WETLANDS

Journal of the Society of Wetland Scientists

VOLUME 30   NUMBER 3   JUNE 2010   (ISSN 0277-5212)

SWS

Competition and Facilitation in Three Marsh Plants in Response to a Water-Level Gradient

Historical Ecology as a Tool for Assessing Landscape Change and Informing Wetland Restoration Priorities

Springer

ORIGINAL PAPER

Factors Influencing Fish Distributions in Shallow Lakes in Prairie and Prairie-Parkland Regions of Minnesota, USA

Brian R. Herwig · Kyle D. Zimmer · Mark A. Hanson · Melissa L. Konsti · Jerry A. Younk · Robert W. Wright · Sean R. Vaughn · Mitchell D. Haustein

Abstract Fish exert strong influences on shallow lakes, but managers lack empirical models useful for predicting fish distributions at landscape scales. We used classification and regression tree analysis (CART), and regression to predict fish presence/absence (P/A), richness, and community composition in 82 shallow lakes distributed among two regions (prairie and prairie-parkland) along the eastern margin of the Prairie Pothole Region in western Minnesota, U.S.A. A CART model for fish P/A using downstream connections to fish sources and maximum depth correctly classified ≥92% of our study sites, indicating the rare fishless sites observed in our study were either isolated or shallow. Fish richness was positively related to both lake and watershed size. Given that many fish species have strong negative influences on shallow lake ecological characteristics, we conclude that future conservation efforts should focus on protecting shallow, isolated basins, or reducing surface connectivity among basins as these factors were decisive in promoting fish populations. Such management strategies should help to maintain current levels of fish richness and enhance richness of aquatic birds, amphibians, plants, and invertebrates.

Keywords Cart · Connectivity · Fish communities · Isolation

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Introduction

Fish community structure in lakes reflects a dynamic interplay of isolation and extinction (Magnuson et al. 1998), habitat complexity (Tonn and Magnuson 1982), regional species pools (Jackson and Harvey 1989; Griffiths 1997; Irz et al. 2004; Mehner et al. 2007), stocking (Radomski and Goeman 1995), productivity (Persson et al. 1992; Jeppesen et al. 1997, 2000; Mehner et al. 2005), and presence of piscivores (Tonn and Magnuson 1982; Rahel 1984). Extinction factors include features of the lake itself, such as surface area, habitat heterogeneity, depth, winter hypoxia, pH, watershed position, and water chemistry (Tonn and Magnuson 1982; Rahel 1984; Marshall and Ryan 1987; Robinson and Tonn 1989; Magnuson et al. 1998; Mehner et al. 2005). Isolation features reflect lake proximity to, and

extent of connectivity among, surface waters containing source fish populations (Tonn and Magnuson 1982; Magnuson et al. 1998; Hershey et al. 1999; Spens et al. 2007). Fish assemblages in lakes also reflect regional and geographic patterns of fish distributions when larger spatial scales are considered (Jackson and Harvey 1989; Irz et al. 2004; Mehner et al. 2007). Obviously, in a broad sense, fish assemblages reflect numerous influences that vary greatly among lakes and geographic regions, due to natural gradients, anthropogenic disturbance, and climate fluctuation. This means that dominant constraints on fish presence and community characteristics in a given lake or region may be far less influential elsewhere.

Factors influencing fish community patterns in deeper lakes have received vastly more study than for shallow lakes and permanent wetlands. The limited work done in northern prairie wetlands and shallow lakes of central North America suggests that winter hypoxia and occasional drying are the most important factors influencing fish distributions (Peterka 1989). Isolation and extinction, and geomorphic setting probably also influence fish presence and community structure in shallow lakes, but the relative importance of these factors in the Prairie Pothole Region (PPR) of North America is unknown. Compared to larger, deeper lakes, PPR lakes are more productive, smaller, and shallower, thus fish populations are more susceptible to winterkill (extinction). These lakes are also extremely prone to fish colonization events (less insular than deep lakes) because landscape relief is low, anthropogenic connectivity (drainage, ditching) is extensive, and extreme precipitation dynamics are typical (Hanson et al. 2005). Collectively, these processes may be so dynamic that extinction and colonization rates may never reach equilibrium (*sensu* MacArthur and Wilson 1967), thus predictive models of fish occurrence and community structure developed elsewhere may not be useful here.

