

SPATIOTEMPORAL VARIATION OF FISH ASSEMBLAGES
IN MONTANA PRAIRIE STREAMS

by

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ABSTRACT

Fisheries biologists must be certain that their samples represent true parameters to make sound management decisions. A large-scale effort was conducted in the past decade to sample Montana prairie stream fish assemblages. This effort focused on sampling as many streams as possible, mostly during summer. Longitudinal sampling within drainages and replication of sites across time was minimal. Consequently, the spatiotemporal variation of prairie stream fish assemblages in Montana is not well understood. The objectives of this study were to 1) determine the influence of spatial, temporal, and abiotic variables in structuring prairie stream fish assemblages and 2) determine the survey design that best characterizes prairie stream fish assemblages. To assess spatiotemporal variation, lower, middle, and upper sites were sampled on five tributaries of the Yellowstone River during each season over a two-year period. Spatial position explained the greatest amount of variation (18.5%), followed by proportion of fine substrates (13.9%). Season (i.e., temporal variation) was not significant in explaining the overall variation in the fish assemblage. Fish species were associated with lower, middle, and upper spatial positions and along the fine substrates gradient based on abundance by species. A more detailed spatial analysis of fish assemblage variation was conducted by sampling sites arrayed from the confluence to the headwaters on each of the five streams during June and July 2005 and 2006. Species richness varied longitudinally and decreased from downstream to upstream sites. Proportion of fine substrates increased and pool area decreased from downstream to upstream sites. Longitudinal changes in species richness were often associated with longitudinal changes in the proportion of fine substrates. Large river fishes were limited to lower and middle reaches and were only occasionally found in upper reaches. Spatiotemporal and longitudinal findings were consistent among streams of varying watershed sizes. At least lower, middle, and upper sites are required to adequately characterize the fish assemblages of prairie streams and more samples are needed at lower sites than middle or upper sites. Given logistic and monetary constraints, biologists should design their surveys to maximize spatial coverage to adequately characterize fish assemblages of prairie streams.

INTRODUCTION

Prairie ecosystems are one of the most endangered biomes on the continent (Samson and Knopf 1994) and include few remaining naturally functional watersheds because of fragmentation (Dodds et al. 2004). Prairie streams are relatively little understood compared to their forested counterparts (Matthews 1988). Prairie stream fish assemblages exist under unstable flow regimes with large fluctuations in environmental characteristics (Matthews 1988). Prairie streams should be considered a conservation priority because they are part of a dynamic ecosystem that is little understood and already highly endangered.

In the past decade, a large-scale effort has been conducted to document Montana prairie stream fish assemblages. However, the spatiotemporal variation of prairie stream fish assemblages in Montana and the northwestern Great Plains is not well understood because surveying has focused on sampling as many streams as possible, mostly during summer. Longitudinal sampling within drainages and replication of sites across time has been minimal, but the spatial position sampled within a drainage can greatly influence fish assemblages observed (Horwitz 1978; Evans and Noble 1979; Matthews 1986a; Schlosser 1987; Bhat 2004). Additionally, fish assemblages vary across time; thus the timing of sampling influences the fish sampled (Schlosser 1987; Tripe and Guy 1999; Adams et al. 2004; Pegg and McClelland 2004). In most stream studies fish assemblages varied more spatially than temporally in abundance or catch per unit effort (C/f) (Matthews 1990; Meador and Matthews 1992; Williams et al. 1996; Tripe and Guy 1999; Ostrand and Wilde 2002). However, fish assemblages varied more temporally than

spatially in C/f in three disturbed Mississippi coastal streams (Adams et al. 2004).

Understanding spatiotemporal variation in fish assemblages is essential in establishing standardized long-term data sets (Tripe and Guy 1999) and assessing anthropogenic and natural changes in fish assemblages (Tripe and Guy 1999; Adams et al. 2004; Bramblett et al. 2005).

Determining the underlying mechanisms that structure fish assemblages is important to fisheries biologists interested in making generalizations to other systems and assessing natural or anthropogenic effects. A number of mechanisms and their relationships to each other can influence the structure of fish assemblages including spatial position within a watershed, abiotic and biotic factors, disturbance history, and temporal movements (Vannote et al. 1980; Schlosser 1987; Matthews 1988; Rahel and Hubert 1991; Adams et al. 2004; Dodds et al. 2004; Butler and Fairchild 2005).

The spatial position within a watershed can influence stream fish assemblages (Vannote et al. 1980; Schlosser 1987; Rahel and Hubert 1991). The river continuum concept was developed to conceptualize such longitudinal variation in flowing waters (Vannote et al. 1980). According to it, physical variables vary predictably downstream and changes in the biota are associated with these physical changes (Vannote et al. 1980). Fish assemblages shift from low diversity coldwater assemblages in the headwaters to more diverse warmwater assemblages in lower reaches (Vannote et al. 1980; Rahel and Hubert 1991). Longitudinal changes in fish assemblages are often attributed to biotic zonation or the addition of new species and less often to the replacement of species (Horwitz 1978; Evans and Noble 1979; Rahel and Hubert 1991). In downstream

tributary reaches, species additions may result from greater connectivity with speciose large rivers (Horwitz 1978; Gorman 1986). Similarly, increases in species richness are associated with increases in watershed size and stream order (Lotrich 1973; Gorman and Karr 1978; Evans and Noble 1979; Fausch et al. 1984).

Similar conceptualizations have been developed to describe warmwater or prairie stream fish assemblages focusing on abiotic versus biotic factors (Schlosser 1987) and disturbance (Dodds et al. 2004) regulating mechanisms. It is generally accepted that a combination of abiotic and biotic factors regulate fish assemblages with the relative influence of each varying within streams (Schlosser 1987; Jackson et al. 2001). In general, species diversity and habitat heterogeneity (i.e., depth, current, and substrate) increase downstream (Gorman and Karr 1978) with abiotic factors most important in structuring warmwater fish assemblages in upstream reaches and biotic factors becoming more important downstream (Schlosser 1987). Fish assemblages in headwater reaches are often limited by harsh habitat conditions (Matthews 1988) whereas downstream reaches exhibit more benign abiotic conditions and a gradual increase in species richness (Horwitz 1978; Evans and Noble 1979; Bhat 2004).

The influence of biotic factors on the fish assemblages of prairie streams has not been as clearly demonstrated as for abiotic factors (Matthews 1988). Predation was demonstrated in an experimental stream in Minnesota on two size classes of hornyhead chubs. Smallmouth bass preyed upon hornyhead chubs of both size classes under different light conditions with shallow refugia present (Schlosser 1988). Fish assemblage structure was at least partially a function of predator avoidance behavior of minnow

species in Roubidoux Creek, Missouri (Gorman 1988). Relatively little work has clearly demonstrated an effect of competition in warmwater stream fish assemblages (Jackson et al. 2001). A literature review suggested that resource partitioning, which could be the result of competition, structures fish assemblages (Ross 1986). The drastic decline of the Arkansas River shiner following the introduction of the closely related Red River shiner provides further potential evidence for competition as a structuring mechanism (Matthews 1988).

The variable hydrology of prairie streams can influence fish assemblages (Harrel et al. 1967; Ostrand and Marks 2000; Fritz et al. 2002; Dodds et al. 2004; Ostrand and Wilde 2004). Prairie streams are often intermittent with frequent flooding and drying events (Dodds et al. 2004). A conceptual model to explain prairie stream ecology was developed using a non-equilibrium viewpoint, where streams exist in a balance between flooding and drying (Dodds et al. 2004). Flooding can alter fish assemblages, the effect often depending on the location in the drainage, intensity, and timing of events (Dodds et al. 2004). Prairie stream fishes are capable of rapid recolonization following habitat disturbance (Fritz et al. 2002; Dodds et al. 2004). Fish abundance was reduced in headwater springs of Kings Creek, Kansas, following an unusually high flooding event in 1995; however, populations recovered rapidly (< 3 months) (Fritz et al. 2002).

As streams dry, pools become isolated and physicochemical conditions become harsher (Mundahl 1990; Ostrand and Wilde 2004). Predictable changes in the fish assemblage of the Brazos River, Texas were detected as isolated pools evaporated in headwater reaches (Ostrand and Marks 2000; Ostrand and Wilde 2004). Cyprinid

presence and abundance decreased with increases in specific conductance and decreases in pool volume whereas cyprinodontid populations remained constant or increased (Ostrand and Marks 2000; Ostrand and Wilde 2004). Laboratory results provided further evidence that cyprinodontids were capable of tolerating higher salinities, higher temperatures, and lower dissolved oxygen levels than cyprinid species (Ostrand and Wilde 2001). The fish assemblage of Otter Creek, Oklahoma responded rapidly following a severe drought (Harrel et al. 1967). Otter Creek was sampled in spring following eight months of continuous stream flow and in autumn following a severe drought and two or three days of stream flow (Harrel et al. 1967). Most fish species that were sampled in spring were also sampled in autumn despite extirpation during the drought.

Fish movements may influence observed fish assemblages and are important considerations in spatiotemporal studies. For example, channel catfish migrated downstream to the Mississippi River in autumn and up the Wisconsin River from the confluence in spring for spawning (Pellet et al. 1998). In downstream pools of a Pennsylvania stream, centrarchids were present in spring and autumn and emigrated out of the stream during winter (Butler and Fairchild 2005). In these cases, sampling during one season would have provided an incomplete assessment of channel catfish and centrarchid populations and their use of river-tributary systems.

The spatiotemporal variation of prairie or warmwater fish assemblages has been evaluated in several settings including central and southern Great Plains streams (Meador and Matthews 1992; Williams et al. 1996; Ostrand and Wilde 2002), coastal plains

streams (Adams et al. 2004), Midwestern warmwater streams (Schlosser 1987) and Great Plains large rivers (Barko et al. 2004; Pegg and McClelland 2004). No attempts have been made to describe the spatiotemporal variation of prairie fish assemblages in Northwestern Great Plains streams. These streams often exhibit intermittency, unstable flow regimes, harsh environmental fluctuations, and relatively depauperate ichthyofaunas (Matthews 1988; Bramblett et al. 2005).

Most stream studies have focused on the spatiotemporal variation of fish assemblages in one stream or one stream and a few of its tributaries (Schlosser 1987; Meador and Matthews 1992; Williams et al. 1996; Ostrand and Wilde 2002). To the best of my knowledge, no studies have assessed spatiotemporal variation in multiple streams of varying size that flow directly into the same river. Adams et al. (2004) studied three tributaries to the Tallahatchie River; however, all streams were small (i.e., less than 100 km² watershed size).

The objectives of this study were to 1) determine the influence of spatial, temporal, and abiotic variables (including watershed size) in structuring prairie stream fish assemblages and 2) determine the survey design that best characterizes prairie stream fish assemblages. Multiple approaches were used to address these objectives including a spatiotemporal assessment incorporating spatial and seasonal sampling and a more detailed longitudinal assessment of fish assemblages and abiotic variables during summer. The results of this study will help place the overall Montana prairie fish database into context and allow biologists to make more informed decisions in conserving prairie streams.

STUDY AREA

The study area consisted of tributaries to the Yellowstone River between the towns of Forsyth (rkm 379 [measuring from its confluence with the Missouri River]) and Glendive (rkm 147), Montana. All tributaries share characteristics in common with typical prairie streams including low gradients, temporally variable turbidities, intermittent headwater to middle reaches, and relatively frequent flooding and drying events (Rabeni and Jacobson 1999; Dodds et al. 2004). All of the streams are located in the Northwestern Great Plains ecoregion of the Yellowstone River basin where the terrestrial ecosystem is northwestern mixed grasslands (Woods et al. 1999; Galat et al. 2005). Grazing and row crop agriculture are the dominant land use activities and oil extraction is prevalent within some drainages. The potential species pool is the same for all streams in the region (White and Bramblett 1993).

METHODS

Survey Design

Study streams were selected to investigate spatiotemporal variation in prairie stream fish assemblages. The study streams were selected to represent a gradient of watershed sizes to assess the influence of watershed size on fish assemblage characteristics. Spatiotemporal sites (i.e., lower, middle, and upper sites) were established on each stream and sampled seasonally to determine if fish assemblages varied more among spatial positions or seasons. Longitudinal sites (i.e., 9 or 10 sites dependent upon access and permission) arrayed from near the confluence with the Yellowstone River to the headwaters were established and sampled during summer to characterize the longitudinal variation in fish assemblages in more detail. Logistical constraints prevented sampling all longitudinal sites during spring and autumn. Abiotic variables were measured at spatiotemporal and longitudinal sites to determine the variables associated with changes in fish assemblage characteristics.

Stream Selection

The study streams ($N = 5$) were randomly selected from a sampling frame using a stratified random design to represent a gradient of watershed sizes. The sampling frame was populated based on the following criteria: 1) a tributary connected directly to the Yellowstone River located between Forsyth (rkm 379) and Glendive (rkm 147), Montana, 2) minimal anthropogenic hydrological influences (e.g., irrigation and

reservoirs), 3) large enough to maintain water in some portion of the stream, and 4) small enough to seine in lower reaches near the Yellowstone River confluence.

For streams meeting the specified criteria, watershed size was estimated using the Montana Natural Resource Information System (MNRIS 2007) Topofinder II mapping system and the watershed sizes of the selected study streams were later more accurately estimated using ArcGis 8.3 Geographic Information Systems (GIS) software (ESRI 2002). The sampling frame was stratified by watershed size using 500 km² increments and study streams were randomly selected from each 500 km² stratum. Landowner cooperation and permission was sought for each stream but if access was denied a new stream was randomly selected. The resulting study streams were O'Fallon (4,080 km²), North Sunday (1,937 km²), Cabin (1,026 km²), Cedar (553 km²), and Sweeney (264 km²) (Figure 1). Both forks of Sunday were used in calculating watershed size, because the lowest site was below the fork in the stream. However, even if the south fork of Sunday is excluded from the watershed size calculation, North Sunday remains the second largest stream (1,055 km²). Oil extraction occurred in the Cabin and Cedar drainages.

Site Selection

All sites were established where there was stream access and landowner permission. When establishing a site, if multiple access points were accessible the access point was randomly selected. The midpoint of each site was randomly established upstream or downstream from the access point at a distance from 1 to 250 m. In an effort to maximize the number of species captured, 300-m sites were established. In Wyoming

prairie streams no additional species were detected when seining greater than 300-m reaches (Patton et al. 2000). A total of forty-six sites (i.e., including both spatiotemporal and longitudinal) were established with the majority of sites located on private land ($N = 39$) and the remaining sites on Bureau of Land Management (BLM) ($N = 5$) and state lands ($N = 2$). Fish movement was potentially blocked in Cedar (above longitudinal site 3, site 1 is the most downstream site) and Sweeney (above longitudinal site 4) at low flows, because of culverts and dikes, respectively.

Spatiotemporal Samples. Sites were selected to represent a lower, middle, and upper spatial position on each stream (Figure 1). The lower site was established within the lower five river kilometers from the confluence with the Yellowstone River. The upper site was established at the estimated uppermost location of permanent water, also thought to be the uppermost point of fish distribution. The middle site was established about midway between the upper and lower sites, with the exact location dependent upon access and permission. Spatiotemporal sites were sampled in June, July, August, and October 2005 and 2006 and February and April 2006 and 2007. The timing of sampling was based on the mean monthly discharge of five Montana prairie streams located within or near the study area (Big Dry, Big Muddy, Rock, Rosebud, and Pumpkin; USGS 2007) and logistical constraints. The April (spring) sample coincided with the lower portion of the descending limb of the hydrograph (USGS 2007). July and August exhibited base flows (USGS 2007) and July was randomly selected to represent the summer season. October was selected for the autumn sample to avoid ice coverage that would be expected to occur in November. February was selected as the winter sample.

Summer Longitudinal Samples. Longitudinal sites were arrayed from near the confluence with the Yellowstone River to the headwaters. Ten sites were established on North Sunday whereas nine sites were established on O'Fallon, Cabin, Cedar, and Sweeney because of limited access (Figure 1). For each stream, the stream length from the confluence with the Yellowstone River to the upper spatiotemporal site was divided by 10 to establish strata wherein sites were randomly established. Spatiotemporal sites served as longitudinal sites wherever possible. The lower spatiotemporal site was longitudinal site one and the upper spatiotemporal site was longitudinal site nine. One site was established above site nine on each stream. Sites were sampled in June and July 2005 and 2006.

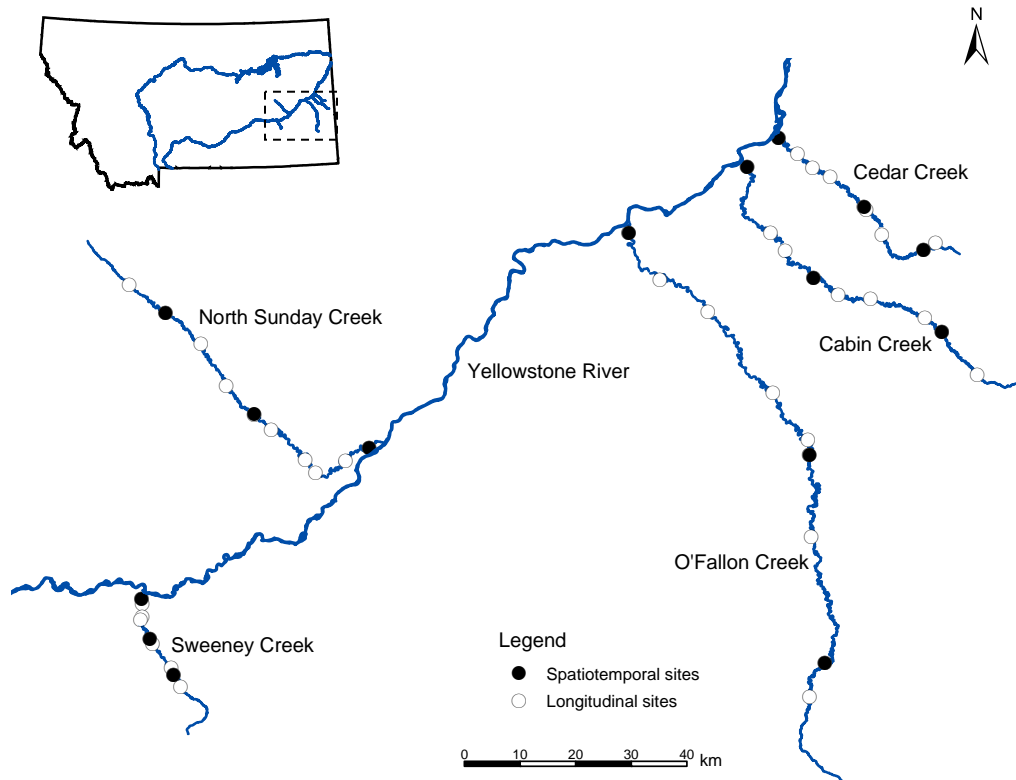


Figure 1. Map of study area illustrating study streams and spatiotemporal and longitudinal sites. The study area in the map inset is designated by the dashed box.

Sampling

Site Setup

All sites were sampled following the Montana Prairie Fish and Habitat Sampling Protocol (Bramblett 2003, Appendix A). Water-quality parameters were measured at the center of the site prior to fish sampling. Conductivity (μmhos), water temperature ($^{\circ}\text{C}$), and dissolved oxygen (mg/L) were measured with a Yellow Springs Institute model 85 meter (YSI 85). Turbidity (NTU) and pH were measured with a LaMotte turbidity meter and Oakton meter, respectively.

Fish Collection and Measurements

A seine (6.1 m x 1.8 m with 0.6-cm bar mesh) was used to sample fish. Seining began upstream and progressed downstream within a site. An effort was made to keep the lead line along the bottom, the float line above the water surface, and the ends of the seine as close to the bank as possible to maximize efficiency. Individual seine hauls were no longer than 60 m and typically 30 m or less depending on the morphological features of the stream reach. If the stream was wider than the seine, multiple seine hauls were performed until the entire width had been sampled. A “kick seine” technique was used in riffle habitats; it involved one person holding the seine against the current in a “U” shape while the other disturbed the substrate immediately upstream of the seine (Matthews 1986b). A dip net (0.30 m x 0.15 m x 0.6-cm bar mesh) was used if the stream was too narrow for effective seining, by passing the dip net downstream through the entire water column.

All fish sampled were placed in 19-L buckets with portable aerators. They were anesthetized with tricaine methanesulfonate (MS-222) to facilitate processing. Species was recorded for each fish sampled. Total lengths were measured (mm) and recorded for thirty randomly selected fish per species and the minimum and maximum lengths of each species sampled were recorded. *Hybognathus* spp. that were less than 55 mm were classified as juvenile *Hybognathus* spp. because of the difficulty in identification. All fish except voucher specimens were returned to the reach where they were sampled after processing.

Vouchers

An attempt was made to voucher at least three individuals of each species present in each stream for species verification. No vouchers were collected if the species was rare and identification was not questionable. Vouchered specimens were euthanized with an overdose of MS-222 and fixed in formalin for at least 7 d. Formalin was removed from the specimens by soaking them in water over a period of 2 d, changing the water at least four times. The vouchered specimens were then preserved and stored in 70% ethanol or 40% isopropanol solutions (Appendix A).

Habitat

Habitat assessment was modified from the Environmental Monitoring and Assessment Program (EMAP) protocol (Lazorchak et al. 1998) and was performed identically at spatiotemporal and longitudinal sites. Habitat measurements started at the downstream end of the site and proceeded upstream. Transect measurements ($n = 11$) were collected at 30-m intervals. Wetted width was recorded to the nearest 0.1 m. Substrate and depth (measured to 0.05 m) were recorded at five locations along the transect (i.e., left bank, left center, center, right center, and right bank). Substrate was classified according to size and included bedrock ($>4,000$ mm), boulder (250 mm to 4,000 mm), cobble (64 mm to 250 mm), coarse gravel (16 mm to 64 mm), fine gravel (2 mm to 16 mm), sand (0.06 mm to 2 mm), fines (<2 mm), hardpan (consolidated fine substrate), wood, and other (Lazorchak et al. 1998). The depth and substrate of the thalweg were measured at about 3-m intervals along the entire length of the site.

Discharge measurements were collected at all flowing sites. Wetted width (m) was used to determine the number of locations to obtain discharge measurements by dividing the wetted width into an equal number of cells. Depth (m), velocity (m/s), and distance from bank (m) were measured within each cell. Velocity was measured using a Marsh McBirney model 2000 flow meter. Stage height was recorded at the middle site in each stream from May to November 2006 with TruTrack WT-HR 1000 mm data loggers. The stage height of North Sunday was not recorded after 22 July 2006 because of equipment malfunctions.

