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Relative importance of phosphorus, fish biomass, and watershed land use as drivers of phytoplankton abundance in shallow lakes



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HIGHLIGHTS

- We assessed the relative influence of phosphorus, fish, and watersheds on algal abundance in shallow lakes,
- Algae were best predicted by a model using both phosphorus and fish biomass.
- There was little collinearity between phosphorus and fish biomass, indicating independent influences from each variable.
- · Lake managers should target both fish communities and phosphorus levels in efforts to reduce algal abundance.

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ABSTRACT

Phytoplankton abundance in shallow lakes is potentially influenced by ambient phosphorus concentrations, nutrient loading accentuated by human activities in lake watersheds, and abundance of planktivorous and benthivorous fish. However, few studies have simultaneously assessed the relative importance of these factors influencing phytoplankton abundance over large spatial scales. We assessed relative influences of watershed characteristics, total phosphorus concentrations, and fish biomass on phytoplankton abundance in 70 shallow lakes in western Minnesota (USA) during summer 2005 and 2006. Our independent variables included total phosphorus (TP), benthivore biomass, planktivore biomass, summed planktivore and benthivore biomass (summed fish), areal extent of agriculture in the watershed, region (prairie versus parkland lakes), and year. Predictive models containing from one to three independent variables were compared using an information theoretic approach. The most parsimonious model consisted of TP and summed fish, and had over 10,000-fold greater support compared to models using just TP or summed fish, or models comprised of other variables. We also found no evidence that relative importance of predictor variables differed between regions or years, and parameter estimates of TP and summed fish were temporally and spatially consistent. TP and summed fish were only weakly correlated, and the model using both variables was a large improvement over using either variable alone. This indicates these two variables can independently increase phytoplankton abundance, which emphasizes the importance of managing both nutrients and fish when trying to control phytoplankton abundance in shallow lakes.

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1. Introduction

Freshwater wetlands and shallow lakes are the most numerically abundant lentic ecosystem at the global scale (Wetzel, 1990). These ecosystems provide a number of different services, including serving as habitat for numerous species, improving water quality, and recreation and

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commercial uses for humans (Mitsch and Gosselink, 2000). However, shallow lakes have small water volumes and constant water–sediment interaction, making them vulnerable to degraded water quality as a result of nutrient loading and high phytoplankton abundance. Shallow lakes exist in one of two alternative stable states, either a turbid-water state dominated by phytoplankton, or a clear-water state dominated by submerged macrophytes (Scheffer, 1998). Most ecosystem services of shallow lakes are reduced at high phytoplankton abundance (Moss et al., 1997; Scheffer et al., 2006), causing most shallow lake managers to focus on maintaining a clear-water state with low algal abundance

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and high water transparency. Previous studies demonstrate that phytoplankton abundance is influenced by numerous factors, including nutrient concentrations (Jeppesen et al., 2005), watershed land use (Crosbie and Chow-Fraser, 1999), and fish abundance and assemblage composition (Potthoff et al., 2008). However, few studies have simultaneously assessed the relative importance of these and other factors as drivers of algal abundance in shallow lakes, making it difficult for shallow lake managers to allocate resources in efforts to favor high water transparency.

One problem with assessing multiple variables potentially influencing phytoplankton abundance in shallow lakes is that predictor variables are potentially correlated with each other, making it difficult to identify actual causal factors. For example, total phosphorus (TP) levels in lakes are potentially influenced by agriculture in watersheds (Knuuttila et al., 1994), regional differences in soil and geology (Heiskary et al., 1987), and abundance of benthivorous fish that translocate P from sediments to the water column by bioturbation (Breukelaar et al., 1994) and by feeding on benthic prey and excreting P into the water column (Persson, 1997; Zimmer et al., 2006). However, each of these factors may influence phytoplankton abundance in ways independent of influences on TP. Agriculture in watersheds may also increase phytoplankton abundance by burying benthic algae and macrophytes via sedimentation (Gleason and Euliss, 1998), reducing nutrient competition for phytoplankton. Regional effects on phytoplankton could also include differences in community composition of fish (Herwig et al., 2010) with subsequent impacts on phytoplankton, and benthivorous fish may facilitate higher phytoplankton abundance via top-down effects of young-ofthe-year fish on zooplankton (Khan, 2003). In contrast, planktivorous fish largely increase phytoplankton abundance via consumption of zooplankton in all life stages (Scheffer, 1998).

