

Fish Influences on Amphibian Presence and Abundance in Prairie and Parkland Landscapes of Minnesota, USA

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ABSTRACT.—Many amphibian populations are declining, and increased understanding of the drivers of amphibian presence and abundance will help in their conservation. In 2005 and 2006 we estimated relative abundance of larvae of two common amphibian taxa, Tiger Salamanders (*Ambystoma tigrinum*) and ranid tadpoles (Northern Leopard Frog *Lithobates pipiens* and Wood Frog *Lithobates sylvaticus*), in 75 shallow lakes in prairie and parkland areas in Minnesota. We used a two-step procedure in which we first modeled presence-absence with data from all lakes and then modeled abundance only in lakes where the amphibian taxa were present. For the two amphibian taxa, a generalized linear mixed effects model was used to examine the effects of dynamic factors like fish abundance and static (timeframe of study) variables like fish community type, depth, and adjacent land cover. Fish variables had the greatest influence but differed for the presence and abundance models. Salamander and tadpole presence was inversely correlated to the abundance of benthivorous fish, while salamander abundance was best explained by total fish abundance and tadpole abundance by fish community type. We did not detect influences of land cover types on the amphibian taxa we surveyed. Our findings are important because they complement previous studies documenting that negative correlations with fish extend beyond piscivores to include both planktivores and benthivores. Hydrological changes in our study landscape (e.g., installation of drainage networks, wetland consolidation) associated with agriculture and other land uses have likely increased the distribution and abundance of fish populations, thus dampening amphibian breeding success.

Stocking of predatory fish is one of the best-documented, widespread, and important factors affecting amphibian populations and has been linked to amphibian declines in the western United States (Hayes and Jennings, 1986; Knapp and Matthews, 2000; Vredenburg, 2004; Welsh et al., 2006). More broadly, fish influence amphibian populations negatively through predation, competition, or both (Hayes and Jennings, 1986). Most studies have focused on fish presence-absence, taken a single species approach, or focused only on “predatory” fish species known to prey on amphibians (e.g., Sunfish and Bass [Centrarchidae], Perch [Percidae], Trout [Salmonidae], and Pike [Esocidae]) (Hecnar and M'Closkey, 1997). Very few amphibian studies have assessed influences of nonpredatory fishes (e.g., minnows and Carp [Cyprinidae], Bullheads [Ictaluridae]) or how the relative abundance of different fish guilds affects amphibian populations (but see Eaton et al., 2005; Shulze et al., 2010). Our study is unique in that we encountered a broad range of fish species and fish community types, allowing for informative contrasts that broaden our understanding of the effects of differing fish guilds on amphibians. Specifically, our study focuses on larval populations of two amphibian taxa, Tiger Salamanders (*Ambystoma tigrinum*) and ranid tadpoles (Northern Leopard Frog *Lithobates pipiens*, and Wood Frog *Lithobates sylvaticus*) and how the presence and abundance of these two taxa are affected by different biotic and abiotic environments.

Surrounding land use and land cover (LULC) factors have also been shown to influence amphibian patterns (Knutson et al., 2004), and the type of LULC factors and their spatial scales

of influence vary considerably among species and studies. Previous work has shown the extent of forests, grasslands, and agricultural lands to have strong influences on amphibians (e.g., Guerry and Hunter, 2002; Babbitt et al., 2009; and many others). Northern Leopard Frogs and Tiger Salamanders can be found in a variety of habitats, but both have a known affinity for grasslands (Petranka, 1998) and, in at least one study, Northern Leopard Frogs were shown to be negatively associated with forests (Guerry and Hunter, 2002). Effects of agriculture are generally thought to be negative (Semlitsch, 2000), yet the reported effects of agriculture on amphibians have been contradictory, showing both positive (Gray et al., 2004) and negative (Babbitt et al., 2009) relationships.

Amphibian species occurrence and richness are often best predicted at relatively large spatial scales ranging from 1,000 m (Porej et al., 2004) up to 3,000 m (Houlahan and Findlay, 2003); however, amphibian abundance is often best predicted at small spatial scales ranging from 100–400 m (e.g., around 200 m in Houlahan and Findlay, 2003) and is likely related to the vagility and typical dispersal and migration distances of a species (Semlitsch and Bodie, 2003). Northern Leopard Frogs are highly vagile, capable of movements up to 8 km (reviewed in Smith and Green, 2005), and LULC effects on population abundance have been documented out to 1,000 m (Pope et al., 2000). In contrast, Tiger Salamanders are much less vagile, with mean movement distances in published studies ranging from 60 to approximately 200 m (Semlitsch and Bodie, 2003) and with maximum movement distances of up to 600 m (reviewed in Smith and Green, 2005).

Isolation and habitat size are other important aspects when amphibian populations exhibit metapopulation structure (Bradford et al., 1993). Fragmentation of habitat patches needed to complete the life cycle (aquatic, terrestrial, or both) can increase mortality (Pope et al., 2000). Lehtinen et al. (1999) studied amphibian assemblages in agricultural and urban landscapes in Minnesota and found that amphibian species richness was