Winter Sampling

Spatiotemporal sites were surveyed in February 2006 and 2007; however, fish collections were not made because ice cover made seining impossible. All sites that were accessible were surveyed for the presence or absence of ice. Holes were drilled in the ice at some sites and ice thickness and water depth underneath the ice were measured. Water quality measurements (including dissolved oxygen) of water beneath the ice were not assessed because of technical difficulties (probe freezing) and inaccurate readings.

Analyses

Spatiotemporal

Fish Assemblage Characteristics. Species richness was examined at position (i.e., lower, middle, and upper), season (i.e., spring, summer, and fall), and stream (i.e., O'Fallon, North Sunday, Cabin, Cedar, and Sweeney) levels. Differences in species

richness among spatial positions, seasons, and streams were assessed using a three-factor ANOVA. In the event of interactions among factors, main effects were not interpreted and species richness patterns were examined graphically by spatial position, season, and stream. Species richness by year and cumulative species richness were plotted. Year 1 included summer 2005, autumn 2005, and spring 2006 samples and year 2 included summer 2006, autumn 2006, and spring 2007 samples. Sites were allocated as year 1 or year 2 to depict interannual variation in species richness. Cumulative species richness was calculated as the species richness for years 1 and 2 pooled.

Large River Fishes. A large river guild was established to examine the spatiotemporal use of prairie streams by large river fishes. Fish were classified as large river fishes based on known distributions and life history characteristics (Brown 1971; R. G. Bramblett, Montana State University, personal communication). The large river guild included channel catfish *Ictalurus punctatus*, emerald shiner *Notropis atherinoides*, flathead chub *Platygobio gracilis*, goldeye *Hiodon alosoides*, river carpsucker *Carpionodes carpio*, shorthead redhorse *Moxostoma macrolepidotum*, smallmouth buffalo *Ictiobus bubalus*, and western silvery minnow *Hybognathus argyritis*. Species presence and absence was depicted for each species for all spatiotemporal sites. Large river species richness was evaluated in an identical manner to species richness.

Abiotic Characteristics. Maximum observed water temperature during sampling was assessed by stream. The percent of winter samples with surface ice coverage was calculated by dividing the number of sites with ice coverage by the number of sites

surveyed and multiplying by 100. Differences in ice thickness and water depth beneath the ice among spatial positions, streams, and years were assessed using a three-factor ANOVA for sites with ice coverage. In the event of interactions among factors, main effects were not interpreted and trends in ice thickness and water depth beneath the ice were examined by assessing the mean, minimum, and maximum of each variable by spatial position and stream. Stage height from May to November 2006 was depicted for the middle site of each stream.

Mean wetted width (m) was calculated by averaging the wetted width of all transects ($N=11$), excluding dry transects (i.e., zero widths). Mean thalweg depths (m) were calculated by averaging the depth of all points along the thalweg ($N=300$), excluding dry reaches (i.e., zero depths). Pool volume (m^3) was calculated as the product of the mean wetted width (m), mean transect depth (m), and wetted channel length (m). Pool area (m^2) was calculated as the product of the mean wetted width (m) and wetted channel length (m). Pool area was more strongly associated with fish assemblage characteristic variables than pool volume, thus pool area was used for all analyses. The proportion of each type of substrate was calculated by dividing the number of times a wetted thalweg substrate occurred by the number of wetted thalweg substrate measurements. Substrate was further classified into two categories: fines (i.e., fines and sand substrates) and greater than fines (i.e., bedrock, boulder, cobble, coarse gravel, fine gravel, hardpan, and wood substrates). Discharge (m^3/s) was calculated as the product of the depth (m), velocity (m/s), and width (m) for each cell along the horizontal transect and then summed for the site discharge.

Abiotic variables were examined at position, season, and stream levels.

Differences in abiotic variables among spatial positions, seasons, and streams were assessed using a three-factor ANOVA. In the event of interactions among factors, main effects were not interpreted and trends in abiotic variables were examined by assessing the mean and coefficient of variation (CV) for each variable by spatial position, season, and stream. Means and CVs were calculated using data from April 2006 and 2007 (i.e., spring), July 2005 and 2006 (i.e., summer), and October 2005 and 2006 (i.e., autumn). Dry sites were used to calculate means and CVs for all variables to illustrate the variation across time. Summary statistics for environmental variables were calculated using SAS version 9.1.3 (SAS Institute 2003).

Fish Assemblage and Abiotic Associations. Correlation analyses were used to assess the relationships between fish assemblage (i.e., species richness and species abundance) and abiotic variables (i.e., pool area, mean thalweg depth, mean wetted width, and proportion of fine substrates). Pool area, wetted width, proportion of fine substrates, and abundance were $\log_{10}(X+1)$ transformed to meet the normality assumption required for correlation analysis. Discharge was excluded from this analysis because of a large deviation from normality and lack of improvement following transformations. Other variables measured in the field were excluded from fish assemblage and abiotic association analyses *a priori* because of diel variation in the parameter (e.g., dissolved oxygen and water temperature) or the potential for temporal fluctuations in the parameter associated with spates (e.g., conductivity and turbidity). Dry sites were excluded from correlation analyses. The relationships between species richness and pool area and

proportion of fine substrates were further assessed by performing separate correlation analyses by spatial position, stream, and season. These abiotic variables were selected because they had the strongest correlations with species richness with all streams pooled. Furthermore, pool area was used because it incorporates wetted width and wetted channel length. Each relationship was examined graphically for non-linear relationships. All correlation analyses were performed using SAS version 9.1.3 (SAS Institute 2003).

Canonical correspondence analysis (CCA) was used to identify the variables that best explained the overall variation in the fish assemblage (i.e., identity and abundance of species). Analyses were performed on abundance data by species for all streams pooled and by individual streams. Fish abundance data was $\log_{10}(X+1)$ transformed prior to analyses to dampen the effect of a few sites with high abundances (Ter Braak 1986). Environmental variables were not transformed prior to analyses because the significance of CCA results does not depend on parametric distribution assumptions (Palmer 1993) and exploratory analysis revealed that differences in results were minimal with transformed variables. Rare species (i.e., species that occurred five times or less for all streams or one time or less for individual streams) and sites with no fish present were removed because of their large influence on CCA (Dray et al. 2002). The spatiotemporal distribution of rare species presence was described qualitatively.

Canonical correspondence analyses were performed using the vegan package version 1.8-3 in R version 2.4.0 (R Development Core Team 2006). Inertia is a term used in the vegan package and is defined as the mean squared contingency coefficient. Inertia was used to assess the amount of variation explained by the CCA models by calculating a

value analogous to the coefficient of determination (r^2) (Williams et al. 1996); the amount of constrained inertia (i.e., amount of variability in the fish assemblage that is explained by CCA) divided by the total inertia (i.e., amount of variability in the fish assemblage that could be explained by CCA) (Ter Braak 1986). Significance was determined by running 999 permutations with the predictor variable of interest randomized. The number of times the randomized model exceeded the amount of variation explained by the non-randomized model was summed and one was added for conservative purposes to calculate a P-value. The P-value was compared against $\alpha = 0.05$ for statistical significance. For example, if the randomized model performed better than the non-randomized model 20 times, the calculated P-value would be 0.021 (i.e., $[(20+1)/(999+1)]$) and I would conclude that the non-randomized model was significantly better at explaining the variation in the fish assemblage than the randomized model.

Single variable CCA models were assessed to determine how much variation in the fish assemblage could be explained by individual variables. Variables that were thought to explain variation in the fish assemblage were incorporated in the models and included spatial position (i.e., lower, middle, and upper), season (i.e., spring, summer, and autumn), rank watershed size (i.e., O'Fallon = 1, North Sunday = 2; Cabin = 3, Cedar = 4, and Sweeney = 5), wetted width, mean thalweg depth, pool area, proportion of fine substrates, and discharge. Other abiotic variables were excluded from CCA analyses *a priori* for the same reasons as in the correlation analyses.

A stepwise approach was used to determine the multi-variable models that explained the most variation in the fish assemblage. Of the one-variable models that

were significant, the model that explained the most variation was used as the start model and all remaining variables were added to the CCA model independently. The models were then tested for significance in the same manner as above. The two-variable model that explained the most variation was then used as a start model and the same process was repeated. The multi-variable model selected for further assessment was determined by examining the graph of variation explained versus the number of variables in the model for an inflection point. If no inflection point was present, the model building process ended when the addition of the next variable explained less than an additional five percent of variation.

Graphical interpretation of CCA focused on interpretation of species associations with abiotic variables. Canonical correspondence analysis is a constrained analysis meaning that the abiotic variables are used in constructing the ordination. Thus CCA axes are a function of the abiotic variables used in the model and interpretations of species associations with CCA axes would be redundant. The first two CCA axes were examined because little variation was explained by additional axes.

Summer Longitudinal

Fish Assemblage Characteristics. Species presence and absence by longitudinal position was calculated by combining longitudinal samples from June and July 2005 and 2006. The relationship between species richness and the distance from mouth was assessed using regression analysis by stream. Quadratic regressions were fit for curvilinear relationships when they passed the F test based on the Type I sequential sums

of squares for the added quadratic parameter (Littell et al. 1991). Higher order polynomials were not fit, because the biological interpretation is difficult (Zar 1999). The relationships between species richness and distance from the mouth and relative distance from the mouth were assessed graphically. Relative distance from the mouth was calculated by dividing the distance from the mouth for a site by the distance from the mouth for the uppermost longitudinal site on the stream.

Large River Fishes. The distribution of large river fishes in the study streams were assessed with dot maps for each species, using ArcGis 8.3 software (ESRI 2002). Logistic regression was used to assess the presence or absence of large river fishes as related to the distance from mouth and relative distance from the mouth. The models selected for interpretation (i.e., using distance from mouth or relative distance from mouth as the predictor variable) were determined by the lowest Akaike's information criterion (AIC) value. Logistic regression was performed using the combined data from longitudinal sites sampled in June and July 2005 and 2006 for O'Fallon, North Sunday, and Cabin. Cedar and Sweeney were excluded from the analysis because of potential barriers to fish movement in the lower reaches. Logistic regression analyses were performed separately for all large river species. Simple logistic response functions were plotted using the formula:

$$P = e^{(\beta_0 + \beta_1 X)} / (1 + e^{(\beta_0 + \beta_1 X)})$$

where P = probability of detecting a fish, β_0 = intercept estimate, β_1 = (relative) distance from the mouth estimate, and X = (relative) distance from the mouth (rkm). The

(relative) distance from the mouth where the probability of capturing an individual of the species was 80% and 20% was determined, by solving for X with $Y = 0.80$ and 0.20 .

Abiotic Characteristics. Pool area and proportion of fine substrates were examined longitudinally because of the relatively strong relationships detected with species richness for spatiotemporal sites. Regression analyses were used to investigate the relationship between pool area and proportion of fine substrates with distance from the mouth (rkm) by stream. Regression analyses were performed using data from longitudinal sites sampled in June and July 2005 and 2006. Pool area and proportion of fine substrates for longitudinal sites were calculated identically as for spatiotemporal sites. Dry sites and two outliers on Sweeney (large pool areas during flooding) were excluded from the analyses. Stream channel distance from the mouth was calculated for each longitudinal site using ArcGis 8.3 software (ESRI 2002). All relationships between pool area and proportion of fine substrates with distance from the mouth were fit for quadratic relationships when they passed the F test (Littell et al. 1991). A simple logistic response function was fit for asymptotic relationships using the formula:

$$P = e^{(\beta_0 + \beta_1 X)} / (1 + e^{(\beta_0 + \beta_1 X)})$$

where P = proportion of fine substrates, β_0 = intercept estimate, β_1 = distance from the mouth estimate, and X = distance from the mouth (rkm). The coefficient of determination was calculated by dividing the corrected sum of squares of the model by the corrected total sum of squares. These values were used to calculate an F statistic and then to estimate a P-value. All regression analyses were performed using SAS version 9.1.3 (SAS Institute 2003).

Fish Assemblage and Abiotic Associations. Associations between fish assemblage and abiotic variables were made by visual assessment of species richness, pool area, and proportion of fine substrates with distance from the mouth graphs. Similar relationships between species richness and abiotic variables with distance from the mouth were identified by stream and spatial position. Abrupt changes in abiotic characteristics were examined to see if they occurred at the same distance from the mouth as abrupt changes in species richness.

Survey Effort

The number of samples required to adequately characterize species richness was assessed by graphical interpretation of cumulative species richness curves. Cumulative species richness curves were calculated using spatiotemporal and longitudinal data for lower, middle, and upper spatial positions by stream from June 2005 through April 2007. The first sampling event (June 2005) was used to calculate the beginning species richness value. Each additional sampling event was combined with all prior sampling events to calculate the cumulative species richness up to that point. Cumulative species richness curves were depicted by stream and spatial position and examined for the number of events where the species richness curve appeared to asymptote.

RESULTS

SpatiotemporalFish Assemblage Characteristics

Twenty-four species and 34,867 individuals were collected in the 90 spatiotemporal samples. Nineteen species were native (94% of the individuals) and five non-native (6% of the individuals). Fathead minnow *Pimephales promelas* (29%), sand shiner *Notropis stramineus* (13%), flathead chub (9%), lake chub *Couesius plumbeus* (6%), and plains minnow *Hybognathus placitus* (5%) were the most abundant species and made up about 62% of the total abundance. At least one species was caught at each of the 15 spatiotemporal sites at least once.

A significant interaction between spatial position and stream ($F_{8,45} = 8.81$, $P < 0.01$) indicated that the variation in species richness among spatial positions was not the same for all streams. Species richness varied more within and among streams than among seasons (Figure 2). In general, species richness declined from downstream to upstream and with decreasing watershed size (Figures 2 and 3). Deviations from these trends were largely associated with Sweeney and North Sunday (Figures 2 and 3). The upstream site on Sweeney had higher species richness than the middle site and although North Sunday was the second largest stream by watershed size, species richness was often lower than the smaller streams (Figures 2 and 3).

The variation in species richness among seasons exhibited no consistent patterns. For example, in lower O'Fallon species richness was highest in the first year of sampling

(i.e., summer 2005 through spring 2006) in autumn (16) whereas in the second year of sampling (i.e., summer 2006 through spring 2007) species richness was highest in summer (13) (Figure 2). Cumulative species richness (i.e., year 1 and 2, pooled) exceeded species richness values of year 1, year 2, or both (Figure 2).

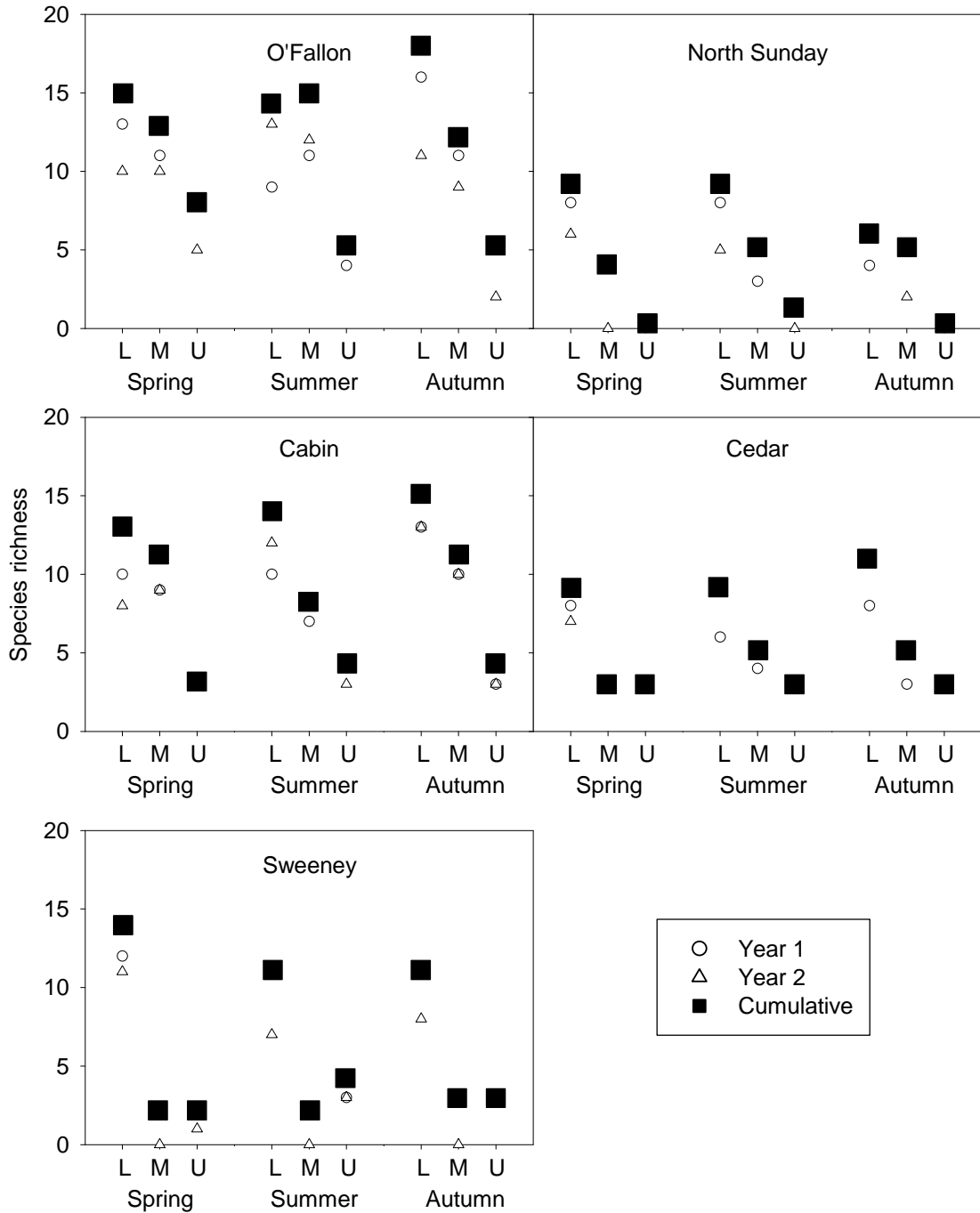


Figure 2. Species richness of lower (L), middle (M), and upper (U) spatiotemporal sites by stream and season. Cumulative species richness is calculated from year 1 and 2 pooled.

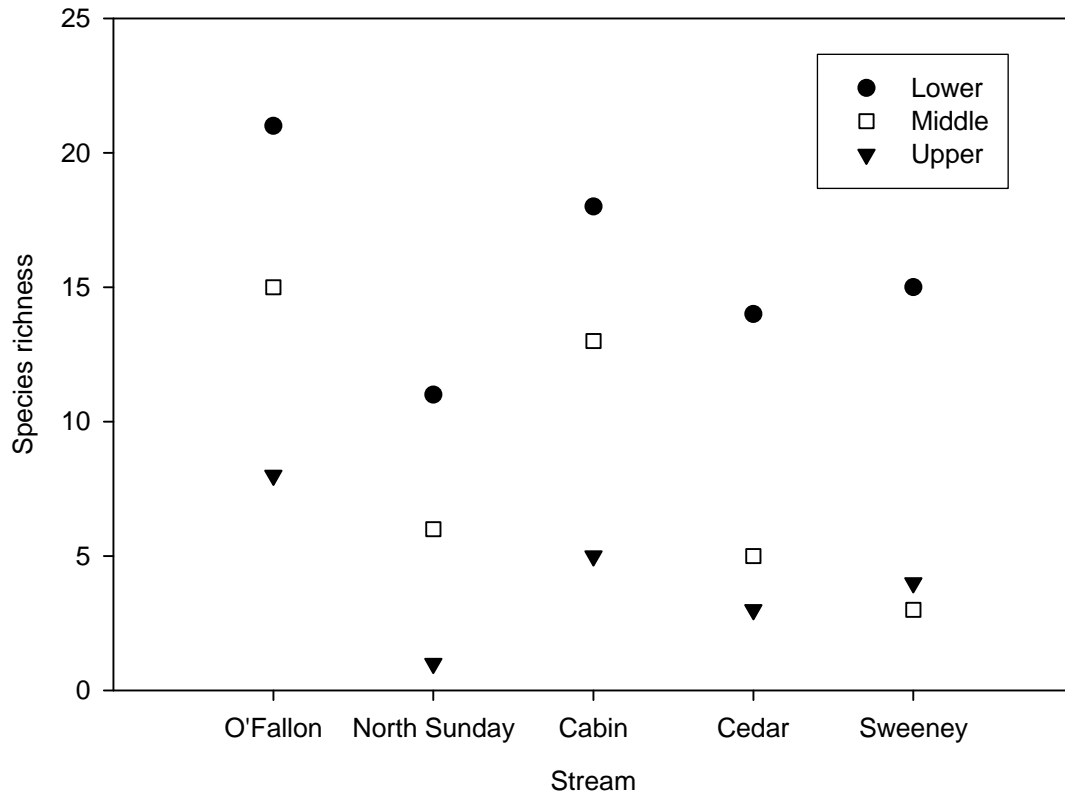


Figure 3. Cumulative species richness of lower, middle, and upper spatiotemporal sites by stream for all seasons and years pooled. Streams are ordered by watershed size (largest to smallest) from left to right.

Large River Fishes. Large river fishes in the five prairie streams made up about 19% of the individuals captured during spatiotemporal sampling (excluding juvenile *Hybognathus* spp., which includes species from both the large river and non-large river groups). Flathead chub were the most abundant (10%) followed by river carpsucker (4%), western silvery minnow (2%), channel catfish (1%), emerald shiner (1%), shorthead redhorse (1%), goldeye (<1%), and smallmouth buffalo (<1%). The presence and absence of large river species sampled from spatiotemporal sites are depicted in maps in Appendix C. Flathead chub and western silvery minnow were sampled in all five

streams, river carpsucker, channel catfish, and shorthead redhorse were sampled in four streams, goldeye and emerald shiner were sampled in three streams and smallmouth buffalo were sampled in two streams. A significant interaction between spatial position and stream ($F_{8, 45} = 5.22, P < 0.01$) indicated that the variation in large river species richness among spatial positions was not the same for all streams. Large river species richness varied more within and among streams than among seasons (Figure 4). Large river species richness declined from downstream to upstream and generally with decreasing watershed size (Figures 4 and 5). Large river species were never present in the upper sites of all streams and were never present in the middle sites of the smallest streams with potential movement barriers (i.e., Cedar and Sweeney) (Figure 4). Large river species richness in North Sunday was lower than expected based on watershed size (Figure 5).