Shallow lake food webs often differ dramatically in response to density and community structure of associated fish populations. Planktivorous fish (categorized as small-bodied plankti-benthivorous fish in our study) are thought to reduce water transparency via predation on zooplankton, favoring shifts towards increased turbidity and loss of submerged vegetation (Scheffer et al. 1993; Scheffer 2004). Common carp *Cyprinus carpio* and black bullhead *Ameiurus melas* (categorized as large-bodied plankti-benthivorous fish in our study) have strong influences on shallow lake phytoplankton, macrophytes and invertebrates through feeding, sediment suspension, and nutrient excretion (Lougheed et al. 1998; Braig and Johnson 2003; Parkos et al. 2003; Miller and Crowl 2006; Roozen et al. 2007). In a recent study of Minnesota shallow lakes, changes in abundance of small- and large-bodied plankti-benthivorous fish were associated with shifts between clear and turbid regimes,

further highlighting the ecological influences of these fishes (Zimmer et al. 2009). Understanding factors influencing fish distributions and communities in shallow lakes is important for management of individual lakes and for maintenance of regional-scale biodiversity because plankti-benthivorous fish can exert dramatic negative influences on abundance of aquatic macrophytes and species richness of aquatic birds, plants, amphibians, and invertebrates (Scheffer et al. 2006).

We used classification tree methods (Breiman et al. 1984) to assess whether landscape and basin features could be used to predict presence/absence of fish and types of fish communities present in shallow lakes of the eastern PPR. We hypothesized that isolation is relatively more important in structuring fish communities in these systems compared to results for deeper temperate lakes. Also, we predicted that fish populations would be present in shallow lake sites where map- and aerial photograph-based surface water connections to source fish populations were identified (e.g., Spens et al. 2007).

Methods

Study Area and Study Sites

Our study was conducted in the eastern part of the PPR of North America, within two distinct ecological zones in western Minnesota, U.S.A. One study area was located within the prairie and the other within the prairie-parkland transition (hereafter parkland) (Fig. 1). These zones reflect gradients in dominant cover types, geomorphic features, climate, and vegetation patterns (Almendinger et al. 2000). Our study landscapes were also positioned in different major river drainages. Prairie and parkland study areas encompass approximately 1,292 km^2 and 1,435 km^2 respectively.

We used a total of 82 shallow lakes (47 prairie, 35 parkland) from two data sets for our analysis. Our main group of shallow lakes consisted of 74 lakes sampled during July 2006. These sites were selected by first identifying all Type 4 and 5 wetlands (sensu Stewart and Kantrud 1971) 2–50 ha in surface area within each study area using a National Wetlands Inventory GIS dataset. 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). The population of candidate shallow lakes for each study area was then stratified and sites were randomly selected based on lake size (open water only) (small, medium, large, overall range 2–50 ha), distance to nearest permanent stream, wetland, or lake (short, medium, long, overall range 0 to 1.8 km), and proportion agriculture within a 500 m buffer surrounding the lake (low, medium,

Fig. 1 Location of the prairie and parkland study areas relative to the three major ecological zones found within Minnesota, USA
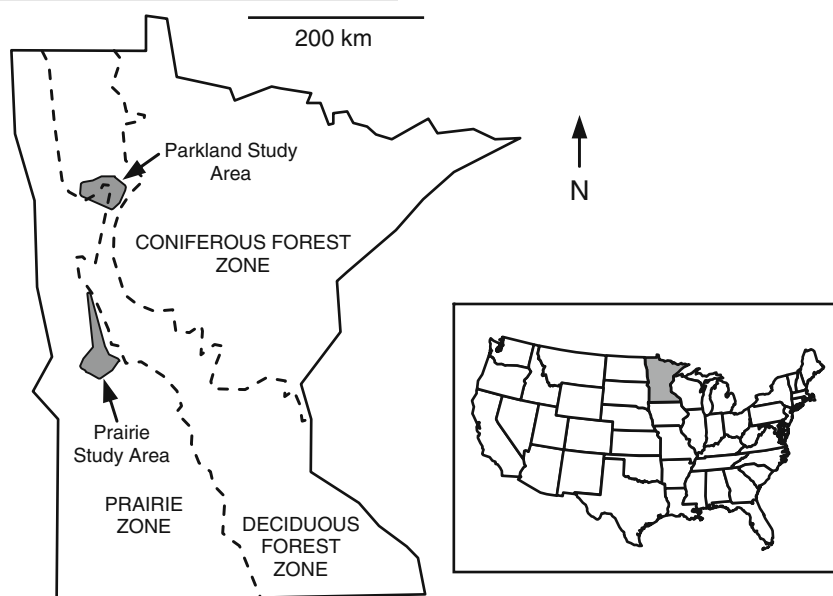
high, overall range 0 to 97%). Because few study sites selected during this process were fishless, we also used a second data set of eight fishless lakes sampled in 1998. These sites were sampled regularly during 1996–2001, and then sporadically during 2002–2004, but remained fishless at all times, thus we assume recursive processes caused these sites to remain fishless, thus should be distinguishable using current analyses.