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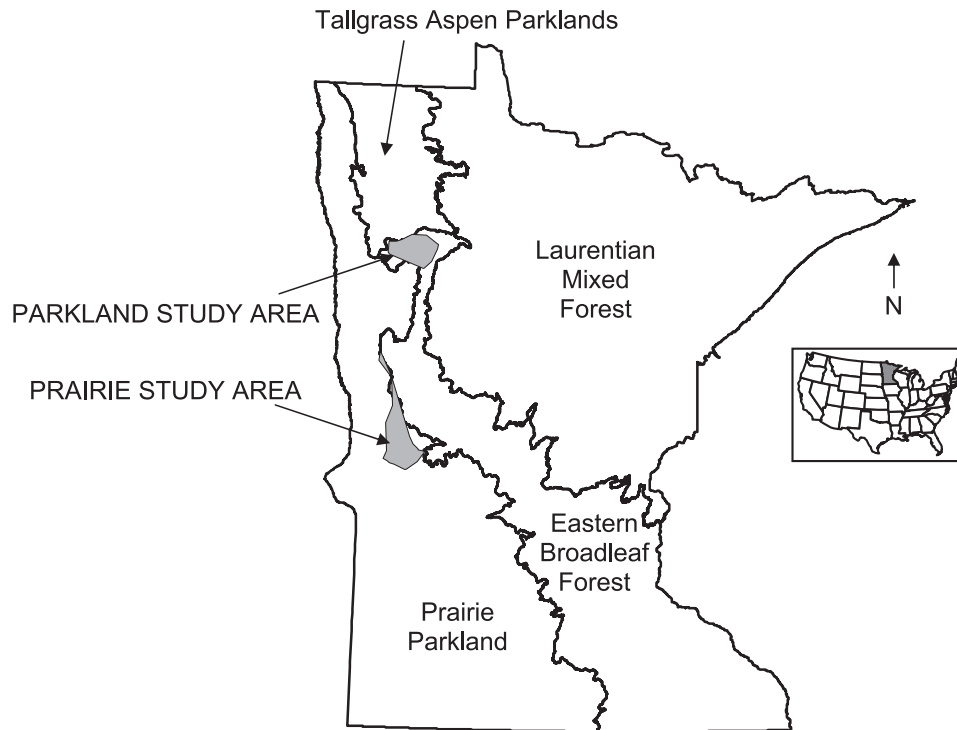


FIG. 1. Map showing the locations of our study areas relative to Minnesota's major ecoregions.

positively correlated with habitat connectivity; as road density and wetland isolation increased, amphibian species richness decreased. Similarly, spatial isolation from other wetlands has been shown to influence patterns of colonization in recently restored wetlands (Lehtinen and Galatowitsch, 2001; Zanini et al., 2009).

Our study evaluated factors influencing presence and abundance of Tiger Salamander larvae and ranid tadpoles (>99% were tadpoles of the Northern Leopard Frog and <1% were Wood Frog) in shallow Minnesota lakes in two consecutive years. We identified two classes of potential influences, those which fluctuated between years (dynamic factors, e.g., fish abundance) and others that remained constant during the time frame of our study (static factors, e.g., land use). We used a sequential model fitting procedure to control for influences of study year and region and to identify variables that best explained variability in amphibian presence and abundance. Our approach explicitly accounted for additional sources of data variability (repeated measures, separate influences of time-varying and static predictors), allowing us to identify meaningful data patterns of amphibian presence and abundance. We hypothesized that aspects of fish populations within lakes would be of primary importance in influencing the responses of our focal amphibian taxa. We evaluated a wide range of candidate lake (e.g., fish communities, fish abundance, total nitrogen, maximum depth) and landscape (e.g., LULC at two spatial scales, lake isolation) variables assessed in recent herpetological literature to identify important patterns and generate hypotheses for further exploration and study.

MATERIALS AND METHODS

Study Area and Study Sites.—Our study was conducted in 2005 and 2006 in the eastern part of the Prairie Pothole Region (PPR) of North America within two distinct ecological zones in northwestern Minnesota, United States. A southern study area with 39

sites was located within the prairie parkland zone (hereafter prairie); our northern area with 36 sites was in a prairie-forest transition zone (hereafter parkland) (Fig. 1). These zones reflect gradients in dominant cover types, geomorphic features, climate (N-S gradients in temperature and E-W gradients in precipitation), and vegetation patterns (Almendinger et al., 2000). Greatest differences in upland cover types between prairie and parkland study lakes were with agriculture and forested land (Table 1). Amount of grassland differed less than 1% between prairie and parkland study lakes at a 1,600-m scale but differed by 6% at the 200-m scale. The prairie and parkland study area encompassed approximately 1,292 km² and 1,435 km², respectively.

We studied 75 lakes selected by first identifying all Type 4 (deep marshes with semipermanent to permanent hydroperiods) and Type 5 (open water wetlands with permanent hydroperiods) wetlands (Stewart and Kantrud, 1971) in the two study areas using an existing National Wetlands Inventory GIS database based on imagery collected 1979–1988. These habitats have traditionally been considered wetlands (Cowardin et al., 1979) but, because our particular study sites are permanently flooded, they have no functional distinction from shallow lakes (*sensu* Scheffer, 2004). We imposed an additional size requirement that all lakes were 2–50 ha. The remaining population of candidate lakes was then stratified among 27 different bins (three levels for each of three factors) that were based on the following characteristics: 1) area of open water (small, medium, large; range 2 to 50 ha); 2) distance to nearest permanent stream, wetland, or lake (small, medium, large; range 0 to 1.8 km); and 3) proportion of agriculture within a 500-m buffer surrounding the lake (small, medium, large; range 0% to 97%). We then randomly selected study lakes from each of the resulting categories (for a total of 39 sites in the prairie and 36 sites in the parkland) until all categories were populated with a maximum of two study sites per category. Physical and

TABLE 1. Average characteristics (minimum-maximum) of lakes in the prairie and parkland study areas during 2005–2006. Surface area includes both open water and wetted zones of emergent aquatic vegetation surrounding study lakes. We used a *t*-test to compare whether variables were different among prairie and parkland lakes. * = significantly different at $\alpha = 0.05$ in both years. ** = significantly different at $\alpha = 0.05$ in 2005 only.