From an applied perspective, concerns for human effects on watersheds and landscapes surrounding shallow lakes historically focused on land use and nutrient input into lakes. However, recent work highlighted the potential importance of anthropogenic alteration of the landscape that increases connectivity among basins and facilitates movement of fish among lakes (Blann et al., 2009; Hanson et al., 2005; Herwig et al., 2010). Thus, lake managers face a bewildering array of potentially interrelated factors driving phytoplankton abundance, as well as anthropogenic alterations to lake watersheds that may influence one or more of the key interrelated variables. This makes it difficult for managers to identify, let alone prioritize, the best management options for shallow lakes.

Here we compared the relative importance of TP, agriculture in watersheds, and fish abundance as drivers of phytoplankton abundance in shallow lakes, and tested whether the relationships we observed were consistent between years and ecoregions. We also assessed relationships among our predictor variables to further clarify the relative importance of each variable for phytoplankton abundance. Our goal was to determine the most parsimonious model for predicting phytoplankton abundance, and to quantify the relative influence of several potential sources of variance in algal abundance. These variables have been assessed in isolation or in mesocosm-scale studies, but we use a holistic approach where we simultaneously measure the influence of several variables at the whole-lake scale over two years.

2. Methods

We studied shallow lakes in two regions of Minnesota; one on the eastern edge of the Prairie Pothole Region (PPR) (Euliss et al., 1999) (hereafter "prairie" lakes), the other in the parkland zone between the PPR and deciduous forest (hereafter "parkland" lakes) (Fig. 1). This allowed us to assess spatial variability in the importance of predictor variables for phytoplankton abundance. Moreover, "region" may in itself be an important driver of algal abundance due to differences in fish community composition, soil characteristics, and other factors that vary at a landscape scale.

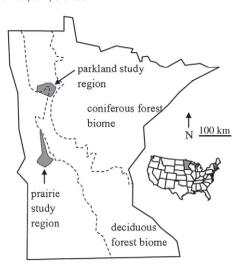


Fig. 1. Location of the parkland and prairie study regions in Minnesota, USA. Dashed lines show approximate boundaries of the three major biomes in Minnesota.

We used stratified-random sampling to select our study lakes from a National Wetlands Inventory GIS database. We stratified potential study lakes into 27 bins based on combinations of the following three variables: 1) lake size (small, medium, large, range 2 to 50 ha), 2) distance to nearest permanent stream, wetland, or lake (short, medium, long, range 0 to 1825 m), and 3) proportion agriculture within a 500 m buffer surrounding the lake (low, medium, high, range 0 to 97%). We randomly selected a maximum of two lakes per bin in each study area, and sampled 35 prairie and 35 parkland lakes in both 2005 and 2006. Our study sites were dispersed across 1292 km² in the parkland region and 1435 km² in the prairie region, and were located on land owned by the federal government (48%), private citizens (41%), and state or municipal government (11%).

Farm Service Agency (FSA) color digital orthophoto quadrangles from 2003 (hereafter "air photos") and GIS were used to estimate surface area of each lake in 2005. ArcView Spatial Analyst (Environmental Systems Research Institute Inc., 2007) and the Minnesota Department of Natural Resources' GIS Hydro Tool were used to delineate watersheds based on hydrologically-corrected digital elevation models, digital raster graphics, air photos from multiple years, and observations from field visits to study lakes in both years. GIS was then used to extract estimated watershed size for each study site. Land use within the watershed of each lake was separated into 13 categories using standardized on-screen digitizing procedures with FSA land use maps and 2003 air photos as primary references. Three lakes had watersheds too large to be hand digitized, so land use was determined from Minnesota Gap Land Cover layers reclassified to match our manuallydigitized cover type categories. For this analysis we used "agriculture in the watershed," which consisted of ha of land used for row-crop agriculture and hay in each lake's watershed. Agriculture consisted largely of corn, soybeans, and small grains, but also likely included some areas hayed on an annual basis.

Fish species composition and wet-weight biomass (CPUE) were sampled in July of both years using two types of gear. Three mini-fyke nets (6.5 mm bar mesh with 4 hoops, 1 throat, 7.62 m lead, with a 0.69 m \times 0.99 m rectangular opening) and one experimental gill net (61.0 m multifilament net with 19, 25, 32, 38, and 51-mm bar meshes) were set overnight in each lake. Fyke nets were set in the littoral zone, while the gill net was set along a 2 m contour, or at maximum depth in lakes less than 2 m deep. Using both types of gear enabled us to capture fish of different sizes, species, and from all major trophic guilds. We summed the biomass of each species captured in each lake using the gill net and three fyke nets set in each lake in each year. We then estimated the total mass of planktivore and benthivore trophic guilds in each lake by summing the mass of all benthivorous and planktivorous fish

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