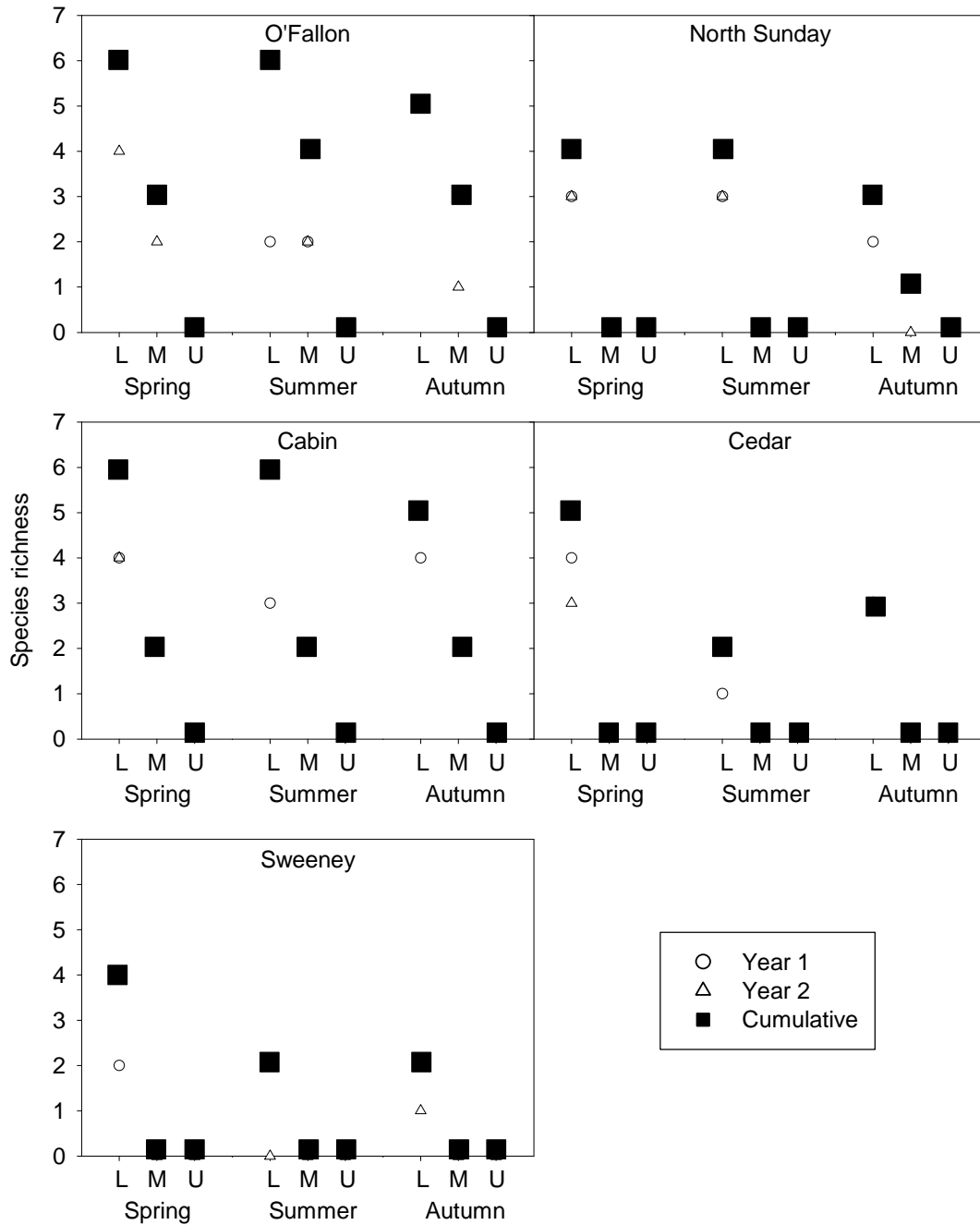


Figure 4. Large river species richness of lower (L), middle (M), and upper (U) spatiotemporal sites by stream and season. Cumulative species richness is calculated from year 1 and 2 pooled.

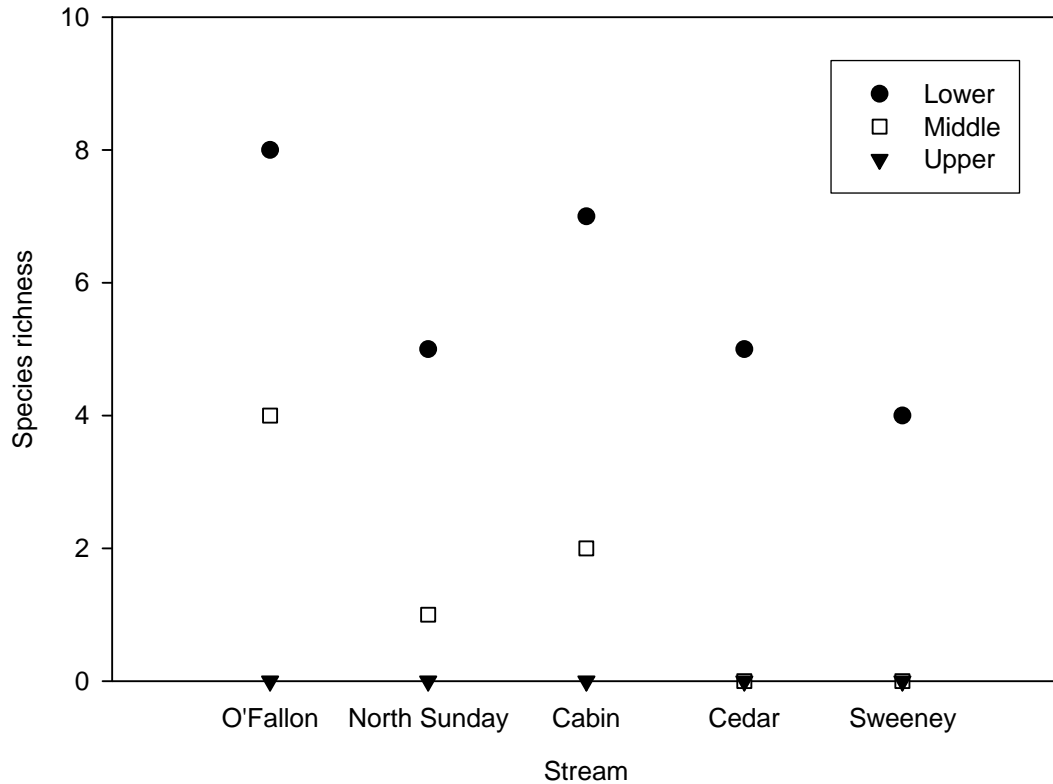


Figure 5. Cumulative large river species richness of lower, middle, and upper spatiotemporal sites by stream for all seasons and years pooled. Streams are ordered by watershed size (largest to smallest) from left to right.

Abiotic Characteristics

The maximum observed water temperature in the largest stream (i.e., O'Fallon) during sampling was 31.1°C (at the middle site, which was flowing) in August 2005.

Similar maximum temperatures were recorded at the other sites and streams.

Eighty-one percent (22 of 27) of winter sites surveyed had surface ice; however, a layer of liquid water was detected beneath the ice at all accessible sites except the upper sites of O'Fallon and North Sunday in 2007 (Table 1). Anchor ice was documented at two of five sites where surface ice did not exist. The five sites where surface ice did not exist

were flooded and included the lower, middle, and upper sites of Sweeney and the lower and middle sites of North Sunday. Significant interactions existed among many of the spatial position, stream, and year factors for ice thickness (spatial position x year; $F_{2,15} = 13.95$, $P < 0.01$, stream x year; $F_{2,15} = 12.42$, $P < 0.01$, spatial position x stream x year; $F_{2,15} = 14.33$, $P < 0.01$) preventing interpretation of main effects. However, there were no significant interactions for water depth beneath the ice and it differed significantly by year ($F_{1,15} = 15.66$, $P < 0.01$) with greater depths in 2006 (mean = 267 mm) than 2007 (mean = 55 mm).

Table 1. Number of holes drilled, mean, minimum, and maximum ice thickness and water depth beneath the ice by stream and spatial position measured at sites with ice coverage in February 2006 and 2007. Streams are ordered by watershed size (largest to smallest).

Variable	Stream	Spatial position	Descriptive statistics			
			N	Mean (mm)	Min (mm)	Max (mm)
Ice thickness	O'Fallon	Lower ^a	1	450	450	450
		Middle	1	200	200	200
		Upper	6	508	250	800
	North Sunday	Lower				
		Middle				
		Upper	1	200	200	200
	Cabin	Lower	4	420	200	700
		Middle	2	425	400	450
		Upper	4	338	100	1000
	Cedar	Lower ^a	3	467	350	550
		Middle ^a	3	417	400	450
		Upper	3	433	400	500
	Sweeney	Lower				
		Middle				
		Upper				
Water depth beneath ice	O'Fallon	Lower ^a	1	200	200	200
		Middle	1	250	250	250
		Upper	6	141	0	350
	North Sunday	Lower				
		Middle				
		Upper	1	0	0	0
	Cabin	Lower	4	300	200	500
		Middle	2	450	200	700
		Upper	4	163	50	400
	Cedar	Lower ^a	3	150	50	300
		Middle ^a	3	333	150	450
		Upper	3	183	100	250
	Sweeney	Lower				
		Middle				
		Upper				

^a Not accessible in February 2007

Stage height (at the middle site of all streams) from May to November 2006 varied the greatest in Cedar (138 to 1,288 mm) and the least in Sweeney (53 to 607 mm) (Figure 6). Peaks in stage height were generally associated with spates. However, a gradual peak in late June in O'Fallon was associated with the inundation of the stage height recorder by a beaver dam (Figure 6). The beaver dam was removed by the landowner in middle to late October (Figure 6). The middle sites of O'Fallon, Cabin, and

Cedar flowed continuously from May to November 2006 whereas North Sunday and Sweeney were often intermittent (Figure 6).

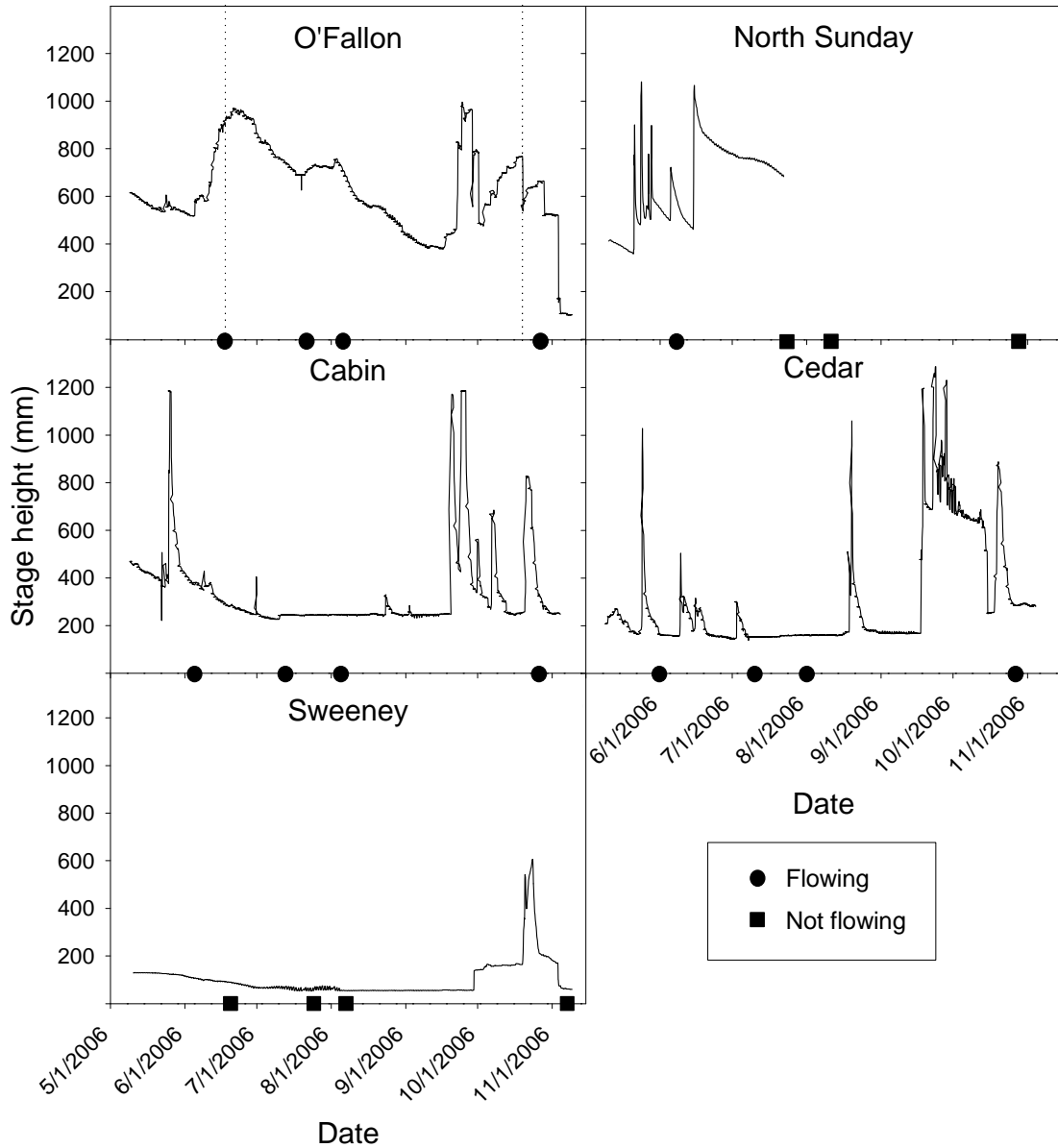


Figure 6. Stage height recorded at the middle site of all streams. Sampling events at middle sites are depicted by circles when the water was flowing and squares when the water was not flowing. The dashed lines in the O'Fallon panel represent the first observation of a beaver dam following stage height recorder installation (left) and the estimated time of beaver dam removal (right). The stage height dataset is incomplete for North Sunday because of equipment malfunctions. Streams are ordered by watershed size (largest to smallest) from left to right.

A significant interaction existed between spatial position and stream for all abiotic variables (wetted width; $F_{8,44} = 30.57$, $P < 0.01$, pool area; $F_{8,44} = 22.26$, $P < 0.01$, discharge; $F_{8,44} = 13.11$, $P < 0.01$, proportion of fine substrates; $F_{8,44} = 14.44$, $P < 0.01$, and thalweg depth; $F_{8,44} = 4.01$, $P < 0.01$) indicating that the variation in abiotic characteristics among spatial positions were not the same for all streams. Abiotic characteristics varied more within and among streams than among seasons (Table 2). In general, from downstream to upstream, wetted width, pool area, and discharge decreased and proportion of fine substrates increased (Table 2). Thalweg depth varied little among spatial positions and did not exhibit any patterns that were consistent across all streams (Table 2). In general, from large to small streams, wetted width, pool area, and discharge decreased (Table 2). The proportion of fine substrates among streams was variable; however, it was greatest in Sweeney for all sites (Table 2). Deviations from the trends in abiotic characteristics within and among streams existed and were often associated with large amounts of water in middle to upper reaches. For example, a large pool area was measured at the middle site in Sweeney during spring, because of flooding and the influence of spreader dikes.

Variation in abiotic characteristics among seasons was often less than variation among spatial positions (Table 2). Seasonal patterns were generally associated with streams drying through the summer. In general, wetted width, pool area, discharge, and thalweg depth decreased from spring through summer (Table 2). However, increases in these characteristics were sometimes measured in autumn (Table 2). Proportion of fine

substrates remained relatively constant among seasons, rarely varying more than 0.15

(Table 2).

Table 2. Mean and coefficient of variation (in parentheses) for habitat variables by stream, spatial position, and season, measured in spring 2006 and 2007, and summer and autumn 2005 and 2006. Values for each season are calculated from a sample size of two. Streams are ordered by watershed size (largest to smallest).

Variable	Stream	Spatial position	Season		
			Spring	Summer	Autumn
Mean wetted width (m)	O'Fallon	Lower	10.5 (1)	10.1 (11)	9.4 (13)
		Middle	4.5 (3)	4.2 (0)	4.2 (0)
		Upper	3.3 (62)	2.5 (49)	3.0 (48)
	North Sunday	Lower	11.3 (1)	7.7 (10)	9.8 (7)
		Middle	2.9 (5)	2.4 (6)	3.0 (2)
		Upper	2.7 (10)	2.3 (20)	1.6 (5)
	Cabin	Lower	5.2 (1)	4.7 (2)	5.0 (1)
		Middle	1.7 (9)	1.7 (0)	1.8 (9)
		Upper	2.5 (20)	1.4 (5)	1.3 (2)
	Cedar	Lower	5.2 (4)	4.0 (15)	4.6 (8)
		Middle	2.9 (9)	2.1 (18)	2.6 (16)
		Upper	2.7 (2)	2.4 (24)	2.4 (17)
	Sweeney	Lower	2.4 (7)	2.3 (11)	2.3 (13)
		Middle	8.0 (80)	1.6 (141)	3.8 (5)
		Upper	6.0 (5)	5.6 (14)	4.9 (1)
Pool area (m ²)	O'Fallon	Lower	3,153 (1)	3,015 (11)	2,815 (13)
		Middle	1,361 (3)	1,249 (0)	1,265 (0)
		Upper	995 (62)	638 (82)	890 (49)
	North Sunday	Lower	3,393 (1)	2,003 (17)	2,954 (7)
		Middle	880 (5)	621 (9)	863 (7)
		Upper	818 (10)	249 (38)	86 (24)
	Cabin	Lower	1,564 (1)	1,418 (2)	1,500 (2)
		Middle	522 (8)	510 (0)	554 (9)
		Upper	764 (20)	410 (5)	391 (2)
	Cedar	Lower	1,564 (4)	1,175 (18)	1,387 (8)
		Middle	874 (9)	619 (18)	765 (16)
		Upper	799 (2)	621 (24)	731 (17)
	Sweeney	Lower	708 (7)	691 (11)	695 (13)
		Middle	2,249 (95)	469 (141)	966 (33)
		Upper	1,799 (5)	1,150 (25)	973 (2)

Table 2. Continued.

Discharge (m ³ /s)	O'Fallon	Lower	0.528 (43)	0.424 (62)	0.050 (19)
		Middle	0.097 (15)	0.004 (101)	0.015 (82)
		Upper	0.005 (141)	0.000	0.000
	North Sunday	Lower	0.170 (18)	0.000	0.026
		Middle	0.001 (77)	0.000	0.000
		Upper	0.000	0.001 (109)	0.000
	Cabin	Lower	0.118 (11)	0.020 (115)	0.048 (74)
		Middle	0.069 (22)	0.007 (46)	0.013 (84)
		Upper	0.076 (81)	0.007 (141)	0.007 (91)
	Cedar	Lower	0.192 (22)	0.004 (141)	0.010 (71)
		Middle	0.157 (34)	0.000 (141)	0.002
		Upper	0.023 (19)	0.000	0.000 (52)
	Sweeney	Lower	0.020 (59)	0.005 (137)	0.007 (2)
		Middle	0.001 (141)	0.000	0.000
		Upper	0.000	0.000	0.000
Proportion of fine substrates	O'Fallon	Lower	0.11 (0)	0.09 (47)	0.15 (5)
		Middle	0.09 (63)	0.04 (71)	0.12 (55)
		Upper	1.00 (1)	1.00 (0)	1.00 (0)
	North Sunday	Lower	0.16 (114)	0.03 (28)	0.36 (62)
		Middle	0.36 (35)	0.34 (58)	0.39 (40)
		Upper	0.85 (1)	0.98 (3)	0.67 (71)
	Cabin	Lower	0.01 (141)	0.01 (141)	0.01 (141)
		Middle	0.03 (28)	0.02 (47)	0.03 (28)
		Upper	0.59 (4)	0.57 (24)	0.58 (14)
	Cedar	Lower	0.23 (6)	0.08 (124)	0.20 (78)
		Middle	0.52 (32)	0.19 (27)	0.48 (15)
		Upper	0.61 (19)	0.52 (40)	0.61 (14)
	Sweeney	Lower	0.47 (17)	0.41 (2)	0.50 (8)
		Middle	1.00 (0)	1.00 (0)	1.00 (0)
		Upper	0.98 (1)	0.98 (1)	1.00 (1)
Mean thalweg depth (m)	O'Fallon	Lower	0.49 (29)	0.46 (18)	0.42 (29)
		Middle	0.42 (27)	0.37 (2)	0.37 (17)
		Upper	0.41 (61)	0.39 (83)	0.46 (52)
	North Sunday	Lower	0.44 (2)	0.34 (4)	0.37 (10)
		Middle	0.42 (4)	0.34 (8)	0.41 (2)
		Upper	0.53 (3)	0.35 (24)	0.18 (24)
	Cabin	Lower	0.38 (1)	0.32 (9)	0.35 (10)
		Middle	0.42 (12)	0.32 (2)	0.33 (13)
		Upper	0.95 (16)	0.64 (1)	0.51 (22)
	Cedar	Lower	0.44 (4)	0.27 (10)	0.32 (11)
		Middle	0.64 (17)	0.40 (32)	0.53 (28)
		Upper	0.47 (3)	0.45 (21)	0.46 (6)
	Sweeney	Lower	0.36 (4)	0.37 (27)	0.33 (0)
		Middle	0.55 (67)	0.14 (141)	0.33 (47)
		Upper	0.54 (8)	0.50 (41)	0.37 (15)

Fish Assemblage and Abiotic Associations

Species richness was significantly correlated with fish abundance and both were correlated with pool area, wetted width, and proportion of fine substrates (Table 3). The correlations between abundance and the abiotic variables were weaker than between species richness and the abiotic variables (Table 3). Among abiotic variables, all relationships were significantly correlated except between thalweg depth and wetted width (Table 3).

Table 3. Correlation coefficients and *P*-values for test $\beta_1 = 0$. All correlations are for linear relationships with $N = 89$. Proportion of fine substrates is abbreviated by fines.