Characteristic	Prairie lakes	Parkland lakes
Maximum depth (m)*	1.8 (0.5–4.6)	2.7 (0.6–7.5)
Surface area (ha)	17.9 (2.3–47.7)	19.6 (3.6–93.1)
Total nitrogen ($\mu\text{g l}^{-1}$)*	2,936 (1,068–5,994)	1,312 (450–2,925)
% Agriculture – 200-m scale*	35.8 (0–77.3)	29.0 (0–73)
% Agriculture – 1,600-m scale*	56.5 (21.1–82.7)	40.3 (8.7–71.9)
% Forest – 200-m scale*	8.4 (0–41.3)	23.8 (0–70)
% Forest – 1,600-m scale*	4.8 (1.5–14.5)	15.7 (1.6–37)
% Grassland – 200-m scale	32.0 (1–69.9)	25.6 (0–78.8)
% Grassland – 1,600-m scale	15.4 (2.9–34.7)	14.8 (3.1–35.7)
Overall fish biomass per unit effort*	30.4 (0–214.3)	7.6 (0–48.5)
Benthivorous fish biomass per unit effort (kg)**	24.4 (0–170.8)	6.1 (0–41.7)
Piscivorous fish biomass per unit effort (kg)*	5.9 (0–66)	1.5 (0–29.7)
Distance to nearest type 4 or 5 wetland (m)	282.2 (15–2,885)	398.6 (45–7,338)

chemical characteristics of our selected study sites are summarized in Table 1.

Data Collection and Development of Predictor and Response Variables.—We sampled larval amphibians and fish concurrently in a single census survey conducted between 10–26 July each year at each lake using two sampling methods. Three mini-fyke nets (6.5-mm bar mesh with 4 hoops, 1 throat, 7.62-m lead, and a 0.69 m \times 0.99 m rectangular frame opening into the trap) were set overnight in the littoral zone of each lake. Additionally, one experimental gill net (61.0 m multifilament net with 19, 25, 32, 38, and 51-mm bar meshes) was set overnight in each lake, either along the deepest depth contour available in lakes less than 2 m deep or along a 2-m contour in lakes with sufficient depth. We counted the number of larval Tiger Salamander, and we combined the number of Northern Leopard Frog and Wood Frog tadpoles captured in three mini-fyke (trap) nets and one experimental gill net set in each lake. Data were summarized as the total number of individuals captured in each lake. Fish species composition and abundance was also determined from catches obtained in the gill and mini-fyke nets deployed overnight in each lake. Similar protocols have been shown to be effective in sampling fish assemblages in small lakes from other regions (Tonn and Magnuson, 1982; Rahel, 1984; Jackson and Harvey, 1989; Robinson and Tonn, 1989), and our protocol enabled us to capture fish of different sizes, species, and from all major trophic guilds (i.e., planktivores, benthivores, piscivores) in the study lakes. Fish data were summarized as the overall biomass catch per unit effort (CPUE) in the four nets for each guild and for all guilds combined (Table 1). Fish species were classified as planktivores, benthivores, or piscivores based on gut content analyses by Verant et al. (2007) for those fish species common to both studies; otherwise our assignments were based on the food habits reported by Simons et al. (2012). We listed the pool of fish species encountered, frequency of fish species sampled in lakes in the parkland and prairie study areas, and categorization of fish species based on dominant feeding characteristics (Table 2).

Lake maximum depth was determined by measuring depths at 6–24 stations spaced throughout the open water zone of each site, with the total number of stations dependent on the bottom morphology we observed. Total nitrogen was estimated each year from three water samples collected from the open water zone of each lake, placed on ice, frozen, and later analyzed using procedures described in APHA (1994) standards. We used the average total nitrogen value across the three samples for each lake. Nitrogen was used as our focal measure of water

quality because it has been shown to be important in regional studies of amphibians (Houlahan and Findlay, 2003; Knutson et al., 2004).

We assessed LULC influences on amphibians by selecting buffer spatial scales that best matched the approximate dispersal distances reported for Tiger Salamanders and Northern Leopard Frogs, 200 and 1,600 m, respectively. Cover-type polygons were hand-digitized into 13 categories based on land use maps (crop compliance photos) obtained from the U.S. Farm Service Agency and on interpretation of 2003 Farm Service Agency digital orthoquad air photos using heads-up digitizing procedures. We used three LULC categories for this analysis: 1) proportion of land used for agriculture (row-crops and hay); 2) proportion of existing forested lands; and 3) proportion of naturally occurring and managed grasslands. Agriculture consisted largely of corn, soybeans, and small grains but also included areas hayed on an annual basis. Dominant trees in forested areas of our parkland study area included sugar maple (*Acer saccharum*), basswood (*Tilia americana*), red oak (*Quercus rubra*), white oak (*Quercus alba*), quaking aspen (*Populus tremuloides*), North American balm of Gilead (*Populus balsamifera* \times *deltooides*), and bur oak (*Quercus macrocarpa*) whereas important trees in the prairie study area included cottonwood (*Populus deltoides*) and black willow (*Salix nigra*) around wetlands and box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*) and bur oak in upland areas. LULC proportions were calculated for each of the two spatial scales (Table 1).

Statistical Analyses.—Amphibian distributions tend to be patchy and temporally dynamic, which leads to abundance data with many zero observations and a strong right-skew that greatly limits the usefulness of many common statistical approaches (Fletcher et al., 2005; Martin et al., 2005). Further, our interests were not only in modeling abundance but also in factors that affect the presence of each species (Table 3). Therefore, we used an approach advocated by Fletcher et al. (2005) in which the ranid tadpole and Tiger Salamander larvae abundance data sets were each split into “presence” and “abundance when present” data sets and analyzed separately.

We started with a “base” generalized linear mixed model (GLMM; Bolker et al., 2009) in which region and year were treated as categorical fixed effects and lake was entered as a random effect to account for repeated measures correlations. To model species presence, we used a separate GLMM for each species consisting of a logistic link function and binomial error distribution:

TABLE 2. List of scientific and common names of fish sampled, the frequency sampled in the parkland ($N = 35$ sites) and prairie ($N = 37$ sites) study areas, and categorization based on dominant feeding characteristics.

