

## Total phosphorus and piscivore mass as drivers of food web characteristics in shallow lakes

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We assessed the relative influence of total phosphorus and piscivore biomass on the abundance of benthivores, soft-rayed planktivores, spiny-rayed planktivores, zooplankton and phytoplankton in 69 shallow lakes in the prairie and parkland areas of Minnesota, USA. Piscivore biomass was the best predictor for three of these response variables, exhibiting a negative relationship with soft-rayed planktivores, a positive relationship with benthivores, and a weaker positive relationship with large-bodied cladocerans. Total phosphorus and piscivores comprised the best model for predicting spiny-rayed planktivores, while neither variable showed any strong relationship to small-bodied cladocerans. Total phosphorus was positively related to phytoplankton abundance, and was the best predictor among all candidate models. Moreover, contrary to predictions of trophic cascade theory, the relationship between chlorophyll *a* and total phosphorus did not differ between lakes with and without piscivores. Our results indicated top-down influences of piscivores extended through parts of two trophic levels, but failed to influence zooplankton – phytoplankton interactions, leaving phytoplankton abundance constrained largely by total phosphorus. Lack of a relationship between piscivores and phytoplankton was likely due to high densities of larval planktivores less susceptible to piscivory, as well as positive influences of spiny-rayed planktivores and benthivores on algal abundance. These results support the idea that top-down influences of piscivores on phytoplankton abundance may be reduced in more diverse fish communities where some prey species are less susceptible to piscivory.

Community structure is simultaneously influenced by top-down and bottom-up forces, and research has examined factors influencing their relative importance for many years (reviewed by Drenner and Hambright 2002). In lakes with strong top-down control, trophic cascade theory predicts that abundant piscivores keep planktivores at low densities, permitting large-bodied zooplankton populations to increase, thus reducing phytoplankton. In contrast, lakes without piscivores should have high abundance of planktivores and phytoplankton, and low abundance of zooplankton (Carpenter and Kitchell 1988, Mazumder 1994). This dichotomy in phytoplankton abundance was traditionally attributed to higher zooplankton grazing in lakes with piscivores, but it may also be due to bottom-up influences associated with consumer-driven nutrient recycling (Vanni and Layne 1997).

Drenner and Hambright (2002) reviewed 17 studies examining cascading effects of piscivores on phytoplankton, and found evidence of phytoplankton reduction due to piscivores in just seven cases. However, they reported that phytoplankton abundance (measured as chlorophyll *a*) per unit phosphorus was significantly lower in lakes with piscivores relative to those without, suggesting some level of top-down control by piscivores. Numerous studies have

examined trophic interactions of piscivores in shallow lakes, as empirical data suggest top-down influences are inversely related to lake depth (Jeppesen et al. 1997). However, indirect influences of piscivores on phytoplankton via predation on planktivores and benthivores in shallow lakes appear to be variable and often short-lived (Søndergaard et al. 1997, Potthoff et al. 2008).

Most research assessing trophic interactions in shallow-water systems has been conducted under experimental conditions where piscivores are either stocked or removed from individual lakes (Søndergaard et al. 1997, Skov et al. 2002). At a broader scale across multiple lakes, influences of natural variability in piscivore abundance are poorly understood. Moreover, research on trophic cascade theory has largely focused on piscivores and planktivores (Carpenter et al. 1985), but trophic interactions in more complex food webs with piscivores, benthivores and planktivores are poorly known.

At the landscape scale, the importance of piscivory on algal abundance in natural systems should be highest in areas where the presence or abundance of piscivores is highly variable among lakes. This is typical within eastern portions of the Prairie Pothole Region (PPR) of North America, a matrix of shallow lakes and grasslands stretching from Alberta to Iowa

across 715 000 km<sup>2</sup> (Euliss et al. 1999). Fish communities in these bodies of water vary dramatically, with species richness ranging from 0 to 11 species (Herwig et al. 2010). Presence of functional guilds is also highly variable, with planktivores and piscivores being most and least common, respectively. These variable fish communities result from landscape and lake features driving colonization and extinction of fish species within individual lakes, as well as biotic interactions among fish species (Herwig et al. 2010).

Phosphorus has long been viewed as the key driver of lake phytoplankton abundance and is thought to regulate intensity of trophic cascade influences on zooplankton and algae in lakes (McQueen et al. 1986). Recent evidence confirms that intensity of trophic relationships fluctuate along total phosphorus (TP) gradients (Jeppesen et al. 2000, 2003). However, trophic responses of plankton and water clarity in shallow lakes are complex and may be difficult to predict, as are responses of these lakes to changes in planktivore and piscivore biomass (Søndergaard et al. 2007). Despite their importance, the influences of piscivore abundance and TP for food web structure in unmanipulated shallow lakes is little studied and achieving sustained improvements in water quality of shallow, eutrophic lakes remains extremely challenging for lake managers (Moss 2007, Søndergaard et al. 2007).

In this study, we assessed the influence of total phosphorus and piscivores on food webs in 69 shallow lakes with fish communities along the eastern edge of the PPR under unmanipulated conditions. We hypothesized that piscivore biomass would have a negative relationship with biomass of benthivores, planktivores and phytoplankton, and a positive relationship with zooplankton biomass. We also hypothesized TP would show a positive relationship with all of our dependent variables in lakes where piscivores were absent or in very low abundance.