	Species richness	Fish abundance ^b	Pool area ^{ab}	Thalweg depth ^a	Wetted width ^{ab}	Fines ^{ab}
Species richness	-	0.63 <0.01	0.44 <0.01	-0.19 0.08	0.34 <0.01	-0.71 <0.01
Abundance ^b		-	0.35 <0.01	-0.09 0.43	0.24 0.04	-0.45 <0.01
Pool area ^{ab}			-	0.23 0.03	0.90 <0.01	-0.33 <0.01
Thalweg depth ^a				-	0.11 0.30	0.22 0.04
Wetted width ^{ab}					-	-0.23 0.03
Fines ^{ab}						-

^a Abiotic variables

^b Variables were \log_{10} transformed

The correlations between species richness, pool area, and proportion of fine substrates were further examined by position, stream, and season categories. Most of the correlations between species richness, pool area, and proportion of fine substrates were not significant when analyzed by position (Table 4). When analyzed by stream, significant positive correlations between species richness and pool area existed for

O'Fallon, North Sunday, Cabin, and Cedar. A significant negative relationship between species richness and pool area was detected for Sweeney (Table 4). Correlations were significant between species richness and proportion of fine substrates by stream and were negative (Table 4). When analyzed by season, most of the correlations between species richness, pool area, and proportion of fine substrates were significant (Table 4).

Table 4. Sample size, correlation coefficients, and P -values for the test $\beta_1 = 0$ for the relationships between species richness, pool area, and proportion of fine substrates for spatiotemporal sites by position, stream, and season. Streams are ordered by watershed size (largest to smallest). Dry sites ($N=1$) were excluded from analyses.

Category	Level	Variable					
		Pool area ^b			Fines ^b		
		N	r	P -value	N	r	P -value
Position							
	Lower	30	-0.05	0.79	30	-0.08	0.68
	Middle	29	-0.04	0.82	29	-0.83	<0.01
	Upper	30	0.40	0.03	30	0.10	0.61
Stream							
	O'Fallon	18	0.73	<0.01	18	-0.84	<0.01
	North Sunday	18	0.75	<0.01	18	-0.77	<0.01
	Cabin	18	0.65	<0.01	18	-0.90	<0.01
	Cedar	18	0.72	<0.01	18	-0.67	<0.01
	Sweeney	17	-0.54	0.03	17	-0.92	<0.01
Season							
	Spring	30	0.22	0.25	30	-0.71	<0.01
	Summer	29	0.60	<0.01	29	-0.71	<0.01
	Autumn	30	0.54	<0.01	30	-0.75	<0.01

^bVariables were \log_{10} transformed

All single variable CCA models (with all streams pooled) were significant with the exception of season (Table 5). Spatial position explained the greatest amount of variation in the fish assemblage (i.e., species identity and abundance), followed by proportion of fine substrates (Table 5). Additional models explained less than 10% of the variation (Table 5).

Table 5. Single variable canonical correspondence analysis model output with percent of variation explained and *P*-value.

Model variable	Percent variation explained	<i>P</i> -value
Spatial position	18.5	0.001
Proportion of fine substrates	13.9	0.001
Pool area	7.3	0.001
Wetted width	6.9	0.001
Thalweg depth	4.4	0.002
Rank watershed size	4.3	0.002
Discharge	4.3	0.002
Season	2.1	0.717

All five stepwise models (varying from one to five variables) were significant (Table 6). No inflection point was detected in the variation-explained plot (Figure 7), thus the two-variable model was selected as the best model because the three-variable model did not explain an additional 5% of variation (Table 6). An additional 6.7% of variation was explained by adding proportion of fine substrates to the spatial position CCA model.

Table 6. Canonical correspondence analysis models and output using a stepwise model building approach. For each model type, the significant model that explained the most variation is presented. The two-variable model was selected as the multivariable model for further assessment. Proportion of fine substrates is abbreviated by fines and rank watershed size is abbreviated by rank WS.

Model type	Model variable(s)	Percent variation explained	<i>P</i> -value
One variable	Spatial position	18.5	0.001
Two variable	Spatial position + fines	25.2	0.001
Three variable	Spatial position + fines + rank WS	29.9	0.001
Four variable	Spatial position + fines + rank WS + pool area	33.3	0.002

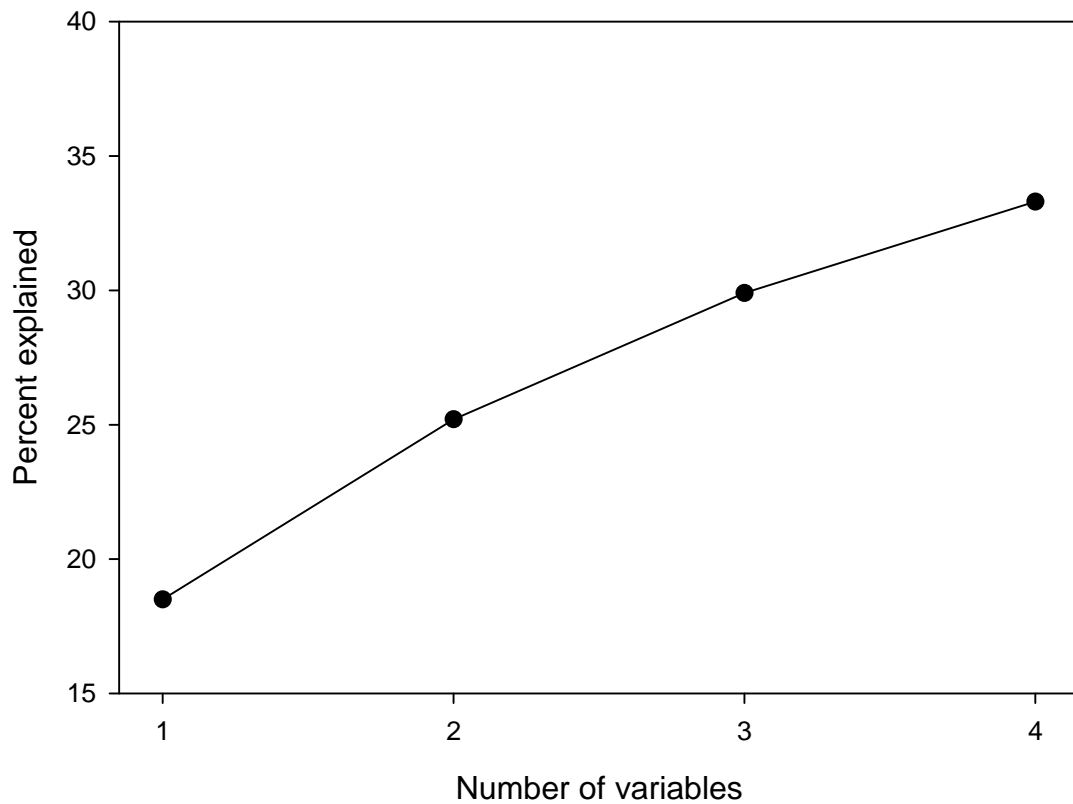


Figure 7. Line plot of the percent of variation explained by the model as a function of the number of variables in the model.

Spatial position and proportion of fine substrates explained 25% of the overall variation in the fish assemblage and CCA axes 1 and 2 represented 92% of this variation. Brassy minnow *Hybognathus hankinsoni*, green sunfish *Lepomis cyanellus*, black bullhead *Ameiurus melas*, and fathead minnow were associated with upper spatial positions (i.e., near the headwaters) with higher amounts of fine substrates (Figure 8). In contrast, stonecat *Noturus flavus*, river carpsucker, western silvery minnow, flathead chub, common carp *Cyprinus carpio*, and sand shiner were associated with lower spatial positions (i.e., near the confluence with the Yellowstone River) with lower amounts of

fine substrates (Figure 8). Longnose dace *Rhinichthys cataractae*, channel catfish, white sucker, shorthead redhorse, and creek chub *Semotilus atromaculatus* were loosely associated with lower and middle spatial positions with lower amounts of fine substrates (Figure 8). Plains minnow and lake chub were loosely associated with middle and upper spatial positions with moderate amounts of fine substrates (Figure 8). The northern plains killifish *Fundulus kansae* was not strongly associated with any spatial positions, although it was associated with moderate amounts of fine substrates. However, these species associated with middle sites, moderate amounts of fine substrates, or both (Figure 8), may alternatively be interpreted as unrelated to these variables (Ter Braak 1987).

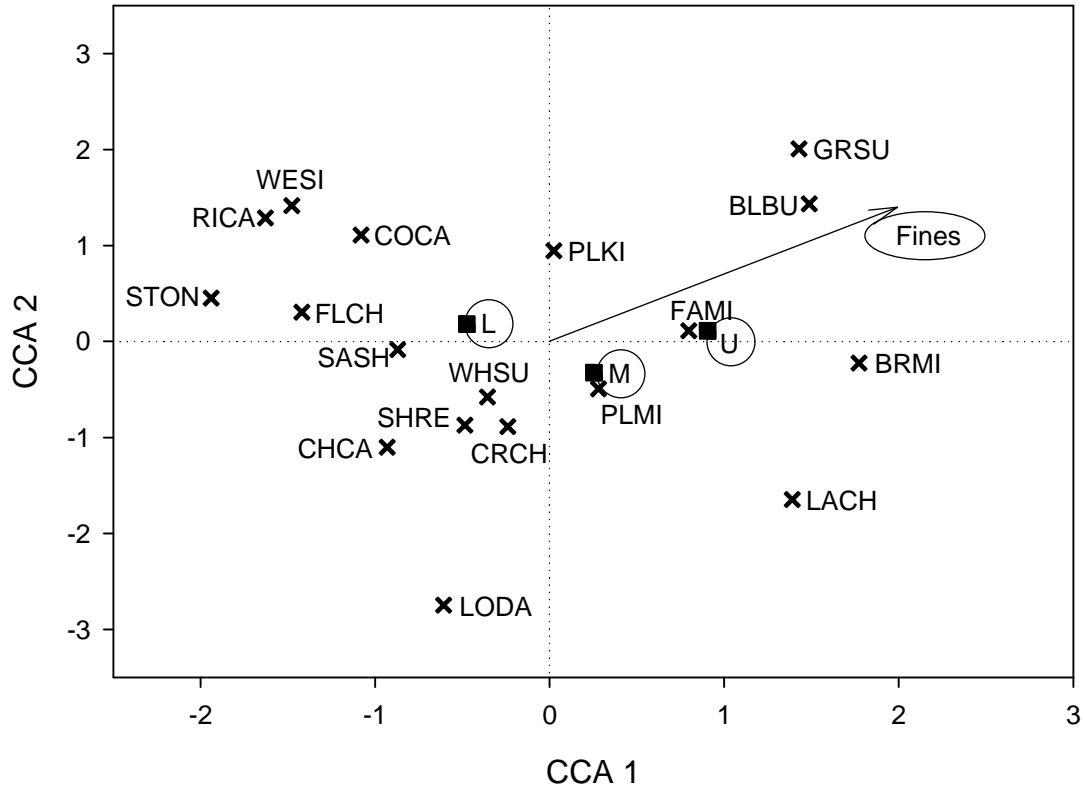


Figure 8. Canonical correspondence analysis ordination plot of fish species (x) and explanatory variables (boxes and arrow) depicted from data sampled in O’Fallon, North Sunday, Cabin, Cedar, and Sweeney. Sites were sampled once a season (excluding winter) from summer 2005 through spring 2007. Abbreviations for fish species are black bullhead (BLBU), brassy minnow (BRMI), channel catfish (CHCA), common carp (COCA), creek chub (CRCH), fathead minnow (FAMI), flathead chub (FLCH), green sunfish (GRSU), lake chub (LACH), longnose dace (LODA), plains minnow (PLMI), northern plains killifish (PLKI), river carpsucker (RICA), sand shiner (SASH), shorthead redhorse (SHRE), stonecat (STON), western silvery minnow (WESI), and white sucker (WHSU). Abbreviations for the explanatory variables (circled) are proportion of fine substrates (Fines), and lower, middle, and upper spatial positions (L, M, and U, respectively).

Although the two-variable model was determined to be the “best” model, the three-variable model nearly met the 5% cutoff (4.7%) and was deemed worthy of interpretation. The three-variable model with spatial position, proportion of fine

substrates, and rank watershed size explained 30% of the overall variation and CCA axes 1 and 2 represented 81% of this variation. Interpretations of species associations with spatial position and proportion of fine substrates were nearly identical to the two-variable model. However, with the three-variable model, species were also associated with watershed size. Stonecat, river carpsucker, western silvery minnow, flathead chub, common carp, channel catfish, sand shiner, and shorthead redhorse were associated with larger watershed sizes and lake chub, plains minnow, and fathead minnow were associated with smaller watershed sizes (Figure 9). Longnose dace, creek chub, white sucker, northern plains killifish, brassy minnow, green sunfish, and black bullhead were located near the center of the watershed size vector indicating they were unrelated to watershed size or related to intermediate watershed sizes (Figure 9). The watershed size vector is smaller than the proportion of fine substrates vector and watershed size was the last variable added, thus it likely had less overall influence in structuring the ordination. Therefore, interpretation with respect to watershed size should be made with caution. For example, brassy minnow was found only in the largest stream, yet is interpreted as being associated with intermediate watershed sizes or unrelated to watershed size. The location of brassy minnow in the ordination is likely because it was sampled only in the upper spatial position where fine substrates was 100% and these variables were more influential in constructing the ordination than watershed size. Similarly, the location of longnose dace is likely a function of the proportion of fine substrates because longnose dace were only found where proportion of fine substrates was low.

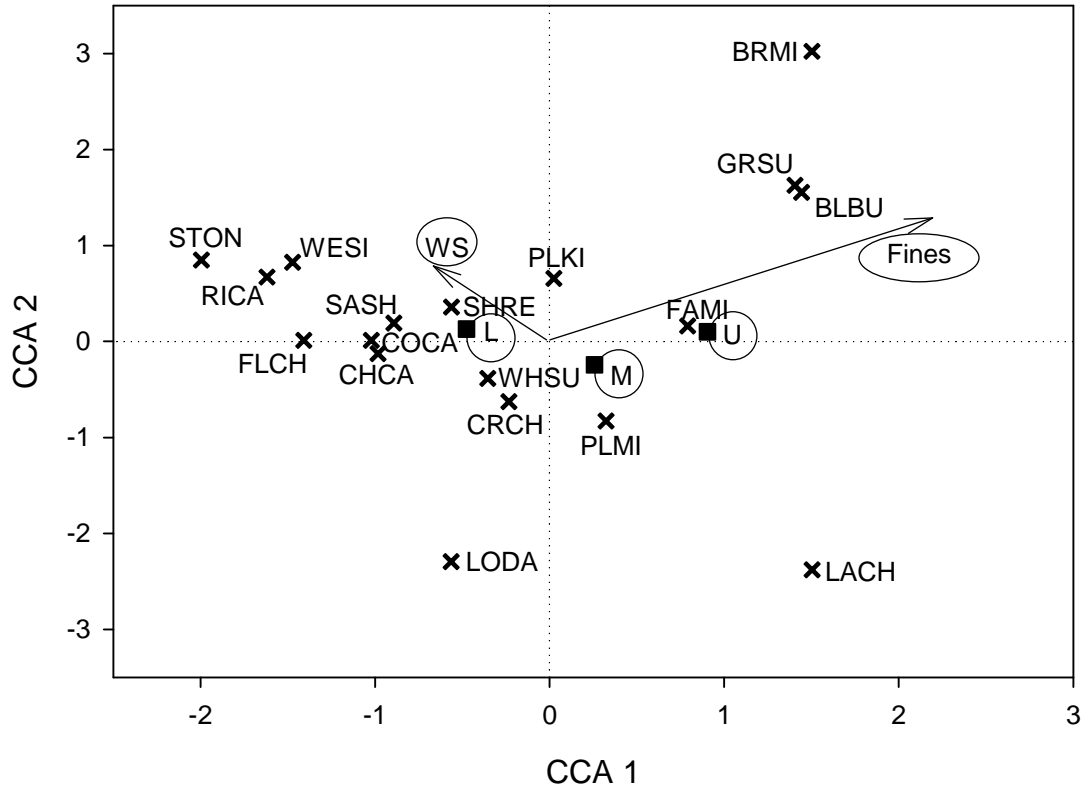


Figure 9. Canonical correspondence analysis ordination plot of fish species (x) and explanatory variables (boxes and arrows) depicted from data sampled in O'Fallon, North Sunday, Cabin, Cedar, and Sweeney. Sites were sampled once a season (excluding winter) from summer 2005 and through spring 2007. Abbreviations for fish species are black bullhead (BLBU), brassy minnow (BRMI), channel catfish (CHCA), common carp (COCA), creek chub (CRCH), fathead minnow (FAMI), flathead chub (FLCH), green sunfish (GRSU), lake chub (LACH), longnose dace (LODA), plains minnow (PLMI), northern plains killifish (PLKI), river carpsucker (RICA), sand shiner (SASH), shorthead redhorse (SHRE), stonecat (STON), western silvery minnow (WESI), and white sucker (WHSU). Abbreviations for the explanatory variables (circled) are rank watershed size (WS), proportion of fine substrates (Fines), and lower, middle, and upper spatial positions (L, M, and U, respectively).

Spatial position was the single variable that explained the most variation in the fish assemblage when CCA analyses were conducted by stream (Table 7). However, the results of the CCA models by stream did differ from the CCA results for all streams

pooled. Proportion of fine substrates was not included in any of the CCA models by stream and season was included in Cabin and season and pool area were included in Cedar (Table 7). Only single variable models with spatial position were significant for O’Fallon, North Sunday, and Sweeney (Table 7). Models by stream explained more variation than models with all streams pooled (Tables 6 and 7).

Table 7. Canonical correspondence analysis models and output by stream using a stepwise model building approach. For each model type (i.e., one variable, two variable, etc.) the selected model was determined as the significant model that explained the most variation. The model building process concluded when the addition of the next variable explained less than an additional 5% of variation. Streams are ordered by watershed size (largest to smallest).

Stream	Model variable(s)	Percent variation explained	P-value
O’Fallon	Spatial position	51.5	0.001
North Sunday	Spatial position	51.7	0.001
Cabin ^a	Spatial position + season	65.2 (55.7)	0.049 (0.001)
Cedar ^a	Spatial position + season	79.4 (61.7)	0.046 (0.001)
Sweeney	+ pool area Spatial position	62.4	0.001

^a Values in parentheses indicate the percent of variation explained and P-value for the single variable models with spatial position.

Goldeye *Hiodon alosoides*, emerald shiner *Notropis atherinoides*, longnose sucker *Catostomus catostomus*, smallmouth buffalo *Ictiobus bubalus*, brook stickleback *Culaea inconstans*, and bluegill *Lepomis macrochirus* were rare species sampled and not assessed using CCA analyses. Of these species only the bluegill is non-native. All of the rare species were sampled only at lower sites except brook stickleback which was sampled only at the upper site in O’Fallon (Table 8). The season when rare species were sampled varied by species (Table 8).

Table 8. Summary table of rare species indicating the stream, spatial position, season, and year where sampled.

Family Common name, <i>Genus species</i>	Spatiotemporal characteristics			
	Stream	Spatial position	Season	Year
Hiodontidae				
goldeye, <i>Hiodon alosoides</i>	O'Fallon	Lower	Summer	2006
	North Sunday	Lower	Summer	2005
	Cabin	Lower	Summer	2006
Cyprinidae				
emerald shiner, <i>Notropis atherinoides</i>	O'Fallon	Lower	Spring	2006
			Summer	2006
			Autumn	2006
			Spring	2007
	Sweeney	Lower	Spring	2007
Catostomidae				
longnose sucker, <i>Catostomus catostomus</i>	Sweeney	Lower	Summer	2005
smallmouth buffalo, <i>Ictiobus bubalus</i>	O'Fallon	Lower	Autumn	2005
	Cabin	Lower	Autumn	2006
			Spring	2007
Gasterosteidae				
brook stickleback, <i>Culaea inconstans</i>	O'Fallon	Upper	Summer	2005
			Autumn	2005
			Spring	2006
			Summer	2006
			Spring	2007
Centrarchidae				
bluegill, <i>Lepomis macrochirus</i>	O'Fallon	Lower	Summer	2006

Summer Longitudinal

Fish Assemblage Characteristics

Twenty-five species and 52,449 individuals were collected from the 178 longitudinal samples. Eighteen species were native (96% of the individuals) and seven non-native (4% of the individuals). Fathead minnow (40%), sand shiner (10%), plains minnow, (10%) flathead chub (5%), and lake chub (4%) were the five most abundant species and made up about 62% of the total abundance. At least one fish was sampled at

each longitudinal site, except for longitudinal site 10 on North Sunday and Cedar where no fish were sampled (Appendix B).

Species richness was negatively related to distance from the mouth for all streams (Figure 10). All relationships between species richness and distance from mouth were fit with a quadratic model, except North Sunday. Watershed size influenced the relationship between species richness and distance from the mouth. For example, species richness remained high farther upstream in streams with larger watersheds (e.g., O'Fallon) than streams with smaller watersheds (e.g., Sweeney) (Figure 11). However, species richness near the mouth and in the headwaters was similar for all streams (Figure 11). North Sunday had lower species richness than expected based on watershed size (Figure 11).