Study sites ranged in surface area (including fringe of emergent vegetation not considered during site selection and including fishless sites) from 4–93 ha in the parkland (mean=19.6 ha) and from 2–48 ha in the prairie (mean= 15.6 ha). Maximum depths ranged from 0.6–7.5 m in the parkland (mean=2.7 m) and from 0.5–4.6 m in the prairie (mean=1.8 m).

Data Collection

Fish species composition was determined from July surveys using two sampling gears deployed overnight. Three mini-fyke nets (6.5 mm bar mesh with 4 hoops, 1 throat, 7.62 m lead, and a 0.69 m by 0.99 m rectangular frame opening into the trap) were set overnight in the littoral zone of each lake. One experimental gill net (61.0 m multifilament net with 19, 25, 32, 38, and 51-mm bar meshes) was set along the deepest depth contour in lakes <2 m deep or along a 2 m contour in sites with sufficient depth. 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 enabled us to capture fish of different sizes, species, and from all major trophic guilds in the study lakes. Fish data were summarized as the total biomass of each species collected in all four nets.

Lake surface area was estimated using digital aerial photographs and GIS software (ArcView 3.3 and ArcGIS 9.2, Environmental Systems Research Institute Inc. 2007), and included both open water and emergent vegetation portions of each lake. Lake maximum depth was determined by measuring depths along parallel transects spaced throughout the open water zone of each site.

We defined lake watersheds as all land and water areas draining surface water into our study sites. Lake watershed areas (hereafter LWAs) were manually delineated as part of MNDNR's statewide Lake Watershed Project (Minnesota Department of Natural Resources 2009). All watershed delineations were reviewed and edited manually in accordance with data sources and additional site-level field knowledge (e.g., presence of culverts identified during field visits, etc.). LWAs of study sites ranged from 2 to 74,003 ha, with a median of 116 ha.

As a final step, flow network lines depicting concentrated water flow across landscapes were created using ArcGIS Spatial Analyst. The flow network is a vector version of the 30-meter flow accumulation grid (raster) built from a specified threshold of contributing grid cells. The flow accumulation grid was built from the hydrologically-corrected digital elevation model created by software that incorporated the DNR 24K Streams and Rivers data set during the interpolation process. Resulting flow networks are synthetic representations of routes followed by concentrated water flow across the landscape. The flow network illustrates flow directionality, and can be used as a tool to help identify inter-basin surface water connections. We used flow network lines, existing stream and river GIS layers, digital color air photos, field knowledge about culverts and fish barriers, and watershed boundaries to identify surface water connections to upstream and downstream fish sources (i.e., Type 4 and 5 wetlands,

lakes, and rivers capable of supporting fish) for each study site. In most cases, surface water connections were directly corroborated in the field. We then classified the surface water connectivity features of each site into one of five categories: a) isolated (no surface water connection), b) seasonal wetland (Type 1–3 wetland) only, c) semi-permanent or permanent wetland (Type 4 or 5 wetland), d) lake, or e) river. Finally, we used ArcGIS to measure shortest distances via surface water connections to nearest upstream or downstream habitats capable of supporting fish (c, d, or e above). In the event of isolated, closed basins, we estimated the nearest distance under assumed extreme high water conditions.

Statistical Analyses

We used negative binomial regression to assess fish species richness relationships with lake size and lake watershed size because it explicitly accounted for the positive integer-valued aspect of responses and provides good fit to the over-dispersed data. We also applied classification and regression trees (CART) (Breiman et al. 1984; De'ath and Fabricius 2000) to construct predictive models for presence of fish in our study sites using JMP® 7.0 Software (SAS Institute 2007). CART analysis is the recursive partitioning of a data set into increasingly homogenous subsets, with the end product being a "tree-like" predictive model. We used the following independent variables to construct a classification tree for fish presence/absence: 1) surface water connection to a upstream fish source (UFS), i.e., upstream Type 4 or 5 wetland, lake, or river, 2) surface water connection to a downstream fish source (DFS), i.e., downstream Type 4 or 5 wetland, lake, or river, 3) distance to the nearest upstream or downstream habitat capable of supporting fish (DNFH), 4) lake surface area (LSIZE), 5) lake maximum depth (ZMAX), and 6) lake watershed area (LWA). We also used CART and the same predictor variables to develop a model for fish community type, a categorical response with four levels (fishless sites, sites with small-bodied plankti-benthivorous fish (primarily soft-rayed minnows) only, sites with small-bodied and large-bodied plankti-benthivorous fish (larger fishes, some having defensive spines) present, and sites with small- and large-bodied plankti-benthivorous, and piscivorous fish present). Sites from both study areas were combined in these analyses.