## Methods

This comparative study was conducted in two areas of western Minnesota. The first area was located in the eastern PPR in an area once characterized by extensive native prairies, now principally agriculture lands (hereafter prairie lakes). The second was along the edge of the PPR, in a parkland area comprised of woodlands, grasslands and agriculture lands (hereafter parkland lakes) (Fig. 1). We studied lakes from both areas because natural levels of nitrogen (N) and phosphorus (P) are higher in prairie lakes (Heiskary et al. 1987). Because lake productivity can influence the strength of trophic interactions (Jeppesen et al. 1997) we felt data from two areas would increase ranges in lake characteristics and contribute to better models. We used a stratified-random selection procedure to select 35 prairie and 34 parkland lakes from a pool of candidate sites identified using geographical information systems. All lakes were sampled during 2006.

The relative abundance of planktivores, benthivores, and piscivores was assessed in July using both mini-fyke and gill nets deployed for 24 h. Each lake was sampled with three mini-fyke nets (6.5 mm bar mesh with four hoops, one throat, 7.62 m lead, and a 0.69 × 0.99 m rectangular opening) set perpendicular to shore, and one experimental gill

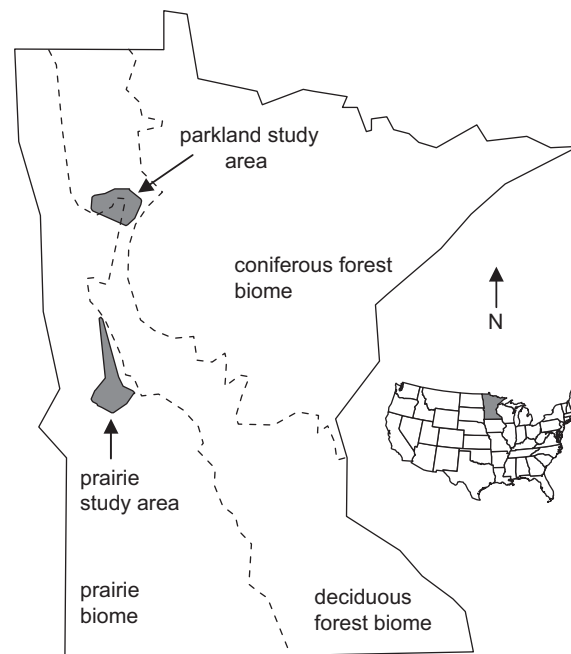


Figure 1. Location of the prairie and parkland study areas in Minnesota, USA. Also shown are the boundaries of the three major biomes found in Minnesota.

net (61 m multifilament net with 19, 25, 32, 38 and 51-mm bar meshes) placed along the deepest contour. Results for each lake were expressed as the total biomass of each fish species captured summed across the three fyke nets and single gill net, and we also estimated average individual fish mass of each species captured. Use of both fyke nets and a multi-panel gill net successfully samples species of fish present in our study sites, and these two techniques have been used to identify patterns of fish community composition in these systems (Herwig et al. 2010). We then determined the total biomass of planktivores, benthivores and piscivores for each lake by summing the biomass of species in each functional group and expressed results as catch-per-unit of effort (CPUE), with species classified based on diet data from the literature and from fish we have collected from similar systems (Friederichs unpubl.). Fish diets are flexible, and classification of fish species as piscivorous can have a large impact on a study such as ours. However, the two primary piscivorous species in these systems, walleye *Sander vitreus* and northern pike *Esox lucius*, feed heavily on fish at the body sizes we observed, and can have strong impacts on prey species (Skov et al. 2002, Potthoff et al. 2008). In contrast, yellow perch *Perca flavescens* generally do not feed on fish until body lengths exceed 150 mm, and fish do not dominate perch diets until they are 4+ years of age (reviewed by Graeb et al. 2005). Lengths of yellow perch in our study sites averaged 121 mm, so we classified this species as planktivorous. Planktivores were further categorized as soft-rayed or spiny-rayed species, based on presence of spines in fins.

We also assessed the influence of piscivores on densities of larval soft-rayed planktivores in prairie lakes in June by sampling five lakes with soft-rayed fathead minnow *Pimephales promelas* but lacking piscivores and three lakes with fathead minnow and piscivorous walleye. One lake in each of these

two groups also contained low numbers of black bullhead *Ameiurus melas*. Larval fish were sampled using a bow-mounted ichthyoplankton push net (0.5 m diameter, 2 m length, 0.8 mm mesh) pushed along three transects running parallel to shore. Each transect was sampled for one minute, and larval fish in each sample were preserved, identified, and counted. Results were converted to larval fish  $m^{-3}$  using a calibrated flow meter, and averaged across the three samples to produce a single density estimate per lake. We used a t-test to determine whether densities of larval soft-rayed planktivores and biomass of adult planktivores in this subset of lakes differed in the presence or absence of piscivores.

Concentration of TP in the water column and abundance of phytoplankton and zooplankton were assessed in July in each lake. TP was estimated from a water sample collected near the center of each lake just below the surface. Samples were frozen after collection, and later analyzed for TP with high-temperature persulfate oxidation followed by ascorbic acid colorimetry, and TN using Kjeldahl digestion combined with nitrate and nitrite estimates done via cadmium reduction. Zooplankton were collected using an integrated column sampler (Swanson 1978) at five locations per lake. We determined densities of large-bodied cladocerans (*Daphnia* and *Simocephalus*) and small cladocerans (*Ceriodaphnia*, Chydorids, *Bosmina* and *Diaphanosoma*) in each sample and averaged the estimates across the five samples for a single estimate of number  $l^{-1}$  for each lake. Phytoplankton abundance was estimated concurrently with zooplankton via chlorophyll a (chl a) concentrations in the water column. Three water samples were collected from each lake, filtered through GF/F filters, frozen, and the filters analyzed for chl a using alkaline-acetone extraction and fluorometric analysis (Arar and Collins 1997).