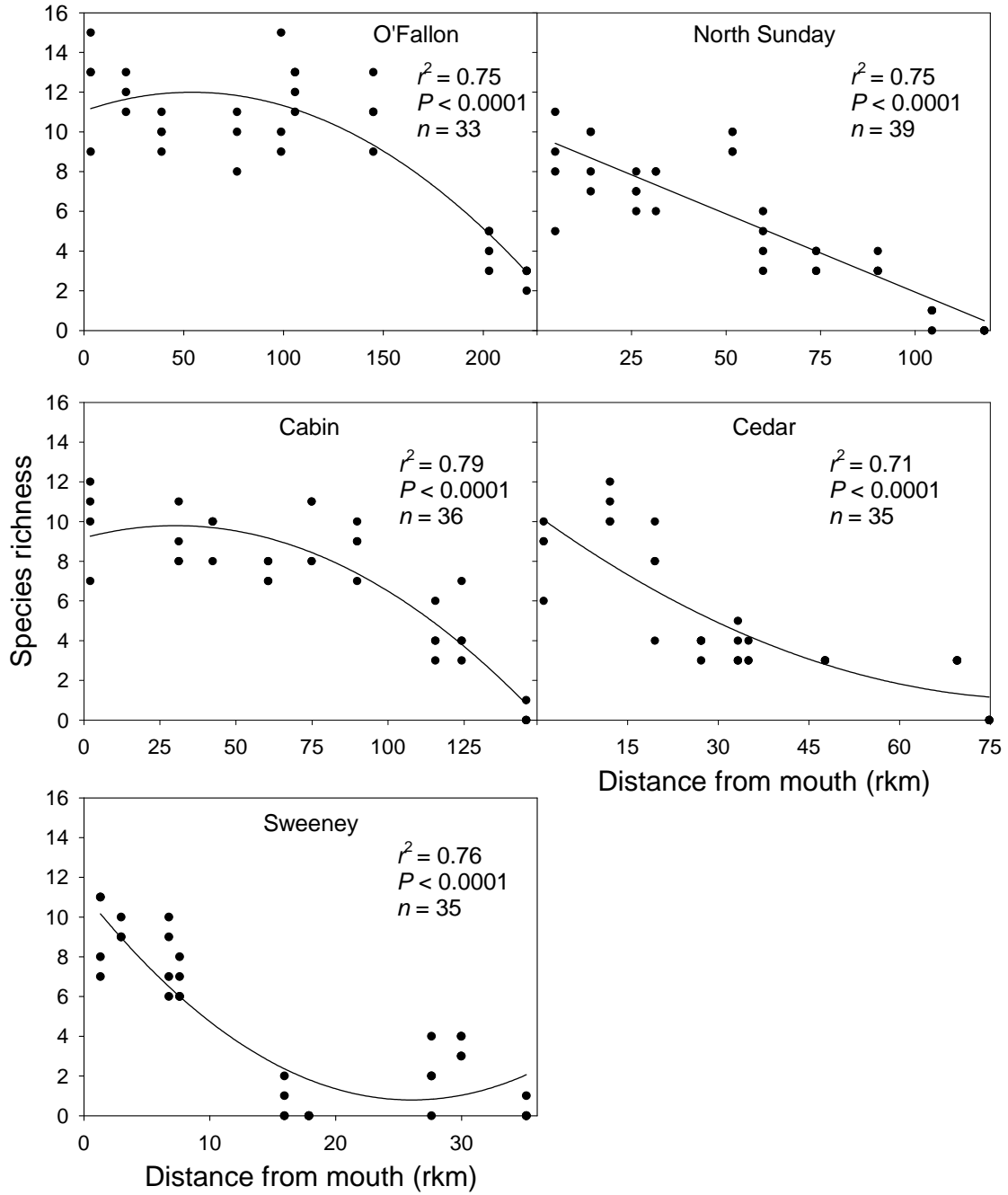


Figure 10. Relationship between species richness and distance from the mouth (rkm) by stream. Streams are ordered by watershed size (largest to smallest) from left to right.

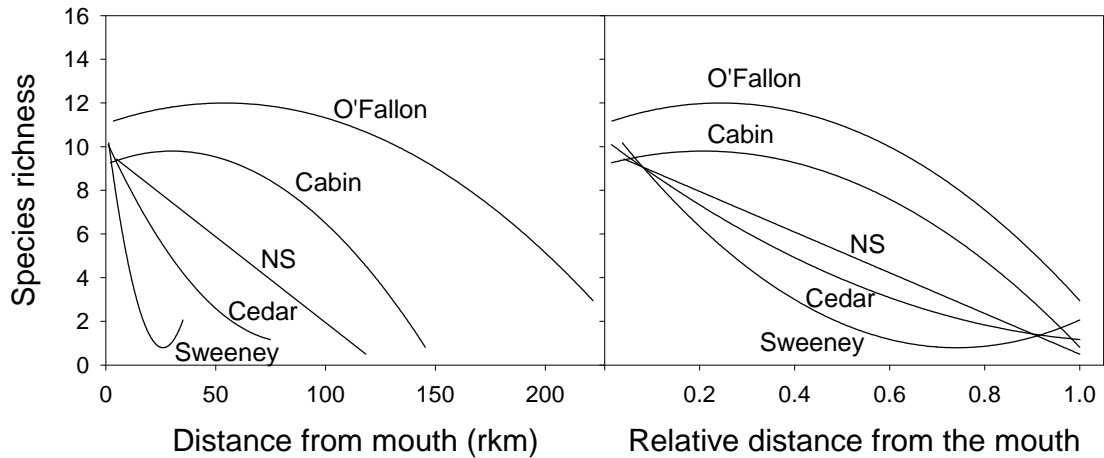


Figure 11. Relationships between species richness and distance from the mouth (rkm) (left) and species richness and relative distance from the mouth (right) for all streams.

Large River Fishes. Large river fishes in the five prairie streams made up about 9% of the individuals sampled from longitudinal sampling (excluding juvenile *Hybognathus* spp.). Flathead chub were the most abundant (5%); followed by river carpsucker (2%), channel catfish (1%), western silvery minnow (1%), shorthead redhorse (<1%), goldeye (<1%), and emerald shiner (<1%). The presence and absence of large river species sampled from longitudinal sites are depicted in a table and maps in Appendix B and C. Channel catfish and western silvery minnow were the only large river species sampled in every stream. Flathead chub and river carpsucker were sampled in four streams (all except Sweeney), shorthead redhorse and goldeye were sampled in three streams (O'Fallon, Cabin, and Sweeney and O'Fallon, North Sunday, and Cabin, respectively) and emerald shiner were sampled in two streams (O'Fallon and Cedar). Large river species richness in the study streams ordered by watershed size (largest to smallest) was O'Fallon (7), North Sunday (5), Cabin (6), Cedar (5), and Sweeney (3). Large river fishes were limited to lower and middle reaches and only occasionally found

in upper reaches. Large river species were generally observed farther upstream in streams with larger watersheds.

Presence of flathead chub, river carpsucker, channel catfish, and western silvery minnow by distance from the mouth were significantly modeled using logistic regression (Figure 12). Flathead chub and channel catfish were more likely to be detected farther upstream than river carpsucker and western silvery minnow (Figure 12). Logistic regression models were not significant for shorthead redhorse, goldeye, and emerald shiner because they were rarely detected at upstream sites (Figure 13).

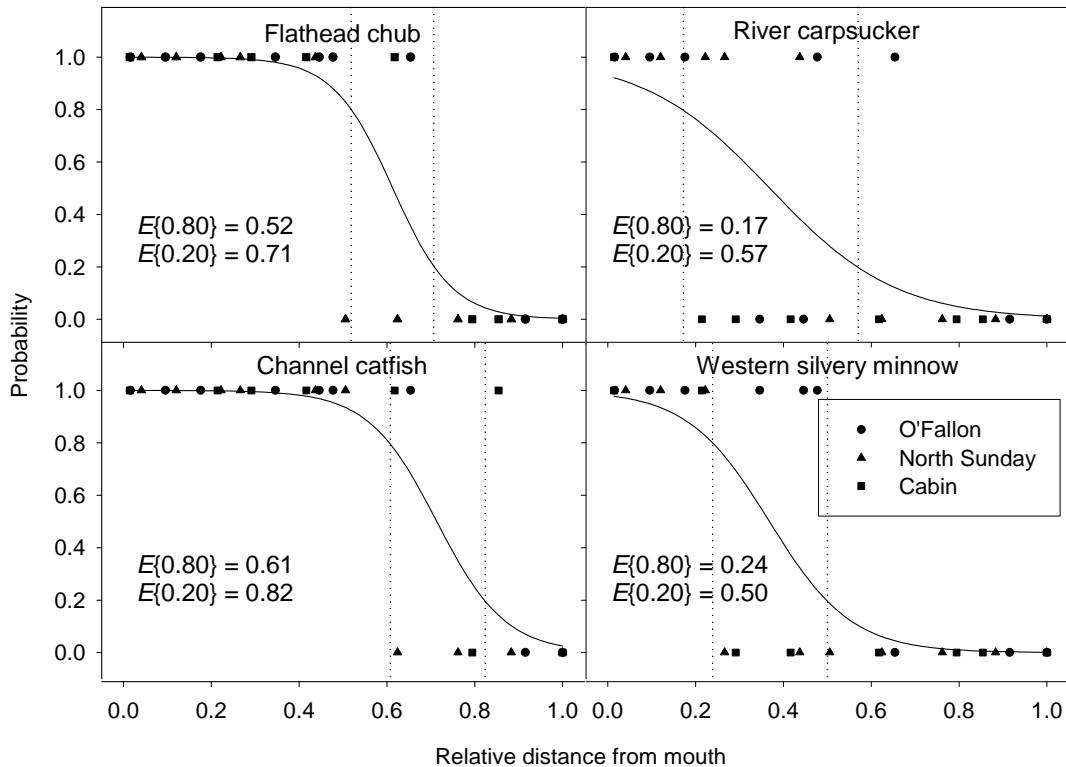


Figure 12. Logistic regression of species presence by relative distance from the mouth for flathead chub, river carpsucker, channel catfish, and western silvery minnow, sampled from O'Fallon, North Sunday, and Cabin in June and July 2005 and 2006. Dotted lines indicate where the probability of capturing the species is 80% (left) and 20% (right).

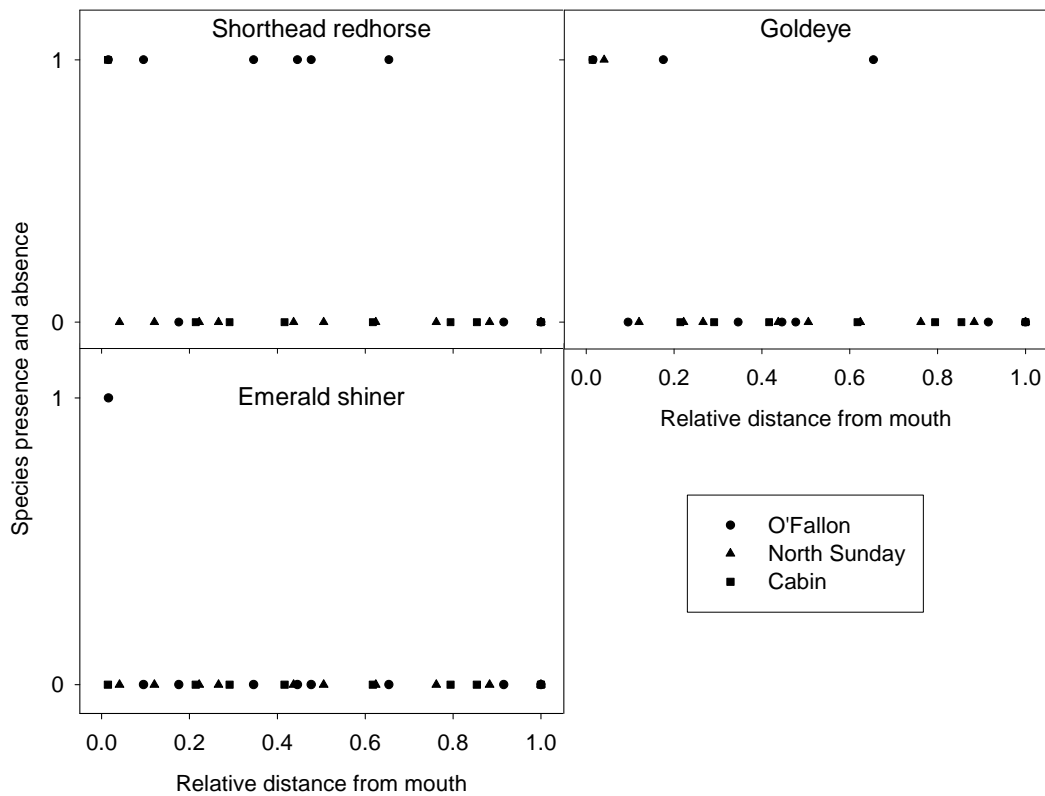


Figure 13. Species presence (1) and absence (0) by relative distance from the mouth for shorthead redhorse, goldeye, and emerald shiner sampled from O'Fallon, North Sunday, and Cabin in June and July 2005 and 2006.

Abiotic Characteristics

Pool area and proportion of fine substrates were the abiotic variables most strongly correlated with species richness and abundance in the spatiotemporal analysis and thus were examined as a function of distance from the mouth. Pool area was negatively related to distance from the mouth for all streams, except Sweeney (Table 9 and Figure 14). Conversely, proportion of fine substrates was positively related to distance from the mouth for all streams (Table 9 and Figure 14). The relationship between proportion of fine substrates and distance from the mouth was best fit with a

quadratic model for O'Fallon, and Cabin and a logistic model for Sweeney (Figure 14).

All other relationships were linear (Figure 14).

Table 9. Regression statistics for linear, quadratic, and logistic relationships between pool area and proportion of fine substrates (Fines) with distance from the mouth (rkm).

Stream	Variable	<i>N</i>	r^2	<i>P</i> -value
O'Fallon	Pool area ^a	33	0.62	<0.01
	Fines ^a	33	0.92	<0.01
North Sunday	Pool area ^a	38	0.85	<0.01
	Fines	38	0.88	<0.01
Cabin	Pool area	35	0.61	<0.01
	Fines ^a	35	0.84	<0.01
Cedar	Pool area	35	0.68	<0.01
	Fines	35	0.51	<0.01
Sweeney	Pool area	27	0.02	0.48
	Fines ^b	27	0.85	<0.01

^a Denotes quadratic relationships.

^b Denotes logistic relationship.

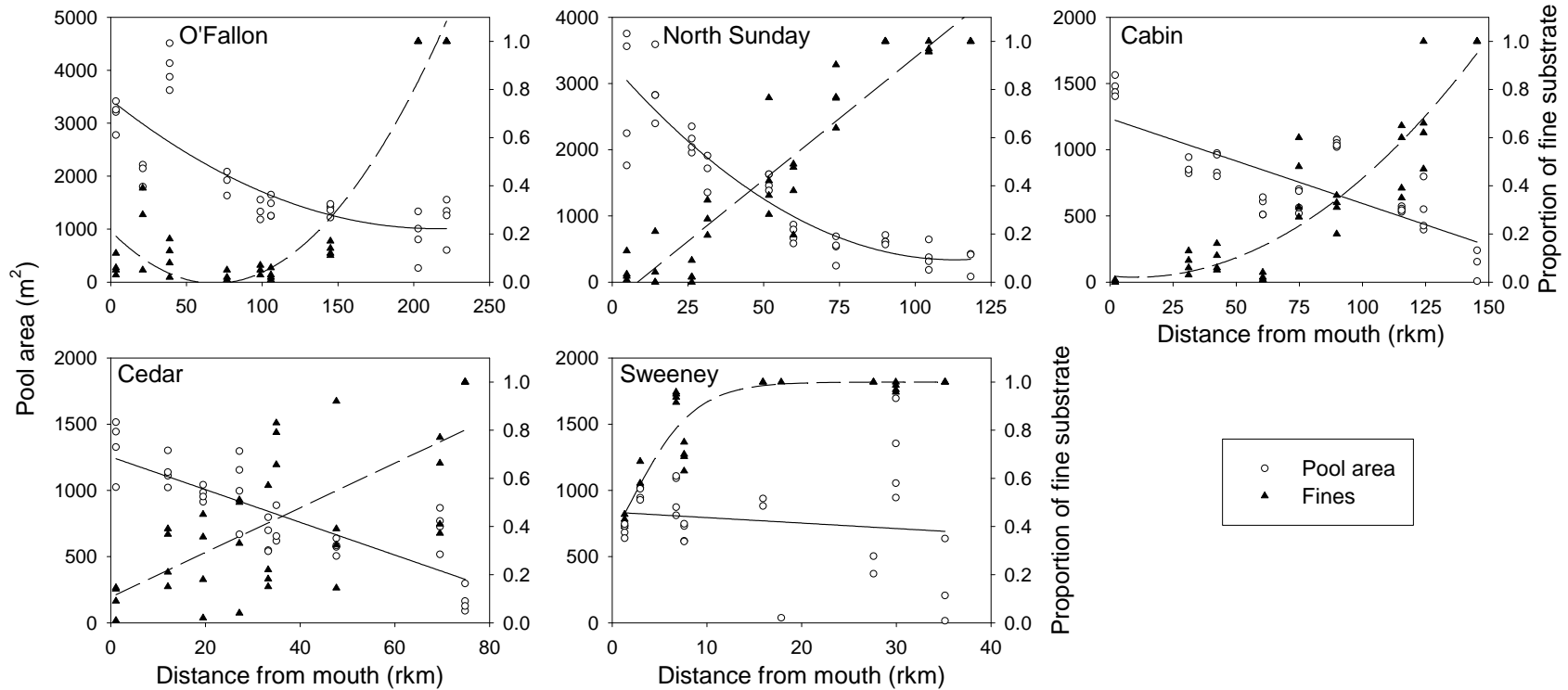


Figure 14. Relationships of pool area (m²) and proportion of fine substrates with distance from the mouth, sampled from longitudinal sites in June and July 2005 and 2006. For all streams, the left y-axis is pool area (m²), the right y-axis is proportion of fine substrates, and the x-axis is distance from mouth (rkm). Linear, quadratic, and logistic regression lines are shown for pool area (solid lines) and proportion of fine substrates (dashed lines). All relationships are significant ($P \leq 0.05$) except for the pool area-distance from mouth relationship in Sweeney. Streams are ordered by watershed size (largest to smallest) from left to right.

Fish Assemblage and Abiotic Associations

Abrupt changes in species richness appeared to correspond with abrupt changes in proportion of fine substrates. High levels of species richness were observed in O'Fallon and Cabin relatively far upstream, before declining. The distance from the mouth where species richness declined in O'Fallon and Cabin corresponded to large increases in proportion of fine substrates (Figures 10 and 14). In contrast to O'Fallon and Cabin, species richness declined relatively quickly in Cedar and Sweeney. The distance from the mouth where species richness began to asymptote at low levels corresponded to potential movement barriers in Cedar and Sweeney and large increases in proportion of fine substrates in Sweeney (Figures 10 and 14). Changes in pool area were not as abrupt as changes in proportion of fine substrates and could not be associated with abrupt changes in species richness. However, in general relationships between species richness and pool area with distance from the mouth were both negative (Figures 10 and 14).

Survey Effort

Cumulative species richness increased with increasing number of sampling events (Figure 15). Species richness curves appeared to asymptote at all sites except lower O'Fallon and lower Cedar (Figure 15). More samples were required to gain a better representation of cumulative species richness at lower sites than middle or upper sites and more samples were required on the largest stream (O'Fallon) than the smallest (Sweeney) stream (Figure 15). In general, to represent most of the species present, four, two, and one sampling event were required for lower, middle, and upper sites, respectively.

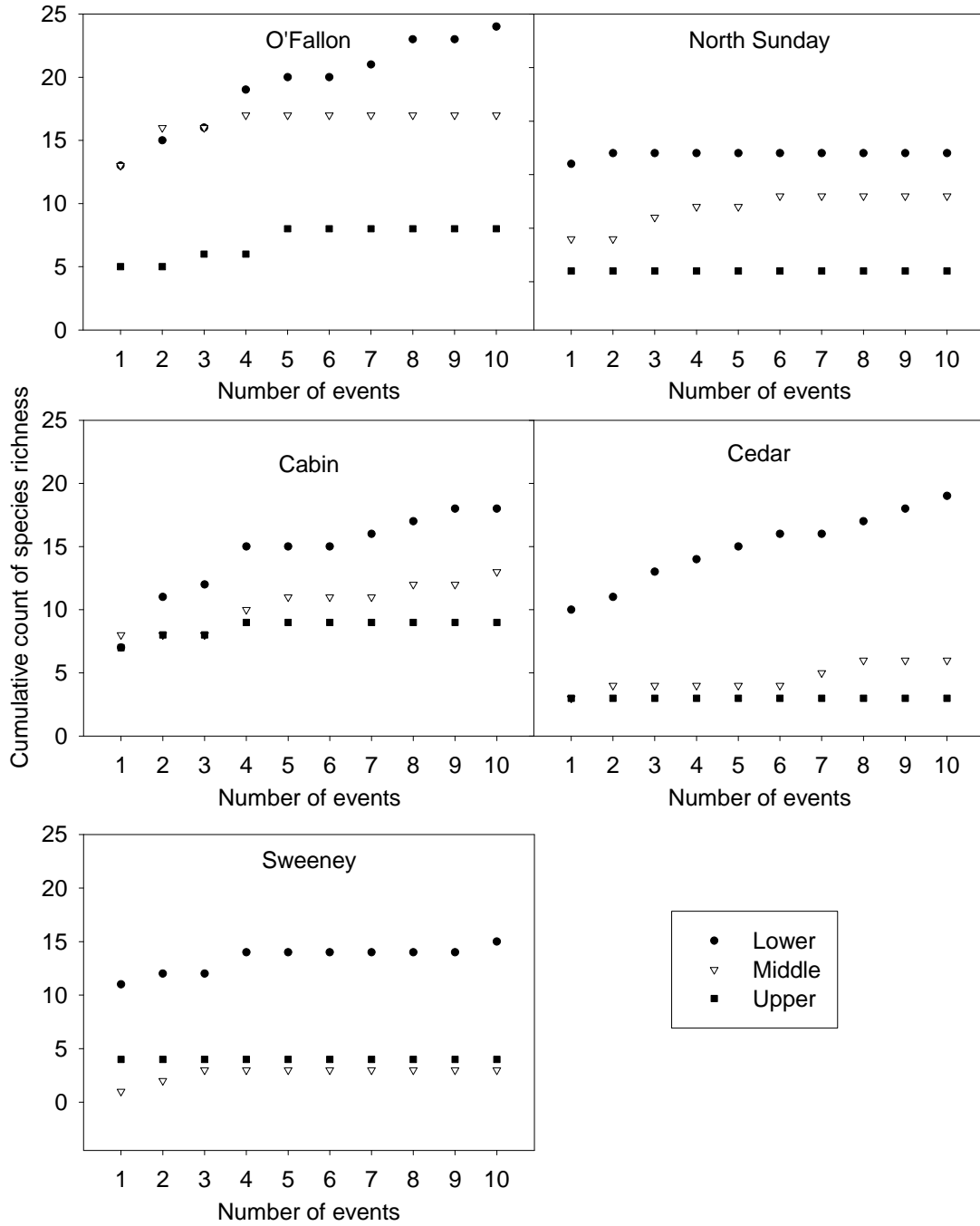


Figure 15. Relationship between the cumulative count of species richness and the number of sampling events by stream and spatial position for spatiotemporal and longitudinal samples. Streams are ordered by watershed size (largest to smallest) from left to right.

