not only minimum average duckweed or metaphyton levels but that also exhibit relatively low interannual variation in those levels (Howard and Harley 1998). Such low levels of among-year variability, if persistent following a lake-level intervention (e.g., drawdown or herbicide treatment), would permit more rapid inference on the success of the intervention. Unfortunately, our design did not typically specify resampling of sites within years and therefore will typically preclude direct inferences on among-year variability within lakes.

A concern with this study is that we treated lakes as ecologically and statistically equivalent. Given the multiple ways in which lakes might vary and the small number of lakes in at least two of the three reaches (Table 1), the validity of these assumptions is not easily addressed. We did adjust for connectivity effects and, for free-floating macrophytes and algae, for SAV levels among lakes; however, lakes varied not only by connectivity and SAV levels but also by sample size, area, depth, contributions from springs, proximity to tributaries, and other variables. Given that the study data derived from few large lakes (Table 1), subsetting the data (e.g., by large

and small lakes) will lead to further imprecision in variance component estimates. Hence, we were unable to fully address this concern.

The study's long-term variance component and scale-related foci make the study unique and yield findings of interest to aquatic plant managers. For example, whole-lake manipulations or herbicide applications are often considered the most efficient and cost-effective way to control nuisance or invasive macrophytes, restore native SAV stands, or enhance recreational use (Zohary et al. 1998, Makarewicz et al. 2007, Kovalenko et al. 2010); however, selection of management approaches for macrophyte or algal control requires a thorough understanding of the variation of macrophyte or algal levels across space and time. Here, we documented substantial levels of variation in free-floating macrophyte cover and filamentous algae at within-lake and, for filamentous algae, at lake-year scales. Given these results, we recommend that efforts to quantify and document factors that underlie variation in duckweed and algal cover (e.g., associations with SAV cover and lake connectivity) be completed prior to initiation of management actions. Failure to plan for spatial and temporal sources of variation in macrophyte or algal cover may compromise efforts to evaluate the success of management actions.

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