Our primary objective was to assess the relative importance of TP and piscivore mass (hereafter piscivores) as drivers of food-web characteristics in shallow lakes. Thus, we used an information theoretic approach (Anderson et al. 2000) to evaluate sets of five candidate models for predicting biomass of chl a, large cladocerans, small cladocerans, benthivores, soft-rayed planktivores and spiny-rayed planktivores in our study sites, and to identify the most parsimonious model for each variable. Our five models consisted of 1) intercept only (hereafter intercept), 2) intercept and TP (hereafter TP), 3) intercept and piscivores (hereafter piscivores), 4) intercept, TP and piscivores (hereafter TP + piscivores), and 5) intercept, TP, piscivores and a TP  $\times$  piscivores interaction (hereafter TP  $\times$  piscivores). Initially, we also fit ecoregion as a fixed effect in all five models to assess spatial variance between the two ecoregions, but it did not improve fit for any of our dependent variables (based on the criteria explained below). Thus, we focused our analyses on the five models described above. We began with the hypothesis that TP  $\times$  piscivores would be the best supported model for all dependent variables, indicating the influence of TP depended on abundance of piscivores. We expected that piscivores would be the best single predictor for all dependent variables, but TP would increase model fit for lakes with low piscivore abundance and in lakes where piscivores were absent.

Model performance was evaluated using  $AIC_C$  (Anderson et al. 2000), and models within 6  $AIC_C$  units of the model with the smallest  $AIC_C$  value (i.e.  $\Delta$ -value  $<$  6) were considered

plausible and retained for inference (Richards 2008). An exception was that complex models (e.g. TP  $\times$  piscivores) had to have lower  $AIC_C$  values than simpler nested models (e.g. TP) to be retained for inference (Richards 2008). Relative support among the five models was assessed using the ratio of Akaike weights ( $w_i$ ) between models (support ratios), providing an estimate of the likelihood of one model relative to another (Anderson et al. 2000). TP can also influence the abundance of piscivores (Jeppesen et al. 2000), so we also assessed the strength of the relationship between TP and piscivore abundance relative to an intercept-only model.

Analysis of chl a and small cladocerans was done using ordinary least square methods. However, large cladocerans, piscivores, spiny-rayed planktivores, soft-rayed planktivores and benthivore data sets contained large numbers of zeroes. Thus, we analyzed these dependent variables,  $Y_i$ , using zero-inflated mixture models (Martin et al. 2005), in which the contribution to the data likelihood was given by:

$$p_i(Y_i|X_i, \beta) \text{ when } Y_i = 0; \text{ and } (1-p_i(Y_i|X_i, \beta)) * f(Y_i|Z_i, \gamma, \sigma)$$

when  $Y_i >$  0, where  $p$  is modeled using a logistic function =  $1/(1 + \exp(X_i, \beta))$ ,  $f$  is the probability density function of a lognormal distribution with mean ( $Z_i, \gamma$ ) and variance ( $\sigma$ ) on the log scale,  $\beta$  and  $\gamma$  are regression parameters,  $X$  is a matrix of covariates used to model the probability  $Y_i = 0$ , and  $Z$  is a matrix of covariates that influence the mean of  $Y_i$  on the log scale when  $Y_i$  is non-zero. We allowed TP, piscivores, and their interaction to enter in both  $X$  and  $Z$  (but, not just in  $X$  or just in  $Z$ ). In essence, mixture models allow independent variables to predict both presence versus absence of the dependent variable in all study sites, as well as the value of the dependent variable in lakes where it was present. We used log transformations of the response variable to meet normality and constant variance assumptions when using ordinary least squares. With both least square and mixture models, we used log transformations of the predictors to improve model fit.

The analyses described above treated piscivores as a continuous variable in our competing models. However, there has been considerable interest in 'even versus odd link' food webs, with top-down theory predicting lower phytoplankton abundance in lakes with piscivores present. We assessed the ability of even versus odd linked food webs and TP to predict chl a using the same information theoretic approach and the five models described above, but treated piscivores as a categorical variable based on presence versus absence in individual lakes. We also used MANOVA to test whether community composition based on biomass of benthivores, soft-rayed planktivores and spiny-rayed planktivores differed between lakes with and without piscivores, and a t-test to test whether the summed biomass of benthivores, soft-rayed planktivores and spiny-rayed planktivores differed between lakes with and without piscivores.

Logistical constraints limited our sampling to a one-time event in July during the peak of the growing season, a period that reflects dominant trophic interactions occurring for the year. Given that shallow lakes are dynamic systems and trophic relationship can change seasonally (Potthoff et al. 2008), our results should be considered a 'snap shot' of food web relationships in these systems.