DISCUSSION

Spatial variation exceeded temporal variation in the fish assemblages of five Montana prairie streams, consistent with most stream studies (Matthews 1990; Meador and Matthews 1992; Williams et al. 1996; Tripe and Guy 1999; Ostrand and Wilde 2002). The previous studies of the spatiotemporal variation in prairie or warmwater stream fish assemblages have focused on the variation within one stream or one stream and a few of its tributaries (Matthews 1990; Meador and Matthews 1992; Williams et al. 1996; Tripe and Guy 1999; Ostrand and Wilde 2002; Adams et al. 2004) and most of these studies have been conducted in the central or southern Great Plains (Meador and Matthews 1992; Williams et al. 1996; Tripe and Guy 1999; Ostrand and Wilde 2002). The current study was conducted in the northwestern Great Plains of Montana on five streams with varying watershed sizes. The similarity among results for Texas, Oklahoma, Kansas, and Montana prairie streams suggests that fish assemblages of prairie streams consistently vary more spatially than temporally, regardless of watershed size and location within the Great Plains. However, greater temporal variation than spatial variation in C/f was detected in three small degraded coastal Mississippi streams (Adams et al. 2004). The increased temporal variation in fish assemblage structure was associated with anthropogenically disturbed habitats (Schlosser 1982; Adams et al. 2004). Although the streams in the current study were not pristine, they were likely less disturbed than the Mississippi coastal streams.

Although spatial variation exceeded temporal variation in the fish assemblages of the current study, temporal variation did exist. Season explained significant amounts of

variation in the fish assemblages in two of five individual stream CCA models. However, the influence of season in explaining the fish assemblage variation was limited, as the addition of season explained only 9.5% and 12.6% more variation in the fish assemblage than spatial position alone, which explained 55.7% and 61.7% of the variation for Cabin and Cedar, respectively. Temporal variation in species richness did not exhibit any discernable seasonal patterns; however cumulative species richness (i.e., all spatiotemporal samples pooled) for a site was greater than individual samples, indicating that the species assemblage varied temporally and sampling multiple times was necessary to get a true picture of the stream's ichthyofauna. For example, the cumulative species richness of the lower O'Fallon site was 21; however, the maximum species richness for a single sample at this site was 16 and the minimum was 9. This variation in species richness was not entirely due to inefficiencies in sampling rare species.

Excluding rare species (defined as those species represented by five individuals or less in a sample because this number of individuals could easily be missed) the cumulative species richness of the lower O'Fallon site was 12, the maximum 9, and minimum 3.

Some of the temporal variation in fish assemblage structure was associated with spawning migrations by adults or possibly movement of juvenile fish into tributaries. The presence of adult channel catfish in spring and early summer, the near absence of adults the rest of the year, and the presence of juveniles throughout the year suggests that channel catfish use prairie streams as spawning and rearing habitat. These findings are consistent with other studies that have documented channel catfish movements into prairie tributaries for spawning (Newcomb 1989; Peters et al. 1991; Pellet et al. 1998).

Channel catfish migrated upstream into the lower Wisconsin River for spawning, before returning downstream to the Mississippi River in autumn (Pellet et al. 1998). Large adult channel catfish were never captured during autumn sampling, thus channel catfish may migrate out of the study streams earlier than in the Wisconsin River. Similarly, channel catfish made upstream movements into tributaries streams in spring and summer for spawning and feeding, followed by downstream movements to larger deep waters in autumn for overwintering in the Missouri and lower Platte rivers (Newcomb 1989; Peters et al. 1991).

The presence and abundance of river carpsucker in the current study exhibited similar patterns to channel catfish; however, adult river carpsucker were rarely sampled. Adult river carpsucker likely spawned in tributary streams and then returned to the Yellowstone River or alternatively they spawned in the Yellowstone River and juveniles then moved upstream into tributaries. River carpsucker displayed a homing tendency associated with spawning in a reservoir-tributary system in North Dakota (Bonneau and Scarnecchia 2002). River carpsucker were sampled in tributaries during the spawning season, released in the reservoir, and recaptured in the tributaries where they were originally sampled (Bonneau and Scarnecchia 2002).

No definitive changes in abundance could be associated with spates using stage height data in 2006; however, the abundance of western silvery minnow appeared to be partially associated with spates in 2005. For example, one western silvery minnow was sampled in lower Cedar during June, July, and August 2005 and 107 adult (i.e., >55 mm) western silvery minnow were sampled in October 2005. The October 2005 sample

followed a large spate, which may have acted as an attractant for spawning to western silvery minnow residing in the Yellowstone River. Some cyprinids are known to synchronize spawning with turbid storm events (Cross and Moss 1987). Emerald shiner were rarely sampled during longitudinal sampling; however, 180 out of the 194 individuals collected during the study were sampled from the lower sites of O'Fallon and Sweeney in April 2007. Upstream spring and autumn migrations into tributaries by cyprinid species have also been documented in other tributary-mainstem systems (Mendelson 1975; Gorman 1986).

Drying and freezing were responsible for some of the temporal variation in the fish assemblage. Substantial drying occurred at the middle site on North Sunday during summer and autumn 2006. During the summer 2006 sample the pool area was reduced to 582 m² before increasing to 908 m² in autumn 2006. Only two species and nine individuals were sampled during autumn 2006 and no fish were sampled in spring 2007 following winter freezing. Drying was also associated with a local extirpation of fish from the upper site of North Sunday where survival was likely limited by abiotic conditions. Despite substantial drying (168 m² pool area) and freezing with no water detected beneath the ice at the upper site of O'Fallon in autumn 2006 and winter 2007, respectively, fish were detected during spring 2007 suggesting the use of nearby refugia or liquid water present beneath the ice but not detected. These examples illustrate the potential for drying and freezing to cause local extirpations, similar to other stream studies where local extirpations were caused by drought and drying (Harrel et al. 1967; Mundahl 1990).

The importance of spatial and temporal factors in explaining fish assemblage variation depends on the spatial and temporal scale of study. For example, spatiotemporal patterns in the fish assemblage of six impounded reaches of the Illinois River, Illinois, were assessed with fish abundance data from 1957 to 2000 (Pegg and McClelland 2004). Two distinct fish assemblages were detected; one prior to 1983 and one after (Pegg and McClelland 2004). The different fish assemblages were associated with improved water quality after policy implementations made in the late 1960s and early 1970s (Pegg and McClelland 2004). A smaller temporal scale of study would have failed to identify the temporal shift in the fish assemblage of the Illinois River.

The greater spatial variation than temporal variation detected in the current study was in part a function of the study design which was conducted over a two-year period. Long-term data may allow for detecting temporal changes in fish assemblage structure associated with increased anthropogenic disturbance (Pegg and McClelland 2004). Lacking long-term data, because the study streams are overall relatively undisturbed (compared to the Illinois River) and non-native species comprised a small percentage of the fish assemblage, it is unlikely that large long-term temporal changes have occurred that would exceed the spatial variation detected. However, Montana was in a drought from at least 2000 through 2006 (MDAC 2005; MFWP 2005-2006). It is possible that species richness and abundance may increase as the drought diminishes and stream levels increase. Higher stream levels may increase connectivity in intermittent reaches, allowing for greater dispersal opportunities, and thus reducing spatial variation in fish assemblages.

Spatial variation in the current study was expected because of differences in habitat and connectivity among sites located near the Yellowstone River to the headwaters. Spatial factors would likely become less important in explaining the variation in the fish assemblage as the spatial scale of study decreases. However, even with a small spatial scale of study if the habitats differed dramatically, the fish assemblage structure would likely also differ. For example, O'Fallon was sampled from rkm 3 to 222 and had large differences in fish assemblages. The lower 100 rkms of O'Fallon were remarkably similar in species richness and fish assemblage composition, but fish assemblages at rkms 145 and 203 varied substantially.

Fish species were associated with spatial positions, similar to other prairie and warmwater stream studies (Schlosser 1987; Williams et al. 1996; Ostrand and Wilde 2002). The associations between species and spatial positions were relatively consistent with a hypothesized model for explaining longitudinal fish species distributions in warmwater streams developed using data from Jordan Creek, Illinois (Schlosser 1987). However, the species pool and stream characteristics in the current study were slightly different than that in Schlosser's (1987) study, resulting in a few deviations from the model. In Schlosser's (1987) model, upper sites were characterized by young cyprinids (age 0-1) and downstream sites shifted toward larger fish with more catostomid and centrarchid species. In the current study, fish assemblages at upper sites were largely made up of cyprinid species, brook stickleback, and non-native green sunfish and black bullhead. Lower sites had more species, larger species, and the addition of more catostomid and ictalurid species. Middle sites were similar to both upper and lower sites,

but were stream specific. Centrarchid species were the main predator in lower sites of the Schlosser (1987) model. The only abundant centrarchid species sampled in the current study was the green sunfish (not a predominant fish species in Jordan Creek) and they were generally limited to upper sites. However, two native ictalurid species (i.e., channel catfish and stonecat) were commonly found at lower and middle sites, perhaps occupying a similar predator niche as the centrarchid species in the Schlosser model (1987).

An important distinction between the results of the current study and the Schlosser (1987) model is that juvenile and adult cyprinids were sampled in upper sites of the current study and mostly juvenile cyprinids were sampled in upper sites of Jordan Creek. The discrepancy is because upstream reaches of Jordan Creek were uniformly shallow limiting adult cyprinid abundance (Schlosser 1987) whereas upstream sites in the current study were comparatively deeper providing habitat for adult survival. Additionally, streams in the current study were often intermittent and much longer (varying from 51 to 250 km) than the perennial 17 km long Jordan Creek (Schlosser 1982). Thus, the opportunity for fish movement was likely greater in Jordan Creek than the streams in the current study.

Distinct fish assemblages by spatial position have been identified in other prairie stream studies (Williams et al. 1996; Ostrand and Wilde 2002). Ten sites dispersed throughout Lagoon Creek, Oklahoma, were sampled each season for a year (Williams et al. 1996). Upstream, midstream, and downstream fish assemblages were identified using CCA analysis (Williams et al. 1996). The midstream sites were dominated by habitat generalists and the downstream sites were dominated by fishes associated with larger

water bodies (i.e., Cimarron River and Keystone Reservoir) (Williams et al. 1996). Similarly, in the current study large river fish were frequently sampled in downstream sites. The upper Brazos River drainage, Texas was sampled seasonally over a two-year period (Ostrand and Wilde 2002). Species diversity increased downstream and species composition shifted from cyprinodontid to cyprinid species (Ostrand and Wilde 2002). The only cyprinodontid species sampled in the current study was the non-native northern plains killifish and they were not strongly associated with any spatial position.

Associations between fish species and spatial positions are often explained by changes in abiotic characteristics (Schlosser 1987; Williams et al. 1996; Ostrand and Wilde 2002). In the Schlosser (1987) model fish assemblage diversity increased downstream with increasing habitat heterogeneity (Schlosser 1987). Habitat heterogeneity was measured as a combination of depth, velocity, and substrate (Schlosser 1987). Habitat heterogeneity was not measured in this study. However, pool area increased and fine substrates decreased downstream, consistent with the trends explained for habitat heterogeneity (Schlosser 1987). In Lagoon Creek, Oklahoma and the upper Brazos River drainage, Texas, abiotic variables were highly successful in explaining the variation in the fish assemblage (greater than 85% for both studies) (Williams et al. 1996; Ostrand and Wilde 2002). Abiotic variables explained most of the variation in the fish assemblage in the upper Brazos River drainage because freshwater and saline spring inputs limited the downstream gradient in salinity and pool volume (Ostrand and Wilde 2002). The large amount of variation explained in Lagoon Creek is likely related to the large number (seven) of abiotic variables used. The success of abiotic variables in

explaining the variation in the fish assemblages of these studies mildly conflict with the results of the current study. The limited success of abiotic variables in explaining the variation in the fish assemblage in the current study is likely because of the additional variability in the fish assemblage and abiotic variables associated with five streams. When assessed by stream, abiotic variables explained more of the variation in the fish assemblage.

Abiotic characteristics varied more within and among study streams than among seasons. Changes in abiotic characteristics that did occur among seasons were generally associated with streams drying through the summer. However, these variables associated with drying through the summer (e.g., wetted width and depth) did not explain much variation in the fish assemblage. Thus, seasonal changes in stream characteristics had a limited effect on the fish assemblage. Instead, longitudinal changes in abiotic variables explained more of the variation in the fish assemblage. Proportion of fine substrates which varied greatly among spatial positions but little among seasons was the variable that best explained variation in the fish assemblage (other than spatial position).

Longitudinal patterns in species richness may be caused by longitudinal changes in habitat and connectivity. In the current study, pool area increased and proportion of fine substrates decreased downstream, providing larger and more suitable habitat, which allowed more species to exist. Alternatively, the strong negative relationship between species richness and proportion of fine substrates and the importance of fine substrates in explaining the fish assemblage variation may have existed simply because of changes in distance from the mouth and not because of fine substrates. However, longitudinal

changes in proportion of fine substrates often closely matched changes in species richness. In O'Fallon and Cabin, distinct declines in species richness in upper reaches of the drainages occurred where sharp increases in fine substrates to near 100% occurred. Similar declines in species richness occurred in Cedar and Sweeney in lower reaches of the drainage where sharp increases in fine substrates often occurred. Species richness declined linearly upstream in North Sunday resembling the linear increase in fine substrates. Low species richness and diversity levels are often associated with high levels of fine substrates from sedimentation (Berkman and Rabeni 1987; Rabeni and Jacobson 1999). Thus, the continued existence of many prairie stream fishes that required cobble and gravel substrates for spawning were likely limited in upper reaches with a lack of diverse substrates (Berkman and Rabeni 1987). For example, longnose dace require gravel substrates for spawning (Brown 1971) and were found only in lower to middle reaches with gravel substrates and riffle habitats. Sharp longitudinal declines in species richness could alternatively be explained by changes in connectivity. The sharp declines in species richness in O'Fallon and Cabin are also associated with where continuous flow ends and intermittency begins. Declines in species richness in Cedar and Sweeney correspond to potential movement barriers because of culverts and spreader dikes, respectively.

The longitudinal location of the transition from gravel to fine substrates may be partially explained by the upstream watershed area. For example, at approximately 60% of the relative stream distance from the mouth, fine substrates increased to near 100% in O'Fallon and Cabin. The watershed area upstream of this point may represent the

minimum size needed to produce flows capable of flushing fine substrates downstream. The much smaller Sweeney is similar in watershed size to the upper 40% of O'Fallon and Cabin, potentially explaining the relatively high amounts of fine substrates observed at the lower site compared to the larger streams. Numerous stock ponds in the upper reaches of prairie streams likely dampen flushing flows, which may allow fine substrates to accumulate farther downstream than under pre-settlement conditions. The relationship between fine substrates and distance from the mouth was linear for North Sunday and Cedar, thus other alternatives to minimum watershed area could help explain longitudinal substrate characteristics (e.g., geology).

Many studies have noted the influence of stream size (measured by stream order or watershed size) on species richness; however, these studies often focus on the changes in stream size within streams (Lotrich 1973; Gorman and Karr 1978; Evans and Noble 1979) and rarely address differences in watershed size among streams (Fausch et al. 1984). The current findings indicate differences in watershed size among streams influenced the fish assemblage. For example, analysis by stream explained a much higher percentage of variation in the fish assemblages (i.e., species identity and abundance) than streams pooled and rank watershed size was included as a predictor variable in stepwise CCA modeling when streams were pooled. These results are consistent with another study that assessed prairie stream fish distributions in Montana and found that watershed scale variables (e.g., watershed area) can be useful in explaining and predicting large-scale fish distributions (Wuellner 2007).

Species richness declined upstream, for all streams, consistent with results from other studies on the longitudinal variation in fish assemblages (Harrel et al. 1967; Horwitz 1978; Evans and Noble 1979; Vannote 1980; Rahel and Hubert 1991). Despite large differences in watershed size, species richness near the Yellowstone River was similar among all streams. Species richness was also similar in headwater reaches among all streams, indicating that the rate of change in species richness as a function of distance from the mouth was greater for smaller streams than larger streams. Distance from the mouth is likely not the variable responsible for longitudinal changes in species richness. A site sampled a large distance from the mouth in Sweeney would have low species richness but a site sampled this same distance from the mouth in O'Fallon would have high species richness. Instead, longitudinal changes in fish assemblage structure are the result of longitudinal differences in habitat structure (e.g., fine substrates and pool area).

Increased species richness downstream was best explained by species additions, consistent with other longitudinal stream assessments (Horwitz 1978; Evans and Noble 1979; Rahel and Hubert 1991) and these additions were often large river species. Large river species were detected with increasing probability downstream. The presence of a large river species does not mean that the species regularly occurred in the stream reach. However, detection of large river species at low abundance is important because these individuals may provide information about historic or future distributions. Species richness increased downstream because of the addition of new species within the warmwater fish assemblage of Horse Creek, Wyoming (Rahel and Hubert 1991). Species richness varied from 22 species in the headwaters to 33 species at the downstream site of

Big Sandy Creek, Texas because of downstream species additions (Evans and Noble 1979). Similarly, increased species richness levels downstream were detected in the fish assemblages of 15 warmwater tributaries to the Mississippi River drainage because of downstream species additions (Horwitz 1978). Longitudinal changes in the fish assemblage could also sometimes be explained by species being absent from downstream reaches. For example, brook stickleback were only sampled in the upper reaches of O'Fallon and brassy minnow were sampled only in middle to upper reaches of O'Fallon except for two individuals sampled at the lower O'Fallon site.

The study streams can be described as adventitious streams because they flowed directly into the much larger Yellowstone River. Adventitious streams compared to headwater streams of similar size, often exhibit seasonal variation in the fish assemblage, especially in lower reaches because of the interaction with large river fishes (Gorman 1986). In this study, large river fish were present in lower reaches, were more common in larger streams, and demonstrated some seasonal variability. North Sunday had lower large river species richness than expected based on watershed size, because it was frequently intermittent throughout the drainage, which likely limited large river fishes to the lower portions of the drainage. Barriers also limited large river species upstream distributions. Culvert barriers and spreader dikes were present in the lower reaches of Cedar and Sweeney, respectively, likely restricting movement and accounting for the relative rarity of large river species in these drainages. Alternatively, these streams may be limited in suitable habitat required for large river fishes and may lack the flow

required to attract large river fishes from the Yellowstone River compared to larger streams.

This study assessed spatiotemporal variation in five Montana prairie streams across a gradient of watershed sizes. Other studies assessing spatiotemporal variation in prairie or warmwater streams have focused on one stream or a few streams of similar size (Schlosser 1987; Meador and Matthews 1992; Williams et al. 1996; Ostrand and Wilde 2002; Adams et al. 2004). The similarity in results among streams of different sizes in this study and among streams throughout the Great Plains and Midwest (Schlosser 1987; Meador and Matthews 1992; Williams et al. 1996; Tripe and Guy 1999; Ostrand and Wilde 2002), demonstrates that a generalization of spatial variation exceeding temporal variation in fish assemblages of prairie and warmwater streams is appropriate.

Research and Management Implications

Understanding the spatiotemporal variation in fish assemblages (i.e., species identity and abundance) is important for establishing standardized long-term data sets (Tripe and Guy 1999) and assessing anthropogenic influences (Tripe and Guy 1999; Adams et al. 2004; Bramblett et al. 2005). Spatial variation exceeded temporal variation in the fish assemblages for five Montana prairie streams. Temporal variation in fish assemblages did exist, but not with the same degree of consistency or magnitude compared to spatial variation. Sampling multiple sites within a stream (e.g., lower, middle, and upper), will provide fisheries biologists with a relatively complete assessment of the fish assemblage. By sampling lower, middle, and upper sites fisheries

biologists will be able to assess connectivity issues, often related to anthropogenic disturbances and thus prioritize restoration projects. For example, sampling multiple sites in the Cedar and Sweeney drainages identified possible migration barriers associated with culverts and spreader dikes. Sampling lower, middle, and upper sites will ensure fish are sampled from a variety of habitats including different substrates that affect fish assemblage structure.

Repeat sampling of sites across time may be necessary depending on agency objectives. Fish assemblage structure is largely dependent on anthropogenic (Karr 2006) and natural disturbance history (Dodds et al. 2004). Sampling a site during a drought, after drying, or after flooding may provide inaccurate estimates of species richness and abundance. Using this information as baseline data for assessment of anthropogenic effects may prove misleading. Additionally, sampling a site once limits the ability to make inferences regarding the life history of fishes sampled (e.g., spawning migrations) and may underestimate the number of species that utilize that site seasonally. Cumulative species richness exceeded species richness of individual samples, demonstrating both temporal changes in the species assemblage and inefficiencies in sampling rare species. More sampling events are required at downstream sites than upstream sites to adequately characterize the fish assemblage. At a minimum, four samples for lower sites, two samples for middle sites, and one sample for upper sites should be collected to represent most of the species present. If sampling can be conducted during only one season, it should be during early autumn because most fish will be recruited to the gear and

environmental variability (i.e., flooding and freezing) that can adversely affect seining efficiency is limited.

Some fishes associated with large rivers use prairie streams as spawning and rearing habitats. Further research is needed to document the life history characteristics of large river fishes in small prairie streams including more detailed analysis of the spatiotemporal use of small streams and determining which species and what proportion of large river fishes exhibit migratory and non-migratory forms. Fisheries biologists given the task of conserving large river fishes should also consider conservation of prairie streams in making management decisions.

The recent efforts in sampling Montana prairie streams have focused on surveying as many streams as possible, mostly during the summer. My results indicate that prairie stream fish assemblages vary more spatially than temporally. Accordingly, given monetary or logistical constraints, sampling multiple sites within drainages will provide more information about the fish assemblage than repeating a sample site over time. If the objective is to document as many species as possible within the drainage, then sampling at least a lower, middle, and upper site within the drainage is the best approach. Sampling the lower site four times, the middle site two times, and the upper site one time will detect most species utilizing those reaches. If time and resources allow, seasonal sampling of sites may detect additional species and provide information about life history characteristics. At a minimum, long-term standardized locations should be established and sampled at an appropriate temporal interval in an attempt to detect anthropogenic disturbances.