We developed both CART models by first splitting our data into learning and validation sets, with 30% of our sites retained for validation. Unique validation sets were used in each analysis. We determined optimum tree size and minimized overfitting in the learning set by overbuilding the trees, and then pruning back until k-folded cross-validation errors (k=25) began to plateau or there was no remaining residual error (Breiman et al. 1984). We

subsequently tested the generality of models by predicting fish presence in lakes from the validation set.

Results

Twenty-five different species of fish were sampled across 74 sites in 2006, with 22 species present in more than one lake (Table 1). Commonly occurring small-bodied plankti-benthivorous species included fathead minnow *Pimephales promelas* (83% of all sites), brook stickleback *Culaea inconstans* (50%), central mudminnow *Umbra limi* (40%), and northern redbelly dace *Phoxinus eos* (29%). The latter three species occurred more commonly, or exclusively, in the parkland study area. Important large-bodied plankti-benthivorous species included black bullhead (60% of all sites), yellow perch *Perca flavescens* (38%), white sucker *Catostomus commersoni* (19%), and common carp (6%), while dominant piscivores included northern pike (21% of all sites), largemouth bass *Micropterus salmoides* (13%), and walleye *Sander vitreus* (13%).

Average fish species richness was higher in parkland (5.6) compared to prairie (4.0) sites (ANOVA: F=6.77, df= 71, P=0.01). The majority of sites in the parkland had >4 species, whereas the majority of prairie sites contained ≤3 species (Fig. 2). Of 74 lakes sampled in 2006, only one site in the parkland and four sites in the prairie were fishless. Maximum richness occurred in the prairie, with three sites having ≥10 species. Analyzing data from all 82 sites, fish richness was positively related to lake size (P<0.0001; Fig. 3a). We also observed a positive relationship between fish richness and LWA (P<0.0001; Fig. 3b).

We used CART modeling to assess patterns in fish presence and community composition. Our first CART analysis predicting fish presence-absence required just two independent variables to fully classify our learning data set, including 9 fishless sites and 49 sites with fish, with 100% accuracy. DFS was the strongest predictor variable, correctly classifying 44 of 58 sites as containing fish populations if DFS was true (Fig. 4). A second and final split identified ZMAX as the best predictor, and correctly classified the remaining 14 sites as fishless or with fish. The resulting tree indicated a ZMAX threshold of 2.15 m for sites with versus without fish if there was no DFS (Fig. 4). This model was robust, as it correctly classified 22 of 24 lakes (92%) in the validation data set. Of the 20 validation sites with fish, one was misclassified as being fishless. Similarly, 1 of the 4 fishless sites was misclassified as having fish present.

Our second CART used basin, connectivity, and watershed predictors to classify lakes based on type of fish community present: fishless (F), small-bodied plankti-benthivorous fish only (SBPB), small-bodied plankti-benthivorous fish + large-bodied plankti-benthivorous fish (SBPB + LBPB), and small-

Table 1 List of scientific and common names of fish sampled, frequency sampled in the parkland (*n*=35 sites) and prairie (*n*=37 sites) study areas, and categorization based on body size and feeding characteristics

Scientific name	Common name	Study area	Number of sites	Categorization[a]
Ameiurus melas	Black bullhead	Parkland	22	LBPB
		Prairie	21	
Ameiurus natalis	Yellow bullhead	Parkland	0	LBPB
		Prairie	2	
Ameiurus nebulosus	Brown bullhead	Parkland	6	LBPB
		Prairie	2	
Aplodinotus grunniens	Freshwater drum	Parkland	0	LBPB
		Prairie	1	
Catostomus commersoni	White sucker	Parkland	10	LBPB
		Prairie	4	
Culaea inconstans	Brook stickleback	Parkland	26	SMPB
		Prairie	10	
Cyprinus carpio	Common carp	Parkland	0	LBPB
		Prairie	14	
Esox lucius	Northern pike	Parkland	6	P
		Prairie	9	
Etheostoma exile	Iowa darter	Parkland	3	SBPB
		Prairie	0	
Hybognathus hankinsoni	Brassy minnow	Parkland	2	SBPB
		Prairie	0	
Lepomis cyanellus	Green sunfish	Parkland	4	LBPB
		Prairie	2	
Lepomis gibbosus	Pumpkinseed	Parkland	5	LBPB
		Prairie	3	
Lepomis macrochirus	Bluegill	Parkland	3	LBPB
		Prairie	7	
Luxilus cornutus	Common shiner	Parkland	0	SBPB
		Prairie	1	
Micropterus salmoides	Largemouth bass	Parkland	4	P
		Prairie	5	
Moxostoma macrolepidotum	Shorthead redhorse	Parkland	0	LBPB
		Prairie	3	
Notemigonus crysoleucas	Golden shiner	Parkland	6	SBPB
		Prairie	4	
Notropis heterolepis	Blacknose shiner	Parkland	1	SBPB
		Prairie	0	
Noturus gyrinus	Tadpole madtom	Parkland	2	LBPB
		Prairie	1	
Perca flavescens	Yellow perch	Parkland	19	LBPB
		Prairie	8	
Phoxinus eos	Northern redbelly dace	Parkland	21	SBPB
		Prairie	0	
Pimephales promelas	Fathead minnow	Parkland	29	SBPB
		Prairie	31	
Pomoxis nigromaculatus	Black crappie	Parkland	1	LBPB
		Prairie	7	
Sander vitreus	Walleye	Parkland	0	P
		Prairie	9	
Umbra limi	Central mudminnow	Parkland	25	SBPB
		Prairie	4	