## Results

We sampled 22 species of fish in our study sites, but the biomass of each of our four groups of fish was dominated by a limited number of species. Piscivores were dominated by walleye and northern pike (51% and 46% of total piscivore mass, respectively), benthivores dominated by black bullhead and common carp *Cyprinus carpio* (76% and 16% of total benthivore mass, respectively), soft-rayed planktivores dominated by fathead minnow and northern redbelly dace *Phoxinus eos* (84% and 10% of total soft-rayed planktivores, respectively), and spiny-rayed planktivores by yellow perch and bluegill *Lepomis macrochirus* (49% and 34% of total spiny-rayed planktivore mass, respectively). Body size of piscivores averaged 926 g for northern pike and 780 g for walleye, while benthivores had the largest mean body mass among prey fish (carp 625 g, black bullhead 120 g), followed by spiny-rayed planktivores (yellow perch 34 g, bluegill 58 g) and soft-rayed planktivores (fathead minnow 2 g, redbelly dace 1 g). Average number of individual fish in each trophic group captured in lakes where they were detected was approximately 2953 soft-rayed planktivores, 133 benthivores, 75 spiny-rayed planktivores and 29 piscivores. Proportion of total biomass represented by the four groups of fish was highly variable among lakes, ranging from 0 to 99% for benthivores, 0 to 100% for soft-rayed planktivores, 0 to 93% for spiny-rayed planktivores and 0 to 96% for piscivores. T-tests indicated no difference in maximum depth ( $p = 0.586$ ), total phosphorus ( $p = 0.564$ ), or total nitrogen ( $p = 0.858$ ) between lakes with and without piscivores, while lakes with piscivores were significantly larger than those without piscivores ( $p = 0.006$ ) (Table 1).

Our results indicated a positive relationship between piscivore biomass and TP (Fig. 2A). However, the overall relationship between TP and piscivores was relatively weak, and the TP model had only 33-fold more support relative to the intercept-only model (Table 2A).

Results for model selection indicated strong relationships between piscivore biomass and soft-rayed planktivores and benthivores, but much weaker relationships between our predictor variables and spiny-rayed planktivores, large cladocerans and small cladocerans. The piscivore model was the most parsimonious for soft-rayed planktivores, and selection criteria based on  $AIC_C$  values rejected all other models (Table 2B, Fig. 2B). The TP and intercept models had  $\Delta AIC_C$  values greater than 2000, and  $AIC_C$  values for the TP + piscivores and TP  $\times$  piscivores models were equal to or larger than the simpler piscivore model. Support ratios indicated piscivores had 10 000-fold more support relative to TP, and more than 2000-fold support over the intercept model. The mixture model indicated a negative relationship between biomass of soft-rayed planktivores and piscivores,

and a negative relationship between probability of soft-rayed planktivores presence and piscivore biomass. The probability that soft-rayed planktivores were present was 98% in the absence of piscivores, and dropped to 40% at the highest observed biomass of piscivores.

The piscivore model was also the most parsimonious model for benthivores, and  $\Delta AIC_C$  indicated all other models were implausible (Table 2C, Fig. 2C). Relative support for the piscivore model was strong; it had approximately 32 000- and 21 000-fold support over the TP and intercept models, respectively. In contrast to soft-rayed planktivores, biomass and probability of benthivore presence was positively related to piscivore mass, with probability of occurrence increasing from 53% to 99% as piscivore mass increased.

Model results for spiny-rayed planktivores showed no clear support for any specific model (Table 2D, Fig. 2D). The TP+piscivores model had the lowest  $AIC_C$  value, but all other models (excluding the intercept model) were within six  $\Delta AIC_C$  values of this top model. Moreover, the TP+piscivores model had just 57-fold more support than the intercept model, indicating the fit for the spiny-rayed planktivores was much weaker than models for soft-rayed planktivores and benthivores. Biomass and probability of being present for spiny-rayed planktivores both showed a negative relationship with TP, while biomass of spiny-rayed planktivores was positively related to piscivore biomass (Table 2D).

Piscivores was the best supported model for large-bodied cladocerans, and  $AIC_C$  values indicated weaker support for all other models (Table 2E, Fig. 2E). Abundance of large cladocerans and probability of occurrence were both positively related to piscivore biomass. However, the piscivore model had just 26-fold more support than the intercept model, indicating a weaker relationship compared to the relationship observed between piscivores and soft-rayed planktivores and benthivores. Similar to large cladocerans, none of the models predicted abundance of small cladocerans very well. The TP  $\times$  piscivore model had the lowest  $AIC_C$  value, but it was within 3  $AIC_C$  units of the intercept only model, and only explained 13% of the variation in small cladoceran abundance (Table 3A) (data not shown).

The TP model had the most support for chl a, and  $\Delta_i$  values indicated no support for any other models (Table 3B–C, Fig. 3). The ratio of support over the intercept only model was  $> 100\ 000$ , as was the support of TP over piscivore biomass. Results for treating piscivore presence as a categorical variable were similar to using piscivore biomass as a continuous variable, with strong support for the TP model over all other candidate models (Table 3C, Fig. 3). Thus, the chl a – total phosphorus relationship was similar in lakes with and without piscivores, indicating three versus four trophic levels was a poor predictor of algal abundance in these systems.

MANOVA indicated a significant difference in biomass of benthivores, soft-rayed planktivores, and spiny rayed planktivores between lakes with and without piscivores ( $p < 0.0001$ ) (Fig. 4A). Soft-rayed planktivores were higher in lakes lacking piscivores, benthivores were higher in lakes with piscivores, while biomass of spiny-rayed planktivores was similar. Summed biomass of benthivores, spiny-rayed planktivores, and soft-rayed planktivores was significantly

Table 1. Average characteristics (1 SE) of lakes with piscivores absent ( $n = 46$ ) and piscivores present ( $n = 23$ ) during 2006.