Scientific name	Common name	Study area	No. of sites	Categorization
<i>Ameiurus melas</i>	Black Bullhead	parkland	22	Benthivore
		prairie	21	
<i>Ameiurus natalis</i>	Yellow Bullhead	parkland	0	Benthivore
		prairie	2	
<i>Ameiurus nebulosus</i>	Brown Bullhead	parkland	6	Benthivore
		prairie	2	
<i>Aplodinotus grunniens</i>	Freshwater Drum	parkland	0	Benthivore
		prairie	1	
<i>Catostomus commersoni</i>	White Sucker	parkland	10	Benthivore
		prairie	4	
<i>Culaea inconstans</i>	Brook Stickleback	parkland	26	Planktivore
		prairie	10	
<i>Cyprinus carpio</i>	Common Carp	parkland	0	Benthivore
		prairie	14	
<i>Esox lucius</i>	Northern Pike	parkland	6	Piscivore
		prairie	9	
<i>Etheostoma exile</i>	Iowa Darter	parkland	3	Planktivore
		prairie	0	
<i>Hybognathus hankinsoni</i>	Brassy Minnow	parkland	2	Planktivore
		prairie	0	
<i>Lepomis cyanellus</i>	Green Sunfish	parkland	4	Planktivore
		prairie	2	
<i>Lepomis gibbosus</i>	Pumpkinseed	parkland	5	Planktivore
		prairie	3	
<i>Lepomis macrochirus</i>	Bluegill	parkland	3	Planktivore
		prairie	7	
<i>Luxilus cornutus</i>	Common Shiner	parkland	0	Planktivore
		prairie	1	
<i>Micropterus salmoides</i>	Largemouth Bass	parkland	4	Piscivore
		prairie	5	
<i>Moxostoma macrolepidotum</i>	Shorthead Redhorse	parkland	0	Benthivore
		prairie	3	
<i>Notemigonus crysoleucas</i>	Golden Shiner	parkland	6	Planktivore
		prairie	4	
<i>Notropis heterolepis</i>	Blacknose Shiner	parkland	1	Planktivore
		prairie	0	
<i>Noturus gyrinus</i>	Tadpole Madtom	parkland	2	Benthivore
		prairie	1	
<i>Perca flavescens</i>	Yellow Perch	parkland	19	Planktivore
		prairie	8	
<i>Phoxinus eos</i>	Northern Redbelly Dace	parkland	21	Planktivore
		prairie	0	
<i>Pimephales promelas</i>	Fathead Minnow	parkland	29	Planktivore
		prairie	31	
<i>Pomoxis nigromaculatus</i>	Black Crappie	parkland	1	Planktivore
		prairie	7	
<i>Sander vitreus</i>	Walleye	parkland	0	Piscivore
		prairie	9	
<i>Umbra limi</i>	Central Mudminnow	parkland	25	Planktivore
		prairie	4	

$$\log_e [p_{i,j,k}/(1 - p_{i,j,k})] = \beta_{P,0} + \theta_{P,j} + \gamma_{P,k} + b_{P,0,i},$$

where $p_{i,j,k}$ is the probability the species is present in lake i in region j in year k , $\beta_{P,0}$ is the intercept parameter, $\theta_{P,j}$ is the region effect for $j = [\text{prairie}, \text{parkland}]$, $\gamma_{P,k}$ is the year effect for $k = [2005, 2006]$, and $b_{P,0,i}$ is a random lake effect for $i = [1, \dots, 72]$ assumed to be distributed Normal $(0, \sigma_P^2)$. To model abundance when present, nonzero abundance observations were \log_{10} transformed for each species and analyzed separately with a GLMM using an identity link function and a Gaussian error distribution:

$$\log_{10} [\text{Abundance}_{i,j,k}] = \beta_{A,0} + \theta_{A,j} + \gamma_{A,k} + b_{A,0,i} + \varepsilon_{i,j,k},$$

where the model parameters are defined as above though they are denoted with an 'A' subscript because they are uniquely estimated in the presence and abundance models; the $\varepsilon_{i,j,k}$ represents the residual error for the observation in the i^{th} lake in

region j in year k and is assumed to be distributed Normal $(0, \sigma^2)$. For each of the four analyses (presence and abundance were modeled separately for each of the two taxa), models calculated region by year averages and predictions of the differences among individual lakes (i.e., realizations of the $b_{P,0,i}$ and $b_{A,0,i}$ lake effects) along with an estimate of the among-lake variability (i.e., the σ_P^2 and σ_A^2 variance parameters).

We then tested whether including dynamic factors (i.e., those variables that changed from year to year) would improve the fit of the models as measured by Bayesian information criterion (BIC) scores (Schwarz, 1978). The BIC has been suggested for model selection when, as in our case, the goal is to find an adequate descriptive model (Taper, 2004). Benthivore CPUE, piscivore CPUE, and total fish CPUE were each added singly as a fixed effect explanatory variable to the initial GLMM, and the BIC score was calculated for each model. A lower BIC score

TABLE 3. Description of covariates analyzed, reference coding used for categorical variables (in parentheses) and statistical transformations applied to continuous variables (log₁₀ or arcsin √).