[a] Abbreviations as follows: *SBPB* small-bodied plankti-benthivorous fish, *LBPB* large-bodied plankti-benthivorous fish, *P* piscivorous fish
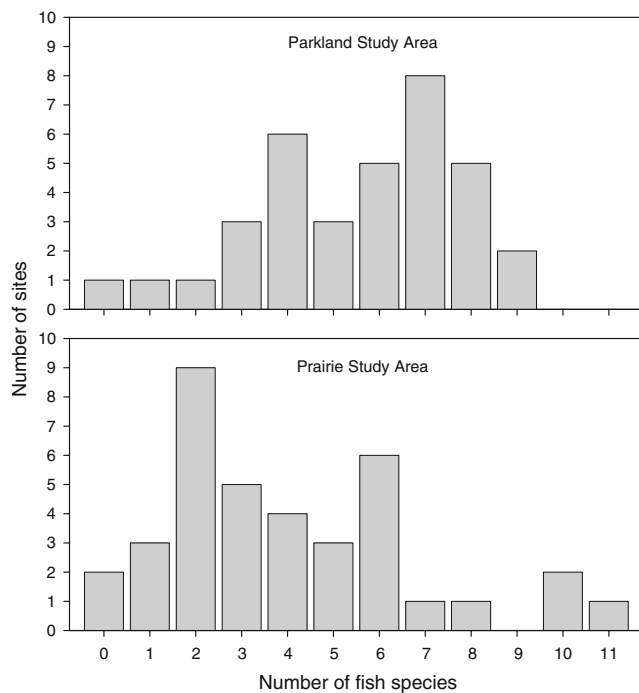
Fig. 2 Frequency distributions showing fish species richness patterns for the **a**) parkland and **b**) prairie study areas for those sites sampled in 2006

bodied plankti-benthivorous fish + large-bodied plankti-benthivorous fish + piscivores (SBPB + LBPB + P). The optimal model split the lakes four times using four independent variables (Fig. 5). DFS was again the strongest predictor variable based on k-folded cross validation. The next splitting variable was LWA. Presence of a DFS and LWA ≥1030.8 ha successfully sorted nine SBPB + LBPB + P sites (out of 20 such sites) into a unique terminal node. No other terminal group in this CART contained only one fish community type. The next two splits of the data were on LSIZE and UFS, respectively. Fishless sites were observed only when there was no DFS and LSIZE was small (<8.66 ha), whereas SBPB + LBPB + P sites were present only when there was either a DFS present, or when there was no DFS and LSIZE was large (≥8.66 ha) (Fig. 5). SBPB + LBPB sites were observed only when DFS was present. Overall, the CART model had the most difficulty distinguishing among SBPB + LBPB, SBPB, and SBPB + LBPB + P sites (Fig. 5, Table 2). The model correctly classified 64% and 63% of learning and validation sites, respectively (Table 2).

Discussion

Earlier accounts of fish distributions in prairie shallow lakes suggest limited fish populations throughout most of the PPR (>80% of sites fishless), often with assemblages

dominated by just fathead minnow and brook stickleback (reviewed by Peterka 1989). Our results indicated a much different picture for shallow lakes in the eastern PPR, where just 4% of the study sites we sampled in 2006 were fishless. Instead, sites with small-bodied plankti-benthivorous fish were common in our study, as were complex multi-species communities including small-bodied and large-bodied plankti-benthivorous fishes, and piscivores. Viewed collectively, our results indicated the importance of interconnectivity among basins (both upstream and downstream connections were important) and key influences of lake size and depth.