	Maximum depth (m)	Surface area (ha)	Total P ( $\mu\text{g l}^{-1}$ )	Total N ( $\mu\text{g l}^{-1}$ )
Piscivores absent	2.3 (0.2)	12.4 (1.6)	115 (21)	2358 (222)
Piscivores present	2.5 (0.4)	20.3 (2.4)	136 (23)	2295 (232)

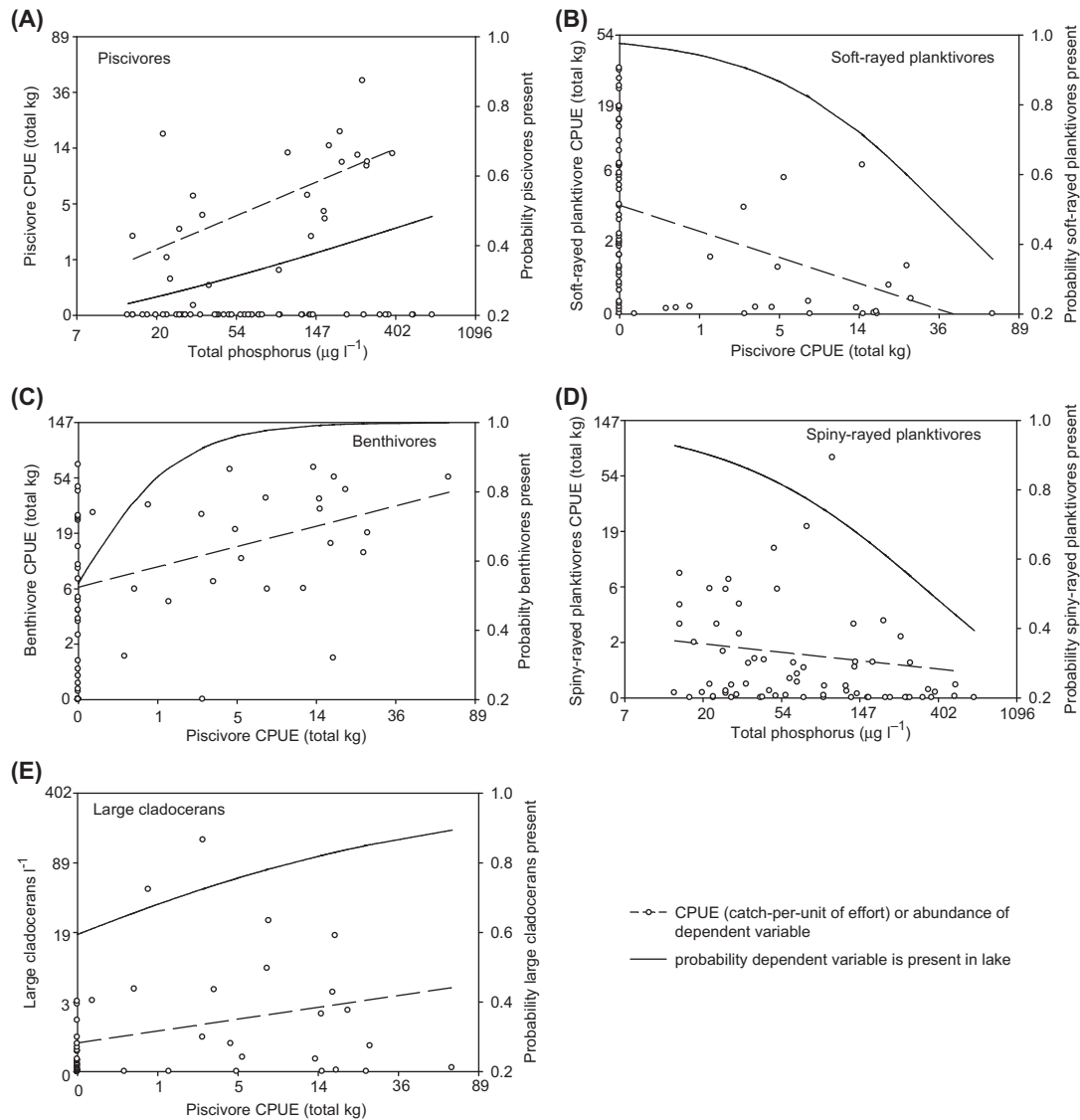


Figure 2. Estimated relationships from ‘best fit’ mixture models for biomass (dotted lines) and probability of being present in a lake (solid lines) for (A) piscivores as a function of total phosphorus, (B) soft-rayed planktivores as a function of piscivore biomass, (C) benthivores as a function of piscivore biomass, (D) spiny-rayed planktivores as a function of total phosphorus while holding biomass of piscivores constant at mean biomass, and (E) abundance of large-bodied cladocerans as a function of piscivore biomass.

higher in lakes with piscivores compared to those without ( $p = 0.020$ ) (Fig. 4B). Data from our subset of eight prairie lakes also indicated that biomass of adult soft-rayed fish was significantly lower in lakes with piscivores compared to those without ( $p = 0.005$ ) (Fig. 5A). However, densities of larval soft-rayed fish did not differ between lakes with and without piscivores ( $p = 0.225$ ) (Fig. 5B).

## Discussion

Our results suggest that trophic interactions associated with unmanipulated communities of piscivores did not extend to influences on phytoplankton abundance in these shallow lakes. Top-down control by piscivores was limited to soft-rayed planktivores, which likely caused the weak positive relationship between piscivore biomass

and large cladocerans. Despite the weak positive relationship between piscivores and large cladocerans, there was no relationship between phytoplankton abundance and piscivores. Influences of piscivores apparently extended through parts of two trophic levels in these systems, but failed to influence zooplankton – phytoplankton interactions. However, our sampling was limited to July, and trophic relationship may differ from those observed here at other times of the year.