Variable	Type	Description
FISHCOMM ^a	Categorical	4 levels: fishless sites (1); planktivorous fish only sites (2); sites with benthivorous and planktivorous fish (3); sites with piscivorous, benthivorous, and planktivorous fish (4)
FISHABUN ^a	Continuous	Log ₁₀ overall fish biomass per unit effort (CPUE)
BENTH	Continuous	Log ₁₀ benthivorous fish CPUE
PISC	Continuous	Log ₁₀ piscivorous fish CPUE
ZMAX	Continuous	Log ₁₀ maximum wetland depth (m)
TN	Continuous	Log ₁₀ total nitrogen concentration (ppb)
AGR200	Continuous	Arccsin √ proportion of agriculture in a 200-m buffer
AGR1600	Continuous	Arccsin √ proportion of agriculture in a 1,600-m buffer
GRA200	Continuous	Arccsin √ proportion of grassland in a 200-m buffer
GRA1600	Continuous	Arccsin √ proportion of grassland in a 1,600-m buffer
FOR200	Continuous	Arccsin √ proportion of forested land in a 200-m buffer
FOR1600	Continuous	Arccsin √ proportion of forested land in a 1,600-m buffer
DNW	Continuous	Log ₁₀ distance to nearest type 4 or 5 wetland
REGION	Categorical	2 levels: prairie (1) and parkland (2)
YEAR	Categorical	2 levels: 2005 (1) and 2006 (2)

^a FISHCOMM = fish community type; FISHABUN = fish abundance.

indicates relatively better fit to the data, and the difference of BIC scores between models (denoted as ΔBIC) gives a measure of the strength of evidence in the data for one model over the other. A ΔBIC value of 2 or less implies the models have essentially the same level of support from the data, while a ΔBIC of greater than 6 implies strong evidence in support of the model with the lower BIC score (Raftery, 1995). If two models had similar support (i.e., ΔBIC < 2), added variable plots (Kutner et al., 2005) were used to visually evaluate the effect of additional explanatory variables on model fit and to determine which model to use for further analyses.

For the best model in each analysis, we then examined the relationships between the predicted lake effects (i.e., the $b_{P,0,i}$ and $b_{A,0,i}$ quantities) and the static variables (i.e., those that varied from lake to lake but did not change appreciably from year to year for a given lake). These lake effects are predictions of how each individual lake differed from the “average” lake during the study and, as such, are useful for investigating relationships between amphibian populations and larger-scale variables that differ among the lakes. Lowess smoothers (Venables and Ripley, 2002) and linear regression models were used to examine the relationships between the best linear unbiased predictors (BLUPs) of the $b_{P,0,i}$ and $b_{A,0,i}$ lake effects and the following variables: average total nitrogen level, maximum depth, distance to nearest Type 4 or 5 wetland, percent agriculture, percent grassland, and percent forest (the percent land cover variables were examined at both 200-m and 1,600-m scales). A one-way ANOVA model was used to examine the relationship between lake effects and fish community type; if significant, the ANOVA model was followed up with a Tukey honestly significant differences multiple comparison test (Kutner et al., 2005) to detect pairwise differences in lake effects between fish community types. All analyses were

TABLE 4. Presence patterns of larval Tiger Salamanders and ranid tadpoles in prairie and parkland study sites. Data are number of sites with taxa present/total number of sites (prairie, parkland).

Year	Tiger Salamander larvae	Ranid tadpoles	Both taxa
2005	(17/37, 12/36)	(12/37, 12/36)	(11/37, 9/36)
2006	(15/39, 6/35)	(11/39, 10/35)	(10/39, 4/35)
Both	(12/37, 6/35)	(7/37, 9/35)	(6/37, 4/35)

performed with version 2.12.0 of the statistical program R (R Development Core Team, 2012); the GLMM models were fit using the lmer function from the lme4 package (Bates and Maechler, 2012).

RESULTS

Overall Distributional Characteristics.—In 2005, larval Tiger Salamanders were present in 17 (46%) prairie and 12 (33%) parkland lakes (Table 4). In 2006, 15 (38%) prairie lakes contained salamanders compared to just 6 (17%) lakes in parkland. Ranid tadpoles were present in a similar number of lakes between years. Tadpoles were present in 12 (32%) and 11 (28%) prairie lakes in 2005 and 2006, respectively. In the parkland, tadpole populations were present in 12 (33%) and 10 (29%) lakes in the two study years. The percentage of sites with both taxa present was higher in the prairie than in the parkland in both 2005 and 2006 (Table 4). Tiger Salamander larvae were present in consecutive years in a greater percentage of prairie versus parkland sites, but differences were more subtle for ranid

TABLE 5. Bayesian information criterion scores for models of presence-absence (P-A) and abundance when present (Abun|P) for Tiger Salamander larvae (TSL) and ranid tadpoles (TDPL). The base model contains year and region as fixed effects and lake as a random effect. Benth = benthivore CPUE, Pisc = piscivore CPUE, and FishAbun = total fish CPUE.

Model	Factors	BIC	ΔBIC
TSL P-A	Base	204.1	47.5
	Base + Benth	156.6	0
	Base + Pisc	172.4	15.8
	Base + FishAbun	161.3	4.7
TSL Abun P	Base	93.2	10.9
	Base + Benth	91.8	9.5
	Base + Pisc	96.3	14
	Base + FishAbun	82.3	0
TDPL P-A	Base	205.3	36.5
	Base + Benth	168.8	0
	Base + Pisc	188.1	19.3
	Base + FishAbun	173.7	4.9
TDPL Abun P	Base	106.5	1.6
	Base + Benth	104.9	0
	Base + Pisc	109.8	4.9
	Base + FishAbun	108.5	3.6

TABLE 6. Parameter estimates for chosen models of larval Tiger Salamander presence-absence (P-A) and \log_{10} abundance when present (Abun|P).

Model	Parameter	Estimate	SE	P
P-A	Intercept	6.23	1.68	0.0002
	Region: parkland	-5.39	1.70	0.002
	Year: 2006	-2.72	1.02	0.008
	Benthivore abundance	-7.51	1.87	<0.0001
Abun P	Intercept	1.83	0.15	<0.0001
	Region: parkland	-0.36	0.13	0.01
	Year: 2006	0.13	0.13	0.33
	Fish abundance	-0.51	0.12	0.0001

tadpoles. Percentage of sites with both taxa present in both years was low and was observed in only 11–16% of sites.