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APPENDICES

APPENDIX A

FISH AND HABITAT SAMPLING PROTOCOL
FOR PRAIRIE STREAMS

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January, 2003

1. **Site location.**-Locate the sampling site using GPS for random sites, or by convenience for non-random sites. The GPS location will be the center of the reach, this is where you place the “F” flag (see Step 2). If the site is dry, shift the reach up or downstream to capture the most wetted channel possible on the parcel of land where you have permission for sampling.
2. **Laying out the sample reach.**-Lay out a 300 m sample reach using a measuring tape and a set of 11 pin flags (labeled A-K). Follow the curves in the stream channel with the measuring tape; do not cut across curves. To avoid spooking fish, walk along the bank, not in the stream. Place a flag every 30 m. The “A” flag will be at the downstream end, the “K” flag will be at the upstream end of the reach. The “F” flag will go in the center of the reach.
3. **Block nets.**-Place block nets (these can be old seines, 1/4” mesh) at the upstream (K flag) and downstream (A flag) ends of the sample reach if the water in the channel is continuous, deeper than 25 cm, and relatively clear. This prevents fish from leaving the sample reach.
4. **Seining.**-Select the seine based on the size of the stream to be sampled. The seine length to be used should be approximately equal to or slightly greater than the stream width, and the seine height should be about 1.5 to 2 times greater than the depth of the stream. Dip nets can be used in very shallow, small habitats. Seining begins at the upstream end (K flag) and proceeds downstream to the A flag. Seining is performed by two people, one on each end of the seine. In pools, the seine is pulled down the stream channel, using the shore and other natural habitat features as barriers. Begin with the seine rolled up on each seine brail. The seine is typically set perpendicular to shore and hauled downstream parallel to shore. As you proceed, let out enough seine so that the seine forms a “U” shape, but not so much that the net is hard to control. Adjust the length of the seine by rolling or un-rolling net on the seine brail. The speed of seining should be fast enough to maintain the “U” shape, but not so fast that the floats become submerged, or that the seine’s lead line come way up off the bottom of the stream. If rocks or other snags are on the bottom, the seine can be lifted off the bottom for a moment to avoid the snag, or one of the netters

can bring the seine around the snag to avoid it, all the while maintaining the forward progress of the seine. Similarly, areas of dense aquatic vegetation can be avoided. It is important not to stop the forward progress, because fish will swim out of the seine. It is better to avoid a snag while keeping moving than to become snagged, which will allow fish to escape. In “snaggy” waters, keep more of your seine rolled up for better control.

Proceed downstream while seining. In narrow streams, the entire channel width is spanned with the seine. In wider streams, one person walks along the shore, while the other wades through the channel. The length of each seine haul will depend on the natural features of the stream channel and shoreline, but seine hauls should not normally be more than 60 or 90 m long. Side channel bars or the end of a standing pool are good areas to haul out or “beach” the seine. Where a large bar or end of a standing pool is present both netters can simply run the net up on the shore. In streams with steep banks or lack of obvious seine beaching areas the “snap” technique can be used. At the end of the haul, the person near shore stops, while the person farthest out turns into shore, quickly, until the seine is up against the bank. The two netters then walk away from each other, taking the slack out of the seine, and keeping the seine’s lead line up against the bank.

In riffles, with moderate to fast current, the “kick seine” technique can be used. The seine is held stationary in a “U” shape, while the other team member disturbs the substrate immediately upstream of the net. Then the net is quickly “snapped” out of the water by both team members using an upstream scooping motion.

Seine the entire 300 m reach, covering the linear distance at least once. If part of the 300 m is dry, just skip it. If the stream is much wider than your seine, do extra seine hauls in the large pools to cover the extra width. Sample all habitat types (shoreline, thalweg, side channels, and backwaters).

After each seine haul, place fish in a bucket. If the water is warm, or you have captured many fish, place fish in a fish bag to keep them alive until seining is completed. If you have to work up fish before seining is completed, release processed fish in an area that has already been seined, as far away from the area remaining to be seined as possible (or outside of the block nets). Large fish such as northern pike, common carp, white sucker, shorthead redhorse, or channel catfish, can be measured, given a small clip to the lower caudal fin and released immediately.

5. ***Processing captured fish.***-Record the species of each fish captured, and measure 20 “randomly” selected fish to the nearest millimeter, total length. If the species of fish is unknown, try to at least record it as Unknown type 1, Unknown type 2, etc. Keep track of and record the minimum and maximum length of each species.

For each species, preserve a subsample of at least 10 individuals per site to serve as voucher specimens. Record a small letter “v” next to the recorded length of the fish that is vouchered to allow for later validation. For *Hybognathus* spp., voucher up to 20 individuals per site. Kill the fish to be vouchered by placing them in a small bucket or 1000 ml nalgene jar with an overdose solution of MS-222. After fish processing is completed, drain the MS-222 solution and place the fish in a 1000 ml nalgene jar with a 10% solution of formalin (in clear water, if possible). For specimens longer than 150 mm, an incision should be made on the right ventral side of the abdomen after death, to allow fixative to enter the body cavity. The volume of formalin solution should be approximately equal to the twice the volume of fish tissue to be preserved, and the fish volume should be considered water when concentrations are determined. For example, if the fish take up 250 ml of the 1000 ml volume, you need about 500 ml of 10 % formalin solution (75 ml formalin and 425 ml water) in the 1000 ml nalgene jar. If necessary, use a second jar to accommodate all of the specimens. Use safety glasses and gloves when pouring formalin. Do not let the fish “cook” in the sun for a while and preserve them later, do it as soon as possible. Label all jars inside and out with Site, Site Number, Lat/Long, Date, Collectors names. Use

pencil on Write-In-the-Rain or high rag paper for inside labels (just put the label right in with the fish), use a sticker label on the outside, cover it with clear (ScotchPad high performance packing tape pad 3750-P). Fish specimens should be left in formalin solution for at least 2-7 days. Fish specimens must have formalin solution soaked out before being handled extensively. Specimens should be soaked in water for at least 2 days, and water should be changed at least four times during this period. After soaking out the formalin, the fish specimens should be placed in either 70% ethanol or 40% isopropanol for long-term storage.

6. **Habitat survey.**-Channel width, depth of water, and substrate will be measured at 11 transects perpendicular to the stream channel (located at Flags A-K), and along the thalweg in 10 thalweg intervals between transects (deepest part of channel). Stream width is measured to the nearest 0.1 m, depth is measured to the nearest cm, and substrate sizes and codes are on the data sheet. One person will be in the stream taking measurements while the other records data. Record the Latitude and Longitude (in digital degrees) of the F flag, the stream name, site number, the date, the flow status (flowing, continuous standing water, or interrupted standing water) and the names of the crew members on the data sheet. Take photographs of the site, capturing as much of the sampling reach as possible. Make sure the date feature on the camera is turned on, to allow for later identification of site photographs.

Transects.-Start on the left bank (facing downstream) at Flag A. Measure and record the wetted width of the channel to the nearest 0.1 m. Measure and record (separated by a comma on the data sheet) five equally spaced depth and substrate measurements across the wetted stream channel:

1. Left Bank-5 cm from the left bank;
2. Left Center-halfway between the Center and the Left Bank;
3. Center-center of the wetted stream;
4. Right Center-halfway between the Center and the Right Bank;
5. Right Bank-5 cm from the right bank

Thalweg.-Begin by recording the depth and substrate 3 m upstream of the transect, in the deepest part of the channel (thalweg). Proceed up the thalweg to Flag B, recording depth and substrate every 3 m along the thalweg. You will record a total of 10 depths and substrates between each pair of transects. If the stream channel is dry, record a 0 for depth, and record the substrate. The last thalweg measurement point should fall on the next upstream transect. The 3 m interval can be estimated, and it is helpful if the data recorder helps to keep the person in the stream from “squeezing” or “stretching” the thalweg measurements.

Repeat this procedure until all 11 transects and 10 thalweg intervals are completed.

Gear List

- 20', x 6' x ¼" heavy delta seines
- 15' x 4' x ¼" heavy delta
- 30' x 6' x ¼" heavy delta (or delta) with 6' x 6' x 6' bag
- Fish bags: nylon diver's bags, ¼" mesh 18" x 30"
- Mudders – 109.00 at Ben Meadows
- Block nets, Tent stakes
- Stream Conductivity meter
- Thermometer
- Turbidity meter (LaMotte, Ben Meadows 224805, \$795.00-might try the “transparency tube” Ben Meadows 224196, \$52.95)
- Waders (breathable waders are essential for this work-Cabelas has them for about \$100/pair), hip boots are usually too low
- Lug sole wading boots (Cabelas)
- Habitat pole (I make habitat poles out of 1.0" OD PVC pipe. 1.5 m long including caps. Score the pipe every 10 cm with a pipe cutter, then use a Sharpie to mark rings around the pole at the scores, and label the pole 10, 20, 30, etc. 5 cm marks are made between the 10 cm rings, you can visually estimate between the 5 cm marks to get to the nearest cm. Spray or brush a

Urethane finish on the pole or your marks will come off fast with sunscreen and bug dope.)

- Metric 30 m tape (Ace Hardware actually carries a tape with metric on one side)
- Measuring boards, one short 300 mm (half a 6" PVC works well for *Hybognathus* "fin flotation", one long, ~0.5-1 m, or you can just use a meter stick for the odd big fish)
- Hand lens
- Small 1 gallon red bucket from Ace Hardware for doping fish
- 5 gallon buckets
- MS-222
- Labels and tape pads for fish samples
- 1000 ml Nalgene jars
- Formalin (buffered is great, but more expensive-I throw a Roloids in each jar of fish to neutralize the acidity)
- Clip board
- 11 Pin flags labeled A-F

APPENDIX B

LONGITUDINAL PRESENCE OF PRAIRIE

STREAM FISHES

Appendix B. Presence of species (X) by stream (listed by decreasing watershed size) and longitudinal position (site 1 is downstream), sampled in June and July, 2005 and 2006. Sample size ($N = 4$, unless otherwise noted) is the same for all species and is depicted only for the first species listed is. Sites not sampled because they were inaccessible are denoted by NS.

Family	Common name, <i>Genus species</i>	Stream	Longitudinal position									
			1	2	3	4	5	6	7	8	9	10
Hiodontidae												
	Goldeye, <i>Hiodon alosoides</i> ^b	O'Fallon	X	a	X	a	a		X	NS		
		North Sunday	X			a						
		Cabin	X	NS								
		Cedar						a		NS		
		Sweeney		a					NS			
Cyprinidae												
	lake chub, <i>Couesius plumbeus</i>	O'Fallon								NS		
		North Sunday				X	X	X				
		Cabin		NS		X	X	X	X	X	X	
		Cedar	X	X	X	X	X	X	X	NS	X	
		Sweeney							NS			
	common carp, <i>Carpiodes carpio</i>	O'Fallon	X	X	X	X	X	X	X	NS		
		North Sunday	X		X	X	X					
		Cabin	X	NS	X	X		X	X			
		Cedar	X	X						NS		
		Sweeney	X	X	X	X			NS			
	western silvery minnow, <i>Hybognathus argyritis</i> ^b	O'Fallon	X	X	X	X	X	X		NS		
		North Sunday	X	X	X							
		Cabin	X	NS	X							
		Cedar	X	X	X					NS		
		Sweeney	X	X	X				NS			
	brassy minnow, <i>Hybognathus hankinsoni</i>	O'Fallon					X	X	X	NS	X	
		North Sunday										
		Cabin		NS								
		Cedar								NS		
		Sweeney							NS			

Appendix B. Continued.

		1	2	3	4	5	6	7	8	9	10
plains minnow, <i>Hybognathus placitus</i>	O'Fallon	X	X	X		X	X	X	NS		
	North Sunday	X	X	X	X	X	X	X	X		
	Cabin		NS	X	X		X	X	X	X	
	Cedar	X	X	X	X	X	X	X	NS	X	
	Sweeney			X				NS			
emerald shiner, <i>Notropis atherinoides</i> ^b	O'Fallon	X							NS		
	North Sunday										
	Cabin		NS								
	Cedar	X							NS		
	Sweeney							NS			
sand shiner, <i>Notropis stramineus</i>	O'Fallon	X	X	X	X	X	X	X	NS		
	North Sunday	X	X	X	X						
	Cabin	X	NS	X	X	X	X	X			
	Cedar	X	X	X					NS		
	Sweeney	X	X	X	X				NS		
fathead minnow, <i>Pimephales promelas</i>	O'Fallon	X	X	X	X	X	X	X	NS	X	X
	North Sunday	X	X	X	X	X	X	X	X	X	
	Cabin	X	NS	X	X	X	X	X	X	X	X
	Cedar	X	X	X	X	X	X	X	NS	X	
	Sweeney	X	X	X	X	X			NS	X	X
flathead chub, <i>Platygobio gracilis</i> ^b	O'Fallon	X	X	X	X	X	X	X	NS		
	North Sunday	X	X	X	X	X					
	Cabin	X	NS	X	X	X	X	X			
	Cedar	X	X	X					NS		
	Sweeney								NS		
longnose dace, <i>Rhinichthys cataractae</i>	O'Fallon		X	X	X	X	X		NS		
	North Sunday	X	X	X	X	X					
	Cabin	X	NS	X	X	X	X	X	X	X	
	Cedar	X	X	X					NS		
	Sweeney	X							NS		

Appendix B. Continued.

creek chub, <i>Semotilus atromaculatus</i>	O'Fallon	X	X	X	X	X	X	X	NS	
	North Sunday									
	Cabin	X	NS	X	X	X	X	X	X	X
	Cedar	X	X	X		X			NS	
	Sweeney	X	X	X	X			NS		
Catostomidae										
river carpsucker, <i>Carpionodes carpio</i> ^b	O'Fallon	X	X	X				X	X	NS
	North Sunday	X	X	X	X	X				
	Cabin	X	NS							
	Cedar	X	X							NS
	Sweeney								NS	
longnose sucker, <i>Catostomus catostomus</i>	O'Fallon									NS
	North Sunday			X			X			
	Cabin			NS						
	Cedar									NS
	Sweeney	X	X						NS	
white sucker, <i>Catostomus commersonii</i>	O'Fallon	X	X	X	X	X	X	X	NS	X
	North Sunday									
	Cabin	X	NS	X	X	X	X	X	X	X
	Cedar	X	X	X					NS	
	Sweeney	X	X	X	X				NS	X
shorthead redhorse, <i>Moxostoma macrolepidotum</i> ^b	O'Fallon	X	X		X	X	X	X	NS	
	North Sunday									
	Cabin	X	NS							
	Cedar									NS
	Sweeney	X	X						NS	

Appendix B. Continued.

Ictaluridae										
black bullhead, <i>Ameiurus melas</i>	O'Fallon			X	X	X	X	X	NS	
	North Sunday		X	X	X	X	X	X	X	
	Cabin		NS	X						
	Cedar								NS	
	Sweeney	X	X	X	X			NS	X	X
yellow bullhead, <i>Ameiurus natalis</i>	O'Fallon								NS	
	North Sunday									
	Cabin		NS							
	Cedar								NS	
	Sweeney		X					NS		
channel catfish, <i>Ictalurus punctatus</i> ^b	O'Fallon	X	X	X	X	X	X	X	NS	
	North Sunday	X	X	X	X	X	X	X		
	Cabin	X	NS	X	X	X	X	X		X
	Cedar		X						NS	
	Sweeney			X				NS		
stonecat, <i>Noturus flavus</i>	O'Fallon	X	X		X				NS	
	North Sunday	X	X							
	Cabin	X	NS							
	Cedar	X							NS	
	Sweeney							NS		
Cyprinodontidae										
northern plains killifish, <i>Fundulus zebrinus</i>	O'Fallon	X	X	X	X	X	X	X	NS	X
	North Sunday		X	X		X				
	Cabin	X	NS	X	X		X	X	X	X
	Cedar	X	X	X	X	X	X		NS	
	Sweeney	X	X	X	X			NS		

Appendix B. Continued.

Gasterosteidae												
brook stickleback, <i>Culaea inconstans</i>	O'Fallon									NS	X	X
	North Sunday											
	Cabin		NS									
	Cedar									NS		
	Sweeney								NS			
Centrarchidae												
green sunfish, <i>Lepomis cyanellus</i>	O'Fallon	X	X	X	X	X	X	X	X	NS	X	X
	North Sunday	X					X	X	X	X		
	Cabin		NS									
	Cedar		X							NS		
	Sweeney	X	X	X	X	X			NS	X	X	
bluegill, <i>Lepomis macrochirus</i>	O'Fallon	X								NS		
	North Sunday											
	Cabin		NS									
	Cedar									NS		
	Sweeney								NS			
Percidae												
yellow perch, <i>Perca flavescens</i>	O'Fallon			X				X	X	NS		
	North Sunday											
	Cabin		NS									
	Cedar									NS		
	Sweeney								NS			

^a Denotes a sample size of $N=1$

^b Denotes large river species

APPENDIX C

MAPS OF SPATIOTEMPORAL AND LONGITUDINAL
PRESENCE OF LARGE RIVER FISHES

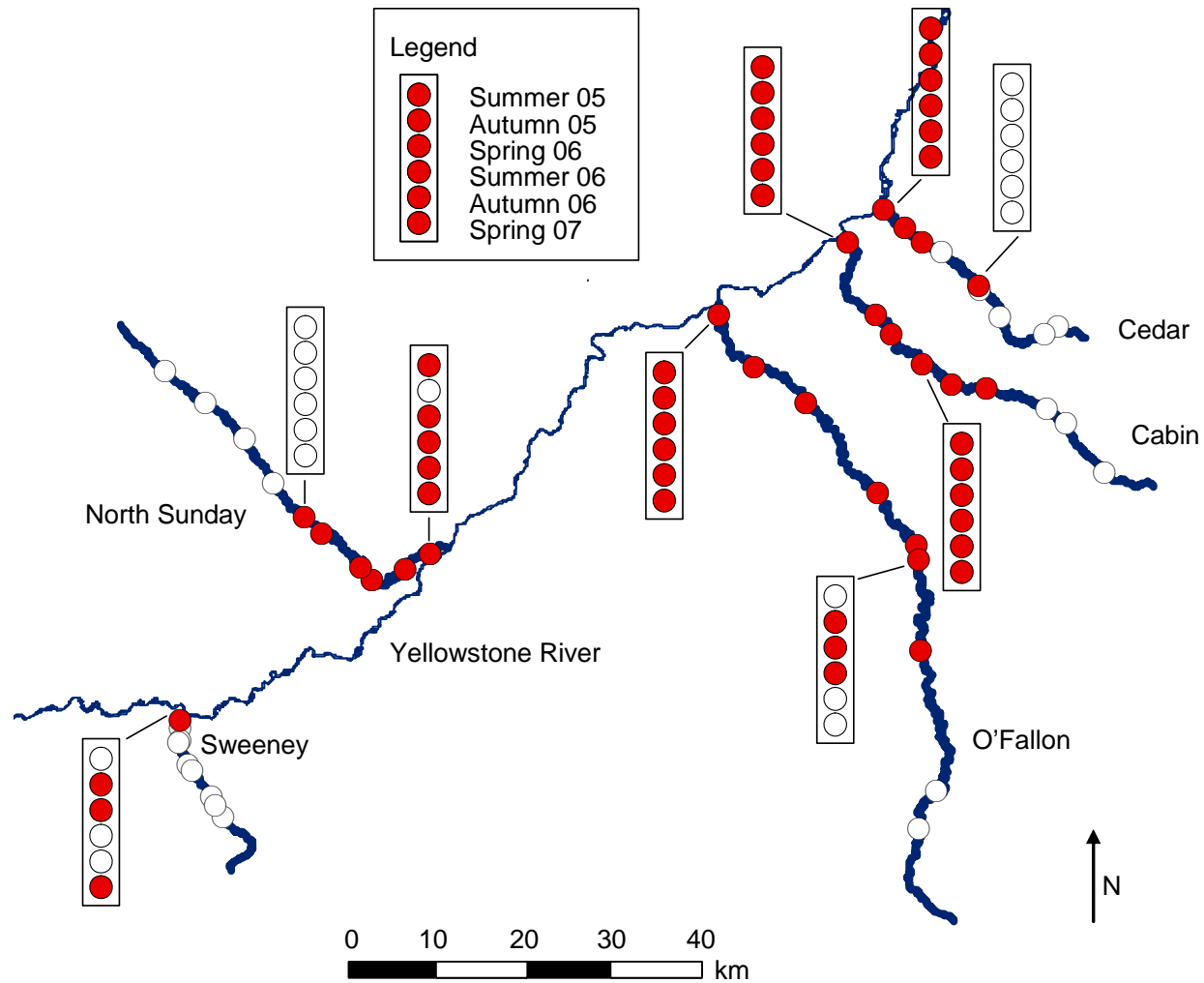


Figure 16. Map of flathead chub presence in longitudinal and spatiotemporal sites, sampled from June 2005 through April 2007. Dots along stream indicate presence (shaded) and absence from all samples. Dots in boxes represent presence (shaded) and absence of flathead chub during spatiotemporal sampling (summer 2005 to spring 2007, from top to bottom).

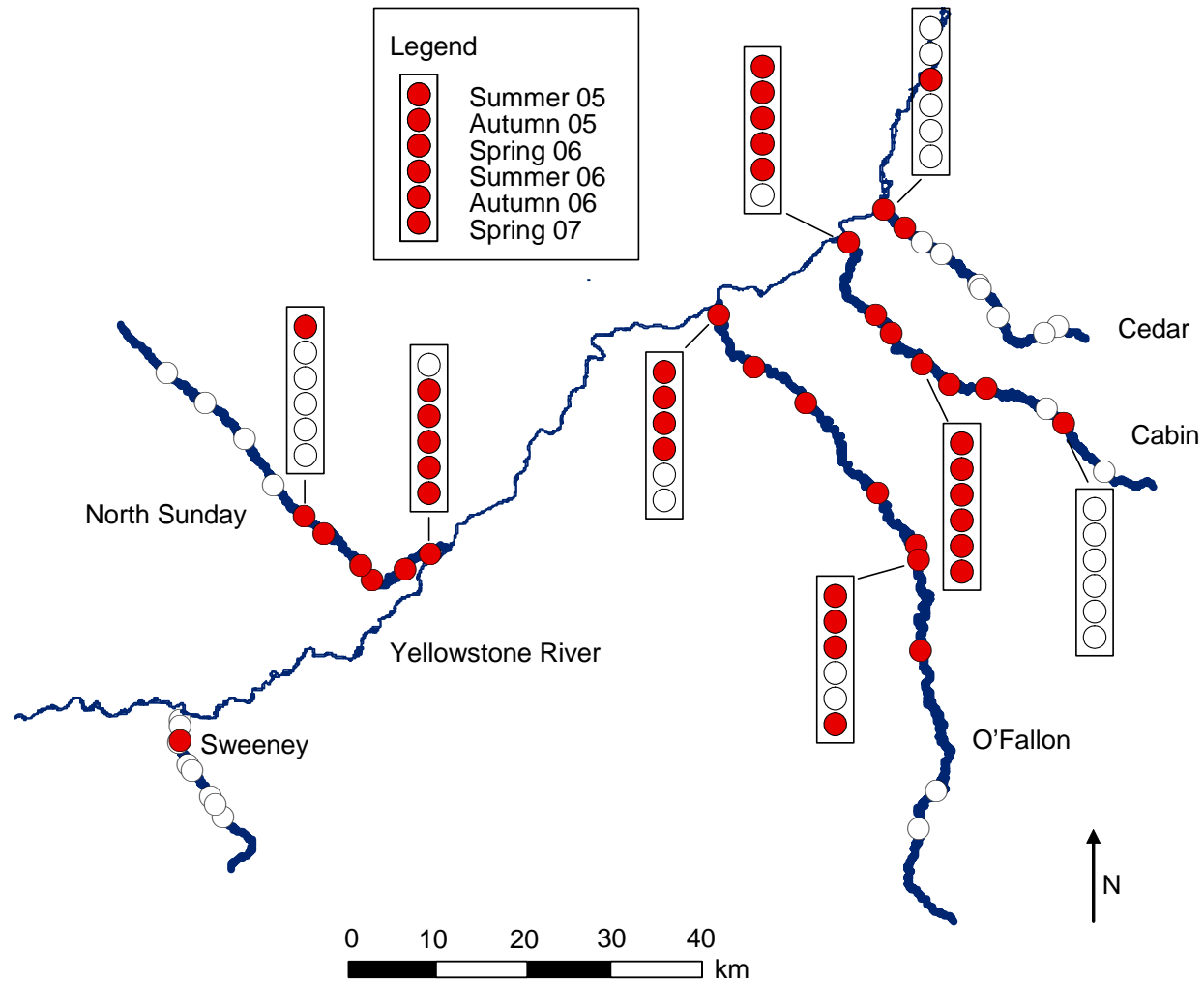


Figure 17. Map of channel catfish presence in longitudinal and spatiotemporal sites, sampled from June 2005 through April 2007. Dots along stream indicate presence (shaded) and absence from all samples. Dots in boxes represent presence (shaded) and absence of channel catfish during spatiotemporal sampling (summer 2005 to spring 2007, from top to bottom).