A strong relationship between TP and piscivores would have made it difficult to decipher the relative importance of these two variables as drivers of food web characteristics in these lakes. However,  $\text{AIC}_C$  values indicated the TP – piscivore relationship was weak, especially relative to relationships observed among other variables. Moreover, with the exception of spiny-rayed planktivores, there was always a substantial difference in the performance of the one

Table 2. Performance of (A) two mixture models attempting to predict biomass and presence versus absence of piscivores, and five mixture models attempting to predict biomass and presence versus absence of (B) soft-rayed planktivores, (C) benthivores, (D) spiny-rayed planktivores and (E) large cladocerans in 69 shallow lakes in 2006. Models are sorted in order of increasing AIC<sub>C</sub> values for each dependent variable, with smaller AIC<sub>C</sub> values indicating more parsimonious models. K is number of parameters in each model,  $\Delta_i$  is differences in AIC<sub>C</sub> values between each model and the most parsimonious model (model with lowest AIC<sub>C</sub> value),  $w_i$  are Akaike weights and represent weight of evidence (out of 1.00) that each model is the best model in the set, and the evidence ratio is the ratio of  $w_i$  between models and shows multiplicative improvement of the best model over all other models. Also shown for the most parsimonious model for each dependent variable are the slope estimates and 95% confidence interval (95% CI) for both the logistic and linear part of the mixture model.

	K	AIC <sub>C</sub>	$\Delta_i$	$w_i$	Evidence ratio	Slope	95% CI
(A) Piscivores: models							
TP	5	107.2	0	0.97			
logistic						0.30	(-0.20, 0.79)
linear						0.22	(0.10, 0.34)
intercept	3	114.2	7	0.03	33		
(B) Soft-rayed planktivores: models							
piscivores	5	219.9	0	0.38			
logistic						-1.02	(-1.73, -0.31)
linear						-0.42	(-0.66, -0.17)
TP + piscivores	7	219.9	0	0.38	1		
TP × piscivores	9	220.8	0.9	0.24	2		
intercept	3	235.4	15.5	<0.01	2321		
TP	5	238.5	18.6	<0.01	10 938		
(C) Benthivores: models							
piscivores	5	223.0	0	0.85			
logistic						1.70	(0.16, 3.23)
linear						0.41	(0.15, 0.66)
TP + piscivores	7	227.2	4.2	0.10	8		
TP × piscivores	9	229.1	6.1	0.04	21		
intercept	3	242.9	19.9	<0.01	20 952		
TP	5	243.9	20.8	<0.01	32 859		
(D) Spiny-rayed planktivores: models							
TP+piscivores	7	213.5	0	0.74			
logistic (TP)						-0.75	(-1.37, -0.14)
logistic (piscivores)						-0.07	(-0.56, 0.42)
linear (TP)						-0.26	(-0.51, -0.01)
linear (piscivores)						0.34	(0.12, 0.57)
TP	5	217.2	3.7	0.12	6		
TP × piscivores	9	217.8	4.3	0.09	9		
piscivores	5	219.3	5.8	0.04	18		
intercept	3	221.6	8.1	0.01	57		
(E) Large cladocerans: models							
piscivores	5	225.6	0	0.75			
logistic						0.96	(-0.27, 2.19)
linear						0.65	(0.07, 1.24)
TP × piscivores	9	229.1	3.5	0.13	6		
TP + piscivores	7	230.1	4.5	0.08	9		
intercept	3	232.1	6.5	0.03	26		
TP	5	235.3	9.7	<0.01	128		

variable models of TP and piscivores, providing further evidence that collinearity among TP and piscivores was low. The weak relationship between TP and piscivores was surprising given results of other studies in shallow lakes (Jeppesen et al. 2000). This suggests that other factors, such as lake isolation, limit the abundance of piscivores in these systems and weaken the TP – piscivore relationship relative to relationships observed in other shallow lakes.

Previous studies reported negative relationships between piscivore and phytoplankton abundance in both shallow and deeper lakes (Carpenter et al. 2001, Lathrop et al. 2002, Skov et al. 2002), and other studies found lower phytoplankton biomass per unit phosphorus in lakes with even link compared to odd

link food webs (Mazumder 1994, Drenner and Hambright 2002). Possible explanations for these differences include different methods for sampling fish communities, and the presence of abundant larval planktivores, spiny-rayed planktivores and benthivores that were not controlled by piscivores in our study. Mehner (2010) also found weak top-down influences of piscivores in European lakes, providing further evidence that cascade effects associated with piscivores may be weaker than cascades observed in lower trophic levels.

Jeppesen et al. (2003) suggested that effects of piscivores in shallow, eutrophic lakes transmit strongly to the zooplankton level (*Daphnia*), but that zooplankton grazing often exerts little control on phytoplankton abundance in

Table 3. Performance of five least-square models attempting to predict (A) small cladocerans and (B, C) chl a. In (A, B), piscivore biomass is included as a continuous variable, whereas in (C) we consider presence versus absence of piscivores (i.e. it is included as a categorical variable).  $r^2$  is the proportion of variance explained; other statistical parameters are defined in Table 2.