Shallow lakes in Minnesota's portion of the PPR of North America have been influenced by a plethora of human activities (e.g., wetland drainage and consolidation), principally to facilitate modern food production (Luoma 1985). Agriculture has resulted in a loss of approximately 66% of wetland area in the U.S. portion of the PPR, and 77% within Minnesota's portion (Dahl 1990; Dahl 1996). Whilst agriculture practices have likely directly impacted wetland
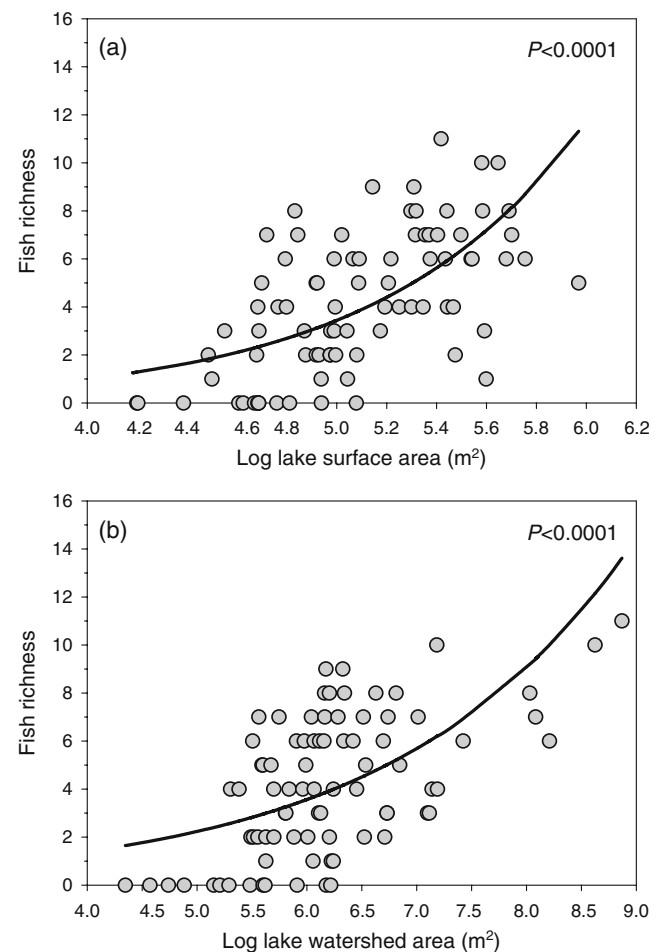

Fig. 3 Negative binomial regression model relationships between fish species richness and **a**) lake surface area and **b**) lake watershed area for 82 study lakes
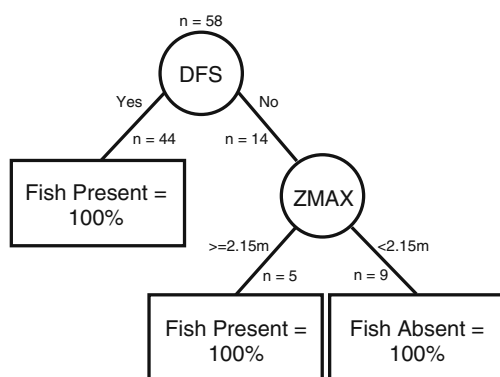
CART model for fish presence - absence

Fig. 4 Classification tree for fish presence or absence resulting from CART analysis performed on training data sites (*n*=58) using six basin, connectivity, and watershed predictor variables. Classification of sites into nodes comprising only one group type required two splits of the data, based on whether the site was connected to a downstream fish source (DFS), and lake maximum depth (ZMAX). Also shown are number of sites corresponding to each split of the data, the splitting value of the environmental variable for each split, and the percentage of lakes at the terminal node with either fish present or absent

quality through increased nutrient loading (Ramstack et al. 2004), installation of drainage tile and ditches, consolidation of wetlands, and other anthropogenic activities (e.g., road and ditch construction, nonnative invasive flora and fauna, intentional fish stocking) have almost certainly modified fish distributions throughout shallow lakes in Minnesota and elsewhere. Consequences of these changes are poorly documented, yet it is plausible that ecological impacts of wetland fishes have increased (reviewed by Bouffard and Hanson 1997), favoring preponderance of turbid, phytoplankton-dominated wetlands with low abundances of invertebrates and submerged aquatic vegetation (Zimmer et al. 2001, 2002, 2003).

Plankti-benthivorous fish have been associated with regime shifts in shallow lakes (Zimmer et al. 2009) and were widely distributed in our study. These fish are pervasive in part because they are less vulnerable to piscivory due to defensive spines (e.g., black bullhead) or fast growth and large adult size (e.g., common carp) (e.g., Hambright 1994). Interestingly, all sites containing populations of piscivores also contained populations of large-bodied plankti-benthivorous fish, and for the reasons just described, piscivores had little effect on overall fish biomass in these sites (Friederichs et al. 2010).