Presence and Abundance Patterns of Tiger Salamander Larvae.—The best model of Tiger Salamander larvae presence included region, year, and benthivorous fish CPUE as explanatory variables (Table 5). Tiger Salamander larvae were present more often in the prairie lakes and more often in 2005 than in 2006, and benthivore CPUE had a dramatic negative influence on presence patterns (Table 6). Predicted probability of Tiger Salamander larvae presence with no benthivores was 1.0 and 0.97 in the prairie in 2005 and 2006 but was just 0.13 and 0.01 at median benthivore CPUE (Fig. 2A). Similarly in the parkland, probability of presence with no benthivores was 0.69 and 0.13 in the two study years but was essentially zero (<0.001) at median benthivore CPUE. Examining relationships among predicted lake effects (i.e., the BLUPs of the $b_{P0,i}$ quantities) from the best model and static variables revealed a significant relationship for fish community type, and the Tukey multiple comparison test showed significantly lower probability of presence in planktivore-only communities ($P = 0.007$ and 0.01 for comparison with planktivore-benthivore and planktivore-benthivore-piscivore communities, respectively). As noted above, the best model of presence contained benthivore abundance as an explanatory variable, so these lake effect comparisons indicate there may be

detrimental effects of planktivores on salamander presence when they are the sole guild present in a lake, but these effects may not be related to planktivore abundance in more-complex fish communities. There was a weak positive relationship between total nitrogen and presence for lakes in the parkland region ($R^2 = 0.14$, $P = 0.026$), and lowess smoothers indicated a linear pattern. Finally, we found a weak negative relationship between salamander larvae presence and maximum depth in the parkland ($R^2 = 0.13$, $P = 0.033$), and lowess smoothers indicated only minor nonlinearity.

The best model of larval Tiger Salamander abundance contained region, year, and overall fish CPUE as explanatory variables (Table 5). This model indicated strong region and year effects, and variability among predicted lake effects was practically zero (less than 1% of unexplained variance was attributed to lake effects). Tiger Salamander abundance was higher in the prairie and higher in 2006, and overall fish CPUE had a strong negative influence on abundance (Fig. 3A, Table 6). Tiger Salamander abundance decreased sharply as fish CPUE increased to 10 kg (Fig. 2B). Because the variance among predicted lake effects was so small, none of the static factors we tested were significantly related to the BLUPs of lake effects on Tiger Salamander abundance.

Presence and Abundance Patterns of Ranid Tadpoles.—The best model of ranid tadpole presence contained region, year, and benthivorous fish CPUE as explanatory variables (Table 5). The model indicated weak effects of region and year with a strong negative effect of benthivorous fish CPUE (Table 7). Predicted probability of ranid tadpoles being present in lakes with no benthivores was 1.0 and 0.89 in the prairie in 2005 and 2006 but was just 0.12 and 0.05 at median benthivore CPUE (Fig. 2C). Similarly, probability of presence in the parkland lakes with no benthivores was 0.86 and 0.82 in the two study years but was extremely low (probability <0.02) at median benthivore CPUE. Examining relationships among predicted lake effects (BLUPs) from the best model and among-lake variables revealed a weak negative relationship between presence and total nitrogen for the prairie lakes only ($R^2 = 0.11$, $P = 0.044$), though lowess

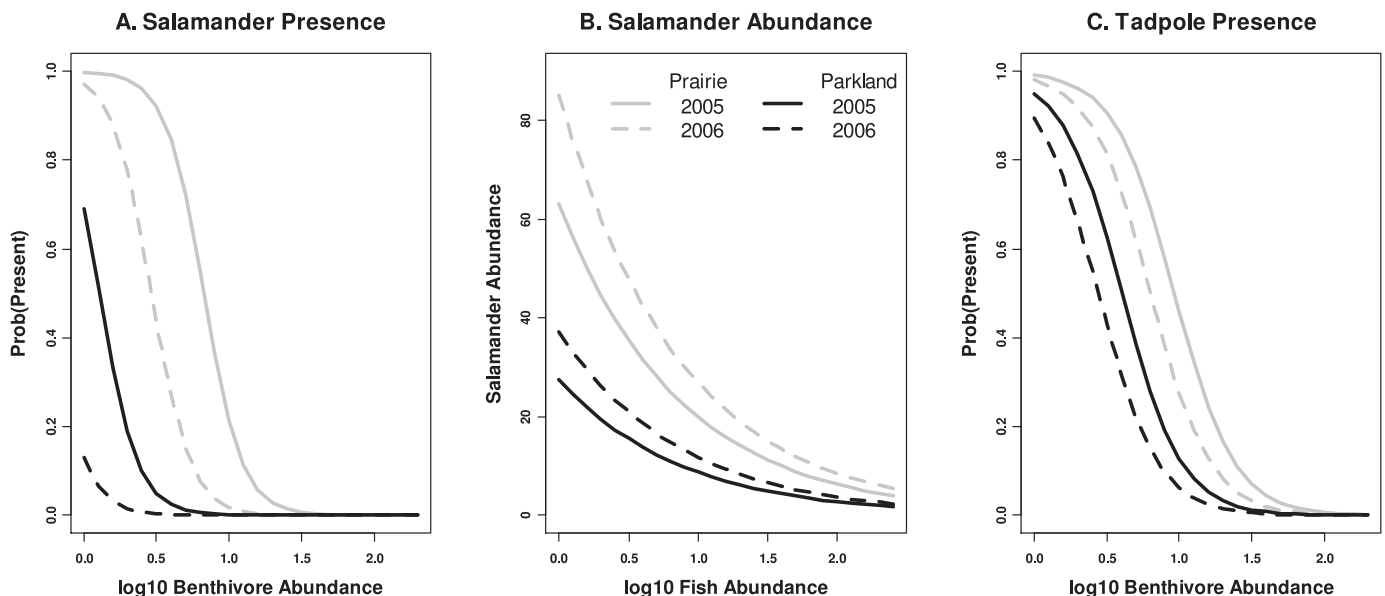


FIG. 2. Relationship between: (A) \log_{10} benthivorous fish CPUE and probability of larval Tiger Salamander presence in prairie and parkland shallow lakes in 2005 and 2006; (B) \log_{10} overall fish CPUE and larval Tiger Salamander abundance; and (C) \log_{10} benthivorous fish CPUE and probability of ranid tadpole presence.