	$r^2$	K	AIC <sub>c</sub>	$\Delta_i$	$w_i$	Evidence ratio	Slope	95% CI
(A) Small cladocerans: models								
TP × piscivores (continuous)	0.13	4	-58.48	0	0.66			
linear (TP)							-0.08	(-0.44, 0.28)
linear (piscivores)							0.47	(0.01, 0.85)
linear (TP × piscivores)							-1.07	(-1.83, -0.31)
Intercept		1	-55.44	3.0	0.14	5		
piscivores (continuous)	0.02	2	-54.82	3.7	0.11	6		
TP	0	2	-53.32	5.2	0.05	13		
TP + piscivores (continuous)	0.03	3	-52.73	5.7	0.04	18		
(B) Chl a: models								
TP	0.64	2	-23.9	0	0.68			
linear (TP)							1.05	(0.86, 1.24)
TP + piscivores (continuous)	0.64	3	-21.8	2.1	0.23	3		
TP × piscivores (continuous)	0.64	4	-19.9	4.0	0.09	8		
piscivores (continuous)	0.07	2	41.7	65.7	<0.01	>100 000		
Intercept		1	44.5	68.4	<0.01	>100 000		
(C) Chl a: models								
TP	0.64	2	-23.9	0	0.69			
linear (TP)							1.05	(0.86, 1.24)
TP + piscivores (categorical)	0.64	3	-21.8	2.2	0.23	3		
TP × piscivores (categorical)	0.64	4	-19.9	4.4	0.08	9		
Intercept		1	44.5	68.4	<0.01	>100 000		
piscivores (categorical)	0.02	2	45.5	69.4	<0.01	>100 000		

these lakes. Little empirical evidence exists with which to evaluate piscivore influences on phytoplankton in shallow lakes in North America. However, given the positive influences of piscivores on large cladocerans in this study, lack of a relationship between piscivores and phytoplankton is perplexing. Potthoff et al. (2008) studied similar prairie lakes in Minnesota with fish communities limited to soft-rayed planktivores (fathead minnow), and introduced young-of-the-year (YOY) piscivores (walleye). The density of large cladocerans in that study averaged 62 l<sup>-1</sup> following piscivore introductions, while controls averaged 3 l<sup>-1</sup>. Lakes stocked with YOY piscivores also showed a significant reduction in phytoplankton abundance relative to control sites. Hence, trophic influences of piscivores extended through the entire food web in the Potthoff et al. (2008) study, yet stopped at the zooplankton level in the current study. However, despite the positive relationship between piscivores and large cladocerans in the current study, only one lake had cladoceran densities higher than 62 l<sup>-1</sup>, while 58 lakes had cladoceran densities lower than the control lakes (3 l<sup>-1</sup>) in the Potthoff et al. (2008) study. Thus, large cladoceran densities may have been too low in our study to exert top-down control on phytoplankton despite the positive relationship with piscivores.

Absence of top-down control on phytoplankton may have been due in part to the inability of piscivores to reduce

abundance of larval and YOY planktivores. Piscivores effectively reduced adult soft-rayed planktivores (fathead minnow), but they had no effect on larval minnows. Hansson et al. (1998) reported that successful biomanipulation is impossible unless piscivores control larval and adult planktivores. In studies of three similar Minnesota lakes, Herwig and Zimmer (2007) estimated that larval fathead minnows accounted for 88% of zooplankton consumption by minnows, despite representing just 19% of total mass of the minnow populations. They also estimated consumption of zooplankton by minnow larvae in one of the three lakes averaged 14.3 kg ha<sup>-1</sup> day<sup>-1</sup> from May through August. The inability of piscivores to control larval planktivores in the present study is likely due to infrequent, limited reproduction by piscivores in our study sites (Friederichs unpubl.). We observed very few YOY piscivores in our study sites, and detected no larval piscivores in the subset of eight lakes sampled for fish larvae. The near absence of YOY piscivores subsequently results in low piscivory on larval planktivores. Thus, piscivores reduce the abundance of adult soft-rayed planktivores, but zooplankton density remains lower than expected due to strong recruitment and resulting high predation from larval planktivores. The cause of infrequent piscivore reproduction is unknown, but it may be due to limited spawning habitat coupled with intense competition and predation from other YOY fishes.

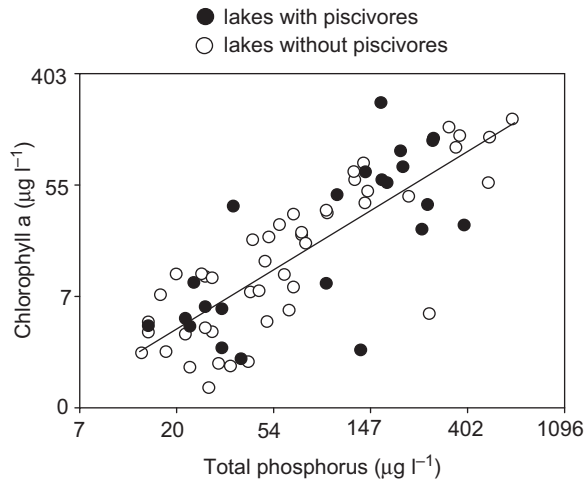


Figure 3. Estimated relationships from least-squares regression for chl *a* levels as a function of total phosphorus. The total phosphorus model was the most parsimonious model regardless of whether piscivore biomass or piscivore presence was used as a predictor variable.

Absence of a relationship between piscivores and phytoplankton could also be due to the inability of piscivores to reduce biomass of adult benthivores and spiny-rayed planktivores. Benthivores increase phytoplankton abundance by increasing internal loading of nutrients via benthic feeding activities (Brabrand et al. 1990, Persson 1997). Additionally, YOY of many benthic fish species consume zooplankton (Khan 2003, Strand 2005), which combined with predation from spiny-rayed planktivores, likely played a role in constraining the abundance of large cladocerans.