Average fish richness in our parkland (5.6) and prairie (4.0) study areas fell within the range reported for smaller North American lakes (2.4 for small Alberta lakes – Robinson and Tonn 1989, 5.3 for small northern Wisconsin lakes – Tonn et al. 1983), but much lower than values from larger lakes (e.g., 10.6 for southern Ontario lakes – Harvey

1981, 13.7 for northern Wisconsin lakes – Rahel 1986). Thus, it seems plausible that the relative importance of processes influencing fish richness and community structure likely differs between smaller, shallower and larger, deeper lakes. Fish assemblages also reflected regional species pools (Jackson and Harvey 1989; Griffiths 1997; Mehner et al. 2007). Species pools differed such that some species were present in only one of the two study areas (e.g., northern redbelly dace in the parkland, common carp and walleye in the prairie). However, most species were present in both study areas but occurred more often in one area (e.g., white sucker and yellow perch in the parkland). Other examples include brook stickleback and central mudminnow, which were more widespread in the parkland, perhaps reflecting their ability to survive anoxic conditions at this more northerly latitude (Klinger et al. 1982). Indeed our observation of small-bodied plankti-benthivorous fish communities (fathead minnow, brook stickleback, and central mudminnow only) in both study areas may reflect these species' ability to survive in low winter oxygen conditions (Klinger et al. 1982).

Magnuson et al. (1998) argued that extinction factors were more important than isolation in predicting the
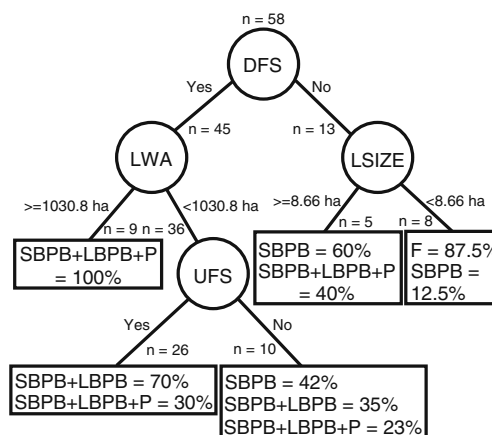
CART model for fish community type

Fig. 5 Classification tree for fish community type resulting from classification and regression (CART) analysis performed on training data sites (*n*=58) using six basin, connectivity, and watershed predictor variables. The optimal classification tree required four splits of the data, using three different independent variables. Connection to a downstream fish source (DFS), lake watershed area (LWA), and lake size (LSIZE), corresponding to the 1st, 2nd, and 3rd + 4th splits of the data, respectively. Inside each "branch" are number of sites corresponding to each split of the data, outside each branch are the splitting values for the environmental variable used at each split, and percentages in the terminal nodes (boxes) indicate the response rate for each response group. Response group abbreviations are as follows: F = fishless, SBPB = small-bodied plankti-benthivorous fish only, SBPB+LBPB = small-bodied plankti-benthivorous fish + large-bodied plankti-benthivorous fish present, and SBPB + LBPB + *P* = small-bodied plankti-benthivorous fish + large-bodied plankti-benthivorous fish + piscivores all present

Table 2 Classification matrix for learning and validation data sets for a CART analysis of four fish community types using selected environmental variables. Fish community types modeled included fishless (F), small-bodied plankti-benthivorous fish (SBPB), small-bodied plankti-benthivorous fish + large-bodied plankti-benthivorous fish (SBPB + LBPB), and small-bodied plankti-benthivorous fish + large-bodied plankti-benthivorous fish + piscivores (SBPB + LBPB + P). Overall, 63% of learning and validation set were correctly classified based on the model depicted in Fig. 5

Actual group	Learning set predicted group				Validation set predicted group				% of sites correctly classified		
	F	SBPB	SBPB + LBPB	SBPB + LBPB + P	F	SBPB	SBPB + LBPB	SBPB + LBPB + P	Learning	Validation	Combined
F	7	0	0	0	4	2	0	0	100	67	85
SBPB	1	14	0	0	0	3	0	0	93	100	94
SBPB + LBPB	0	9	7	0	0	6	6	0	44	50	46
SBPB + LBPB + P	0	8	3	9	0	0	1	2	45	67	48
								All fish community types			
									64	63	63

richness and composition of fish assemblages in lakes, but others have since shown the importance of spatial isolation (Jackson et al. 2001; Olden et al. 2001). Our study points to the importance of both extinction (lake area, depth, and piscivores) and isolation-related variables (watershed area, upstream and downstream fish sources) as important influences on fish presence and community structure in eastern PPR shallow lakes. Surprisingly, distance "as the fish swims" was not an effective predictor of fish populations. Instead, presence of a surface water connection (or "water bridge") between lakes had the most influence on fish distributions. For example, if a downstream connection was present, fish occurred 100% of the time, no matter what the distance was to a permanent water body. When no downstream connection was present, lake maximum depth (an extinction variable) effectively distinguished between sites with and without fish – shallower sites did not have fish while deeper sites did. Possible explanations for this include that fish populations become established during infrequent overland flooding events that are difficult to detect via field observation or using GIS, or are due to stocking, either process of which move fish into these otherwise isolated lakes. Some of these lakes then winterkill, especially those that are shallow. Finally, downstream connections appeared to promote populations of piscivorous fish, similar to the findings of Tonn and Magnuson (1982) for northern pike in small north temperate lakes and findings of Spens et al. (2007) for Swedish lakes.