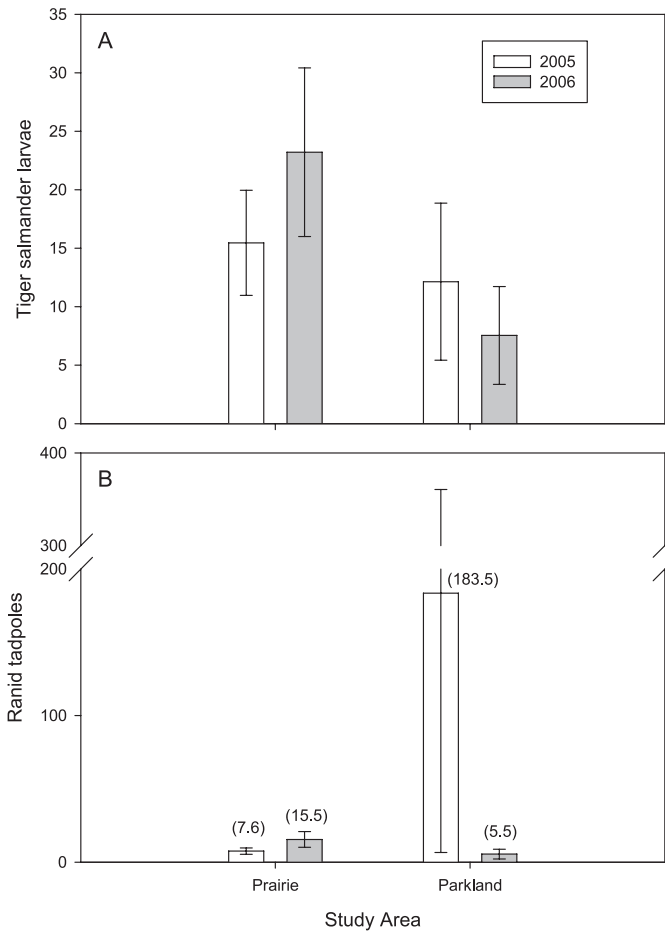


FIG. 3. Mean count \pm 1 SE of (A) larval Tiger Salamanders and (B) ranid tadpoles in prairie and parkland sites in 2005 (white bars) and 2006 (gray bars). Mean values for tadpole counts in parentheses.

smoothers indicated minor nonlinearity in the relationship. This analysis also revealed a weak positive influence of distance to nearest wetland on presence in the parkland only ($R^2 = 0.13$, $P = 0.029$), and lowess smoothers depict a relatively linear positive relationship.

Our analysis of ranid tadpole abundance when present indicated a strong region effect but weak year effects; tadpoles were about three times less abundant in the parkland than in the prairie lakes, this despite the extraordinarily high count from a single lake ($N = 6,374$ tadpoles) that inflated the parkland mean in 2005 (Fig. 3B, Table 7). Adding benthivore CPUE to the base model showed a negative effect of benthivores on tadpole abundance and produced the lowest BIC score, but this reduced BIC scores by only 1.6 (Table 5). After examination of an added-variable plot, we concluded that the improvement in model fit from adding benthivore CPUE to the base model was primarily driven by two outlier points, so we used the base model without benthivore CPUE for further analyses of lake effects. There was moderate variability among predicted lake effects (BLUPs) which was significantly related to fish community type ($P = 0.04$ for one-way ANOVA on 4 df and 25 df). Increasing fish community complexity was associated with lower tadpole abundance; however, the multiple comparison test showed that the only significant difference among fish communities was between fishless lakes and those with a planktivore-benthivore-piscivore community ($P = 0.02$).

TABLE 7. Parameter estimates for chosen models of ranid tadpole presence-absence (P-A) and \log_{10} abundance when present (Abun|P).

Model	Parameter	Estimate	SE	P
P-A	Intercept	1.69	0.85	0.05
	Region: parkland	-1.06	0.98	0.28
	Year: 2006	-0.76	0.61	0.21
	Benthivore abundance	-4.78	1.31	0.0003
Abun P	Intercept	1.46	0.17	<0.0001
	Region: parkland	-0.48	0.21	0.03
	Year: 2006	0.01	0.17	0.95

DISCUSSION

Within-lake factors were generally more important than were surrounding landscape characteristics in influencing amphibian breeding success (presence and abundance) in two Minnesota landscapes dominated by agriculture. In our evaluation of static (including land use, fish community type, and isolation) and dynamic (fish abundance) factors, abundance of benthivorous (bottom-feeding) fish exhibited the most consistent and strongest influences on presence of our amphibian taxa. Negative relationships between fish and amphibian populations are well established in the literature (Bradford, 1989; Hecnar and M'Closkey, 1997; Semlitsch, 2000; Knutson et al., 2004; Werner et al., 2007; Pope, 2008). However, most of these studies focus primarily on influences of large predatory fish (Bass [Centrarchidae], Pike [Esocidae], Trout [Salmonidae] and Sunfish [Centrarchidae]), while a very limited number of studies have assessed influences of planktivorous fish (minnows [Cyprinidae], Yellow Perch *Perca flavescens*) (Zimmer et al., 2002; Eaton et al., 2005). Thus, the strong negative influences of benthivorous fish observed in this study are not well documented in the literature. Moreover, our results show a relationship between abundance of tadpoles and fish guilds present, whereas previous studies have focused on relationships between Leopard Frog occurrence and broad categorizations of fish, e.g., "predatory" fish (Hecnar and M'Closkey, 1997). Our study also explored density-dependent relationships between fish and amphibians, which is an aspect of amphibian ecology that has been rarely assessed in previous studies (but see Welsh et al., 2006; Shulse et al., 2010).