Piscivores likely failed to reduce the abundance of spiny-rayed planktivores and benthivores due to the heightened defenses of these prey fish groups against piscivory, and our results are consistent with other studies showing effects of piscivory are often limited to small, soft-bodied species (Tonn and Magnuson 1982, Chapleau et al. 1997). Adult benthivores and spiny-rayed planktivores in our study sites were larger and better defended against predation via spines

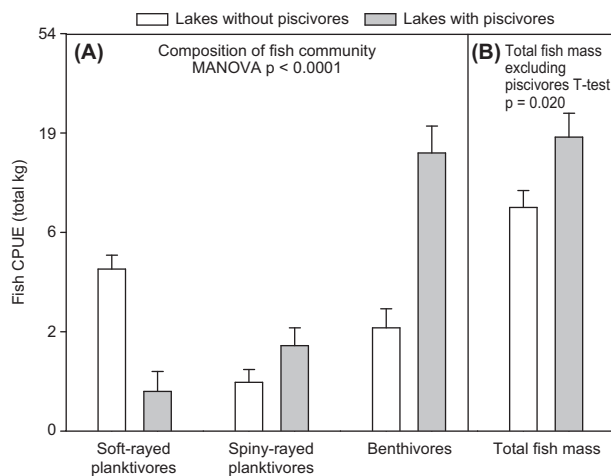


Figure 4. Geometric means of (A) soft-rayed planktivores, spiny-rayed planktivores, and benthivores in lakes with and without piscivores, and (B) summed biomass of soft-rayed planktivores, spiny-rayed planktivores, and benthivores in lakes with and without piscivores ( $\pm 1$  SE).

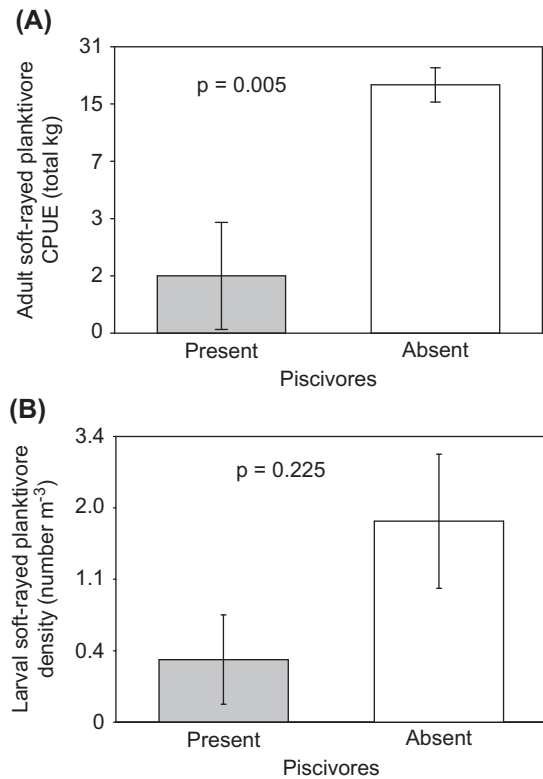


Figure 5. Geometric means of (A) adult soft-rayed planktivore biomass and (B) larval soft-rayed planktivore density in three lakes with piscivores and planktivores and five lakes with planktivores only ( $\pm 1$  SE).

and barbs relative to soft-rayed planktivores, making them less vulnerable to piscivory (Hambricht 1991, Nilsson and Brönmark 2000). Overall, the net result is a shift in species composition of the fish community, with soft-rayed planktivores the dominant fish in lakes without piscivores, while benthivores dominate lakes with piscivores, and total biomass of fish is higher in lakes with piscivores compared to lakes lacking piscivores. Predator-prey relationships among piscivores, benthivores, soft-rayed planktivores, and spiny-rayed planktivores suggests influences of piscivores on phytoplankton abundance in our study sites would be most pronounced in lakes with soft-rayed fish only. However, none of the lakes in this study had fish communities limited to piscivores and soft-rayed planktivores: benthivores were always found with piscivores, and only six lakes had piscivores, soft-rayed planktivores and benthivores present but not spiny-rayed planktivores.

Distributions of soft-rayed planktivores, spiny-rayed planktivores, benthivores and piscivores were highly variable among our study sites, likely due to predation effects as well as landscape and basin features that determine the probability of colonization and extinction (Magnuson et al. 1998, Hershey et al. 1999). Our previous work has shown that the positive relationship between occurrence of benthivores and piscivores in these systems is related to lake morphometry and surface connectivity (Herwig et al. 2010). Lakes supporting high biomass of piscivores must be sufficiently deep to maintain adequate dissolved oxygen levels in winter year after year, or be colonized on



an annual basis. These same features result in a high probability of benthivores being present, and benthivore biomass is high due to high winter oxygen levels and defenses against piscivores. In contrast, soft-rayed planktivore occurrence and biomass showed a negative relationship with piscivore biomass, likely due to predation effects. Interestingly, spiny-rayed planktivore presence and biomass showed little relation to piscivore biomass, and only a weak relationship with TP. Thus, the important factors driving their distribution and biomass are largely unknown in these systems.

Our results indicate piscivores shifted the community composition of potential prey fish in these systems, but failed to influence phytoplankton abundance. This result supports the idea that cascading effects of piscivores are dampened in more diverse fish communities that have prey species less vulnerable to piscivory (Hambright et al. 1991, Nowlin et al. 2006, Mehner 2010). Consequently, in diverse systems such as the ones we studied, influences of piscivores on phytoplankton abundance may be weaker than influences of nutrients, planktivores, and benthivores.

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