Shallow lake fish communities in the eastern PPR do not appear to be dispersal-limited to the extent typical for lentic fish communities (Shurin et al. 2009), especially compared to landscapes with less surface connectivity (e.g., Magnuson et al. 1998). In our study, connectivity among basins was an important mechanism contributing to fish presence, community structure, and richness. Indeed, widespread drainage, ditching, and consolidation in the eastern PPR (Dahl 1990, 1996; Prince 1997) has accentuated the natural propensity for permanent hydrological regimes and spilling among basins, a known characteristic of shallow lakes along eastern margins of the PPR (Leibowitz and Vining 2003; Hanson et al. 2005). Considering the potential for impacts of fish populations in shallow lakes, managers interested in promoting ecological integrity of these lakes should focus on protecting shallow, isolated basins from anthropogenic connectivity (similar to what has been advocated for limiting northern pike in Swedish lakes; Spens et al. 2007). In our study, such sites were most likely to be fishless, or support low density small-bodied plankti-benthivorous fish communities, which in turn are more likely to have high submerged macrophyte abundance and higher richness of waterbirds, plants, invertebrates, and amphibians (Scheffer et al. 2006). Although connectivity almost certainly contributes to higher regional fish richness in our current Minnesota landscape, the resulting persistent fish populations and higher fish biomass probably results in lower diversity of invertebrates, amphibians, plants, and birds via cascading fish feeding effects on these shallow lake food webs (Scheffer et al. 2006). We argue that when naturally flat landscape topography and ditching cause a high frequency of hydrological linkage among surface waters, the net benefit of additional connectivity will generally be negative due to the spread and maintenance of detrimental fish populations. Indeed such connectivity has likely contributed to the spread of common carp, and could facilitate future invasive fish introductions as well (Marchetti et al. 2004). Subsequent impacts are likely to be negative for both native fish populations and associated aquatic food webs.

Land use policies and management activities focused on stemming future ditching and/or interrupting connectivity among basins (e.g., elimination of ditches and culverts,

installation of fish screens and velocity barriers) should benefit shallow lakes, potentially shifting the dominant structuring mechanisms towards extinction-related processes as observed for small lakes in pristine environments (Magnuson et al. 1998). This may also help buffer future impacts of climate changes predicted for our region. Climate is variable across the PPR, reflecting strong north-south temperature and east-west precipitation gradients, the latter which has steepened in the twentieth century, resulting in relatively wet and stable conditions in Minnesota compared to areas north and west within the PPR (Hanson et al. 2005; Johnson et al. 2005; Millett et al. 2009). According to the latest assessments from the Intergovernmental Panel on Climate Change, nearly all of the Atmosphere-Ocean General Circulation and Regional Climate models have projected mean annual warming throughout the USA to exceed 2°C over the next century (Christensen et al. 2007). Other predictions increasingly supported by current models include increased winter and annual precipitation (up to 20%), decreased summer precipitation at mid latitudes, increased frequency of intense precipitation events, increased risk of droughts, as well as decreased snow depth and duration of snow cover (Christensen et al. 2007). Because fish colonization and extinction processes are inextricably linked to surface connectivity and climatic variability, human-induced climate change could influence fish distributions. For example, decreased snow depth and duration of snow cover could reduce frequency of fish winterkills (Danylchuk and Tonn 2003), while increased frequency of either deluge or drought could discriminate for or against fish populations (Hanson et al. 2005), or influence fish community compositions in currently unknown ways.

Our study represents an important step towards increasing our understanding of processes influencing fish species distributions in shallow lakes. Not only do our results offer insight into fish assemblages, they also have implications for identifying, conserving, and managing fishless basins. Collectively, this provides important baseline information allowing planners and managers to adapt to potential future changes in climate and land use practices. Future studies should more explicitly examine the complex interactions among potential climate change impacts, hydrological regimes (Johnson et al. 2005), inter-basin connectivity (Hanson et al. 2005), winterkill processes (Danylchuk and Tonn 2003), and resulting fish distributions.

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