For Tiger Salamanders we observed decreasing abundance with increasing overall fish abundance. Tiger Salamanders (and salamanders generally) are sensitive to predation by fishes, and our data support other studies indicating that fish reduce salamander populations (Petranka 1983; Semlitsch, 1988; Zimmer et al., 2002; Shulse et al., 2010). Decreased abundance of amphibians, with increasing fish abundance or fish community complexity, could arise from avoidance of wetlands with fish (Resetarits and Wilbur, 1991), competition for shared invertebrate resources (Deutschman and Peterka, 1988; Joseph et al., 2010), or direct predation on eggs or larvae (Bradford, 1989; Hecnar and M'Closkey, 1997; Vredenburg, 2004). More study is needed to clarify possible roles of avoidance, competition, and predation. Our results provide some support for the avoidance hypothesis (i.e., lower probability of occurrence as benthivore abundance increases), but there also appears to be a density-dependent relationship, especially for Tiger Salamanders. We did not assess mechanisms in our study, but it is plausible that benthivorous fish feeding along bottom substrates of lakes could negatively affect young amphibian larvae occurring in these habitats. Direct predation, competition for food, alteration of either localized (disruption of oxygen microlayers and sediment deposition on eggs and young larvae) or general

habitat conditions (system-wide turbidity) could all be limiting the survival of larvae.

Region and year were also important sources of variability in our data set. Recruitment patterns in many amphibian populations are temporally variable due to brief periods of synchronous breeding, absence of breeding, or use of different breeding habitats (Pechmann et al., 1991; Hecnar and M'Closkey, 1996), any of which may be responsible for fluctuations in occurrence of Tiger Salamander larvae in breeding ponds between years. We observed that both Tiger Salamanders and tadpoles were generally more abundant in our prairie lakes than in parkland sites. The number of lakes with Tiger Salamanders present was higher in 2005, though the abundance of Tiger Salamanders where present was lower in 2005 than 2006. These findings highlight the temporal and spatial dynamics of amphibian populations, which are evident when larger regional scales were taken into consideration and when sites were sampled in subsequent years (Pechmann et al., 1991; Hecnar and M'Closkey, 1996).

We did not detect influences of LULC patterns on amphibians in our study. This contrasts with the findings of many other studies (Guerry and Hunter, 2002; Houlahan and Findlay, 2003; Knutson et al., 2004; Babbitt et al., 2009). Both Northern Leopard Frogs and Tiger Salamanders are known grassland associates (Harding, 1997; Knutson et al., 2004), yet we were unable to detect a grassland association for either species. Interestingly, the amount of grassland within 200 m, the typical migration distance for Tiger Salamanders (Semlitsch and Bodie, 2003), and within 1,600 m, bounding typical migration distances for Northern Leopard Frogs (Pope et al., 2000), differed little between study areas and were more extensive than we expected, averaging 29% at the 200-m scale and 15% at 1,600 m. We speculate that perhaps the grassland extent, and habitat matrix in general, may be meeting minimum habitat requirements and thus is not a limiting factor. Moreover, Tiger Salamanders and Leopard Frogs have been shown to thrive in agricultural areas if suitable breeding habitat exists (Koloszvary and Swihart, 1999; Knutson et al., 2004). The strongest influences of agriculture on amphibians in our study sites may be indirect, occurring through ditching and consolidation of wetlands, thus favoring deep and interconnected wetlands and lakes that promote the establishment of fish populations in shallow Minnesota lakes (Herwig et al., 2010). Herwig et al. (2010) showed that fish populations and complex fish communities were more likely to be present in deeper lakes and when upstream and downstream connections to other permanent wetlands, lakes, or rivers were present. Semlitsch (2000) suggested that practices that promote fish colonization (stocking, hydrologic alterations, or increased connectivity) induce habitat fragmentation for many amphibian populations, and we believe a similar situation exists in the PPR of Minnesota, United States. Here, fishes are widely distributed in permanent shallow lakes (just one and four sites were fishless in the parkland and prairie, respectively), and the distance to nearest permanent wetland is relatively great (median: 411 m, average: 718 m). Even if a breeding adult were to immigrate successfully to a new and seemingly suitable permanent wetland, it is likely to contain fish—and evidence presented here and elsewhere suggests that amphibian recruitment will suffer. Fortunately, considerable numbers of temporary to semipermanent wetlands (which we did not assess) still exist in some regional landscapes, many of which are likely to be fishless. These habitats constitute important breeding and foraging habitats for amphibians and likely serve as stepping stones during dispersal and migration;

thus, they should be incorporated into future studies and conservation planning efforts.

Our data indicate that the influences of fish extend beyond piscivorous fish (large-gaped fish capable of eating fish and amphibians) to include planktivorous (small-bodied fish such as minnows) and benthivorous fish (bottom-feeding fish such as White Sucker, Black Bullhead, and Common Carp), the latter of which were particularly important in influencing amphibian presence in our study lakes. Given that fishless habitats are rare in our study landscape and that benthivorous fish populations are widespread (Herwig et al., 2010), we suggest that amphibian conservation efforts emphasize maintaining existing fishless habitats, limiting future fish colonization by establishing or maintaining fish barriers, and eliminating fish populations when practical. Biomanipulation using piscivorous fish is another important management tool that can be used to improve lake ecological features (Potthoff et al., 2008), but stocking of piscivorous fish into previously fishless basins should be strongly discouraged. Nine of our study sites received sanctioned stocking of Walleye, *Sander vitreus*, but all contained antecedent fish populations. Policy makers should pay careful attention to fish stocking practices and should consider the indirect impacts of agricultural drainage, ditching, and wetland consolidation practices for native amphibian populations.

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