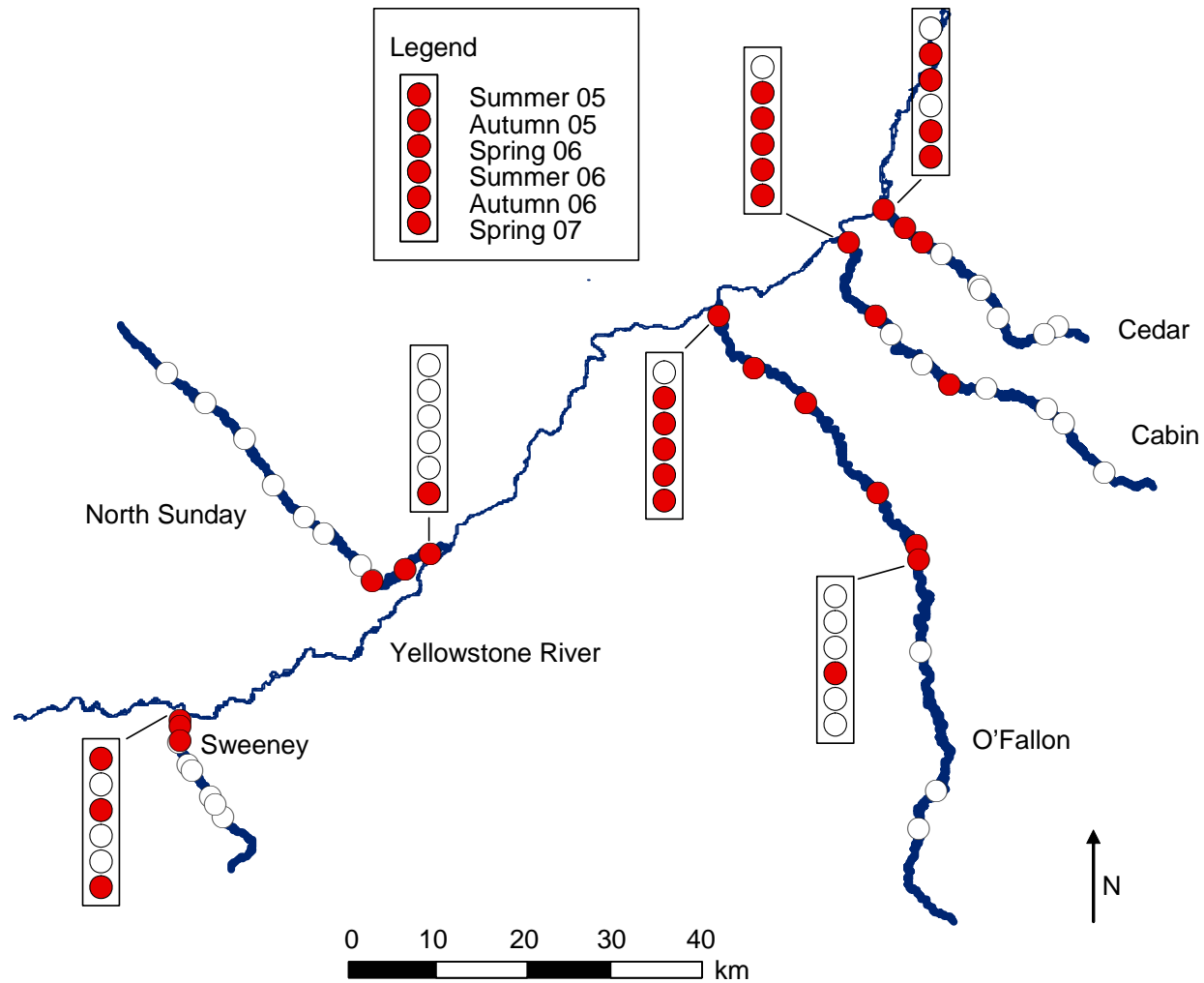


Figure 18. Map of western silvery minnow presence in longitudinal and spatiotemporal sites, sampled from June 2005 through April 2007. Dots along stream indicate presence (shaded) and absence from all samples. Dots in boxes represent presence (shaded) and absence of western silvery minnow during spatiotemporal sampling (summer 2005 to spring 2007, from top to bottom).

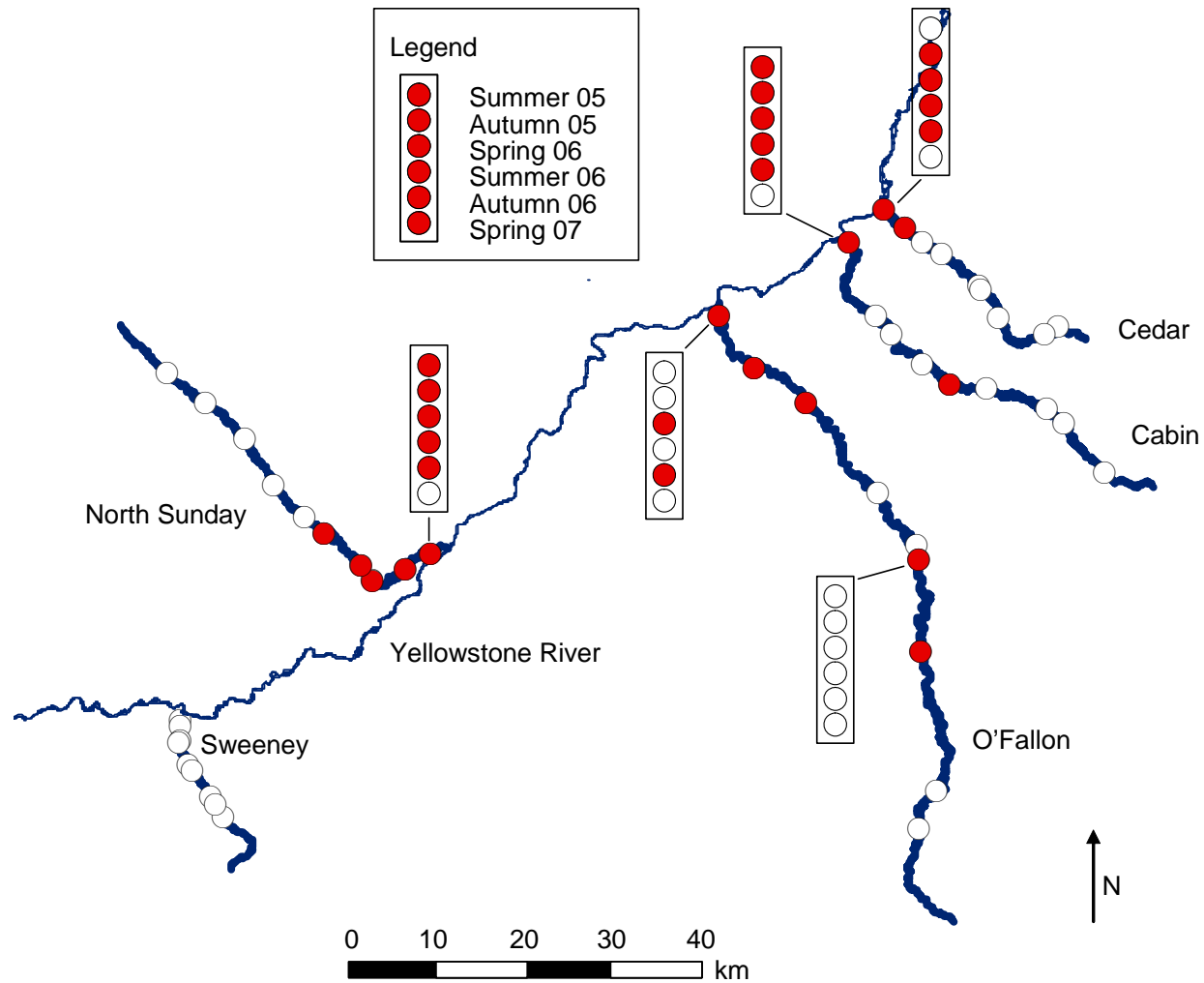


Figure 19. Map of river carpsucker presence in longitudinal and spatiotemporal sites, sampled from June 2005 through April 2007. Dots along stream indicate presence (shaded) and absence from all samples. Dots in boxes represent presence (shaded) and absence of river carpsucker during spatiotemporal sampling (summer 2005 to spring 2007, from top to bottom).

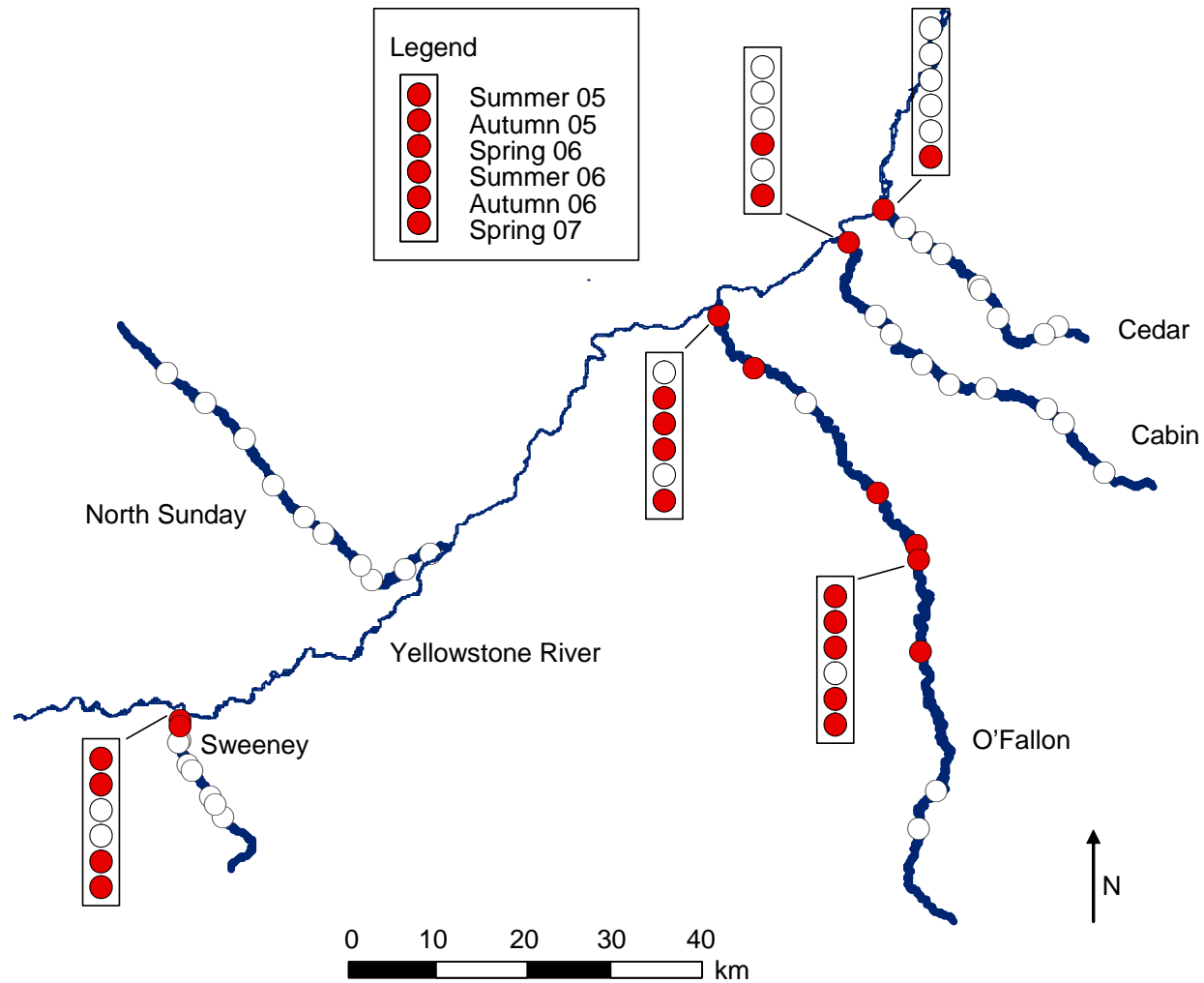


Figure 20. Map of shorthead redhorse presence in longitudinal and spatiotemporal sites, sampled from June 2005 through April 2007. Dots along stream indicate presence (shaded) and absence from all samples. Dots in boxes represent presence (shaded) and absence of shorthead redhorse during spatiotemporal sampling (summer 2005 to spring 2007, from top to bottom).

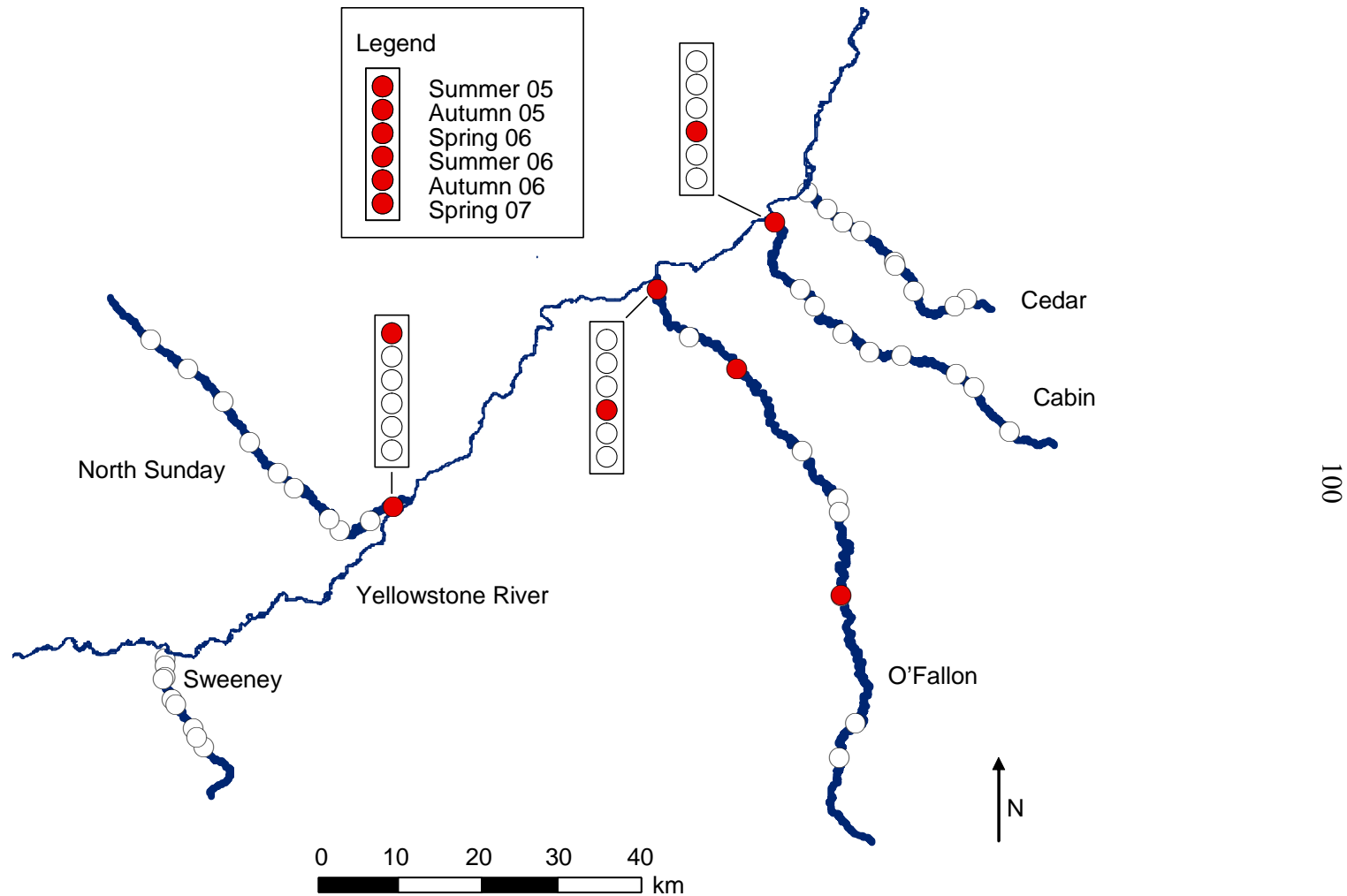


Figure 21. Map of goldfish presence in longitudinal and spatiotemporal sites, sampled from June 2005 through April 2007. Dots along stream indicate presence (shaded) and absence from all samples. Dots in boxes represent presence (shaded) and absence of goldfish during spatiotemporal sampling (summer 2005 to spring 2007, from top to bottom).

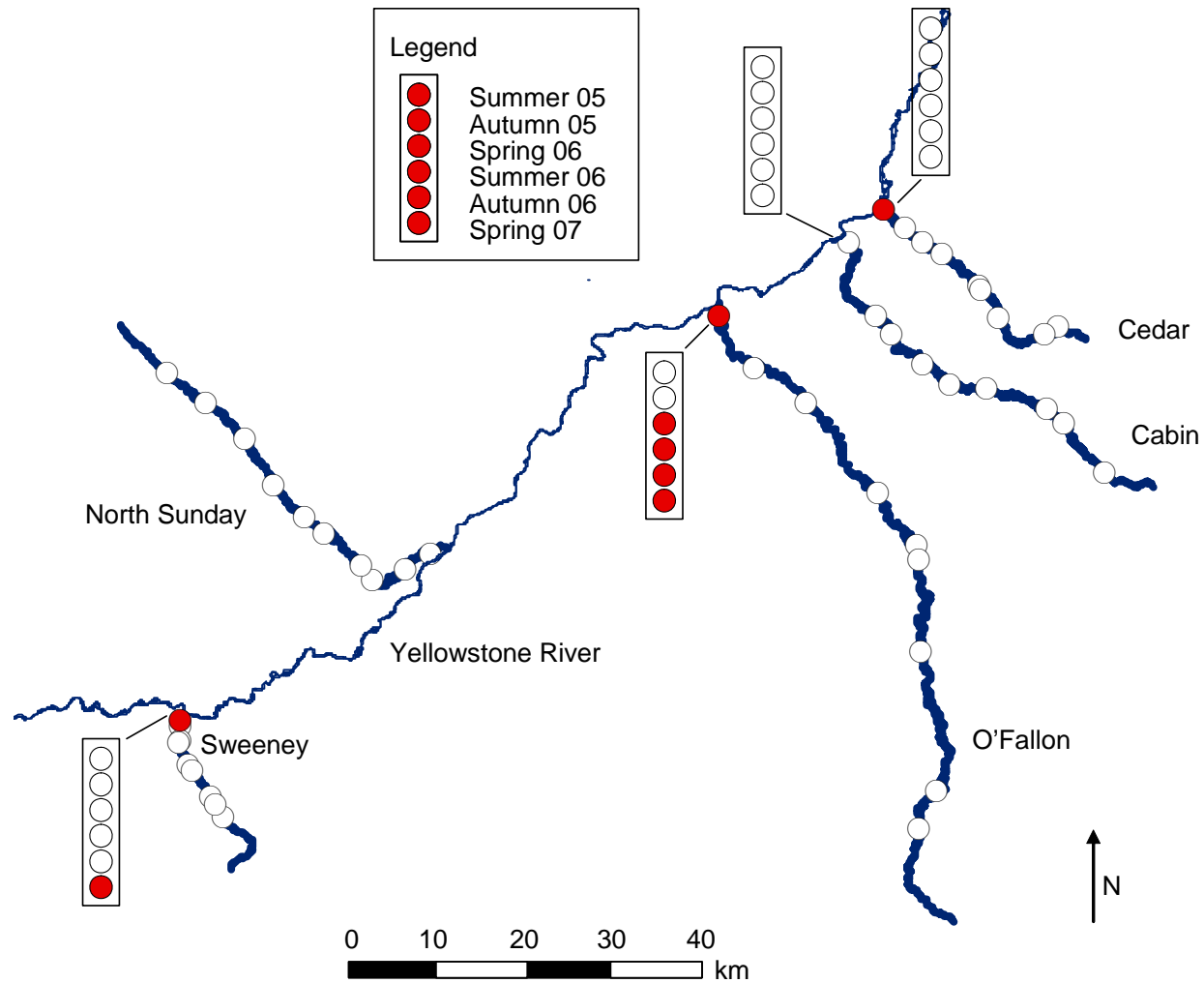


Figure 22. Map of emerald shiner presence in longitudinal and spatiotemporal sites, sampled from June 2005 through April 2007. Dots along stream indicate presence (shaded) and absence from all samples. Dots in boxes represent presence (shaded) and absence of emerald shiner during spatiotemporal sampling (summer 2005 to spring 2007, from top to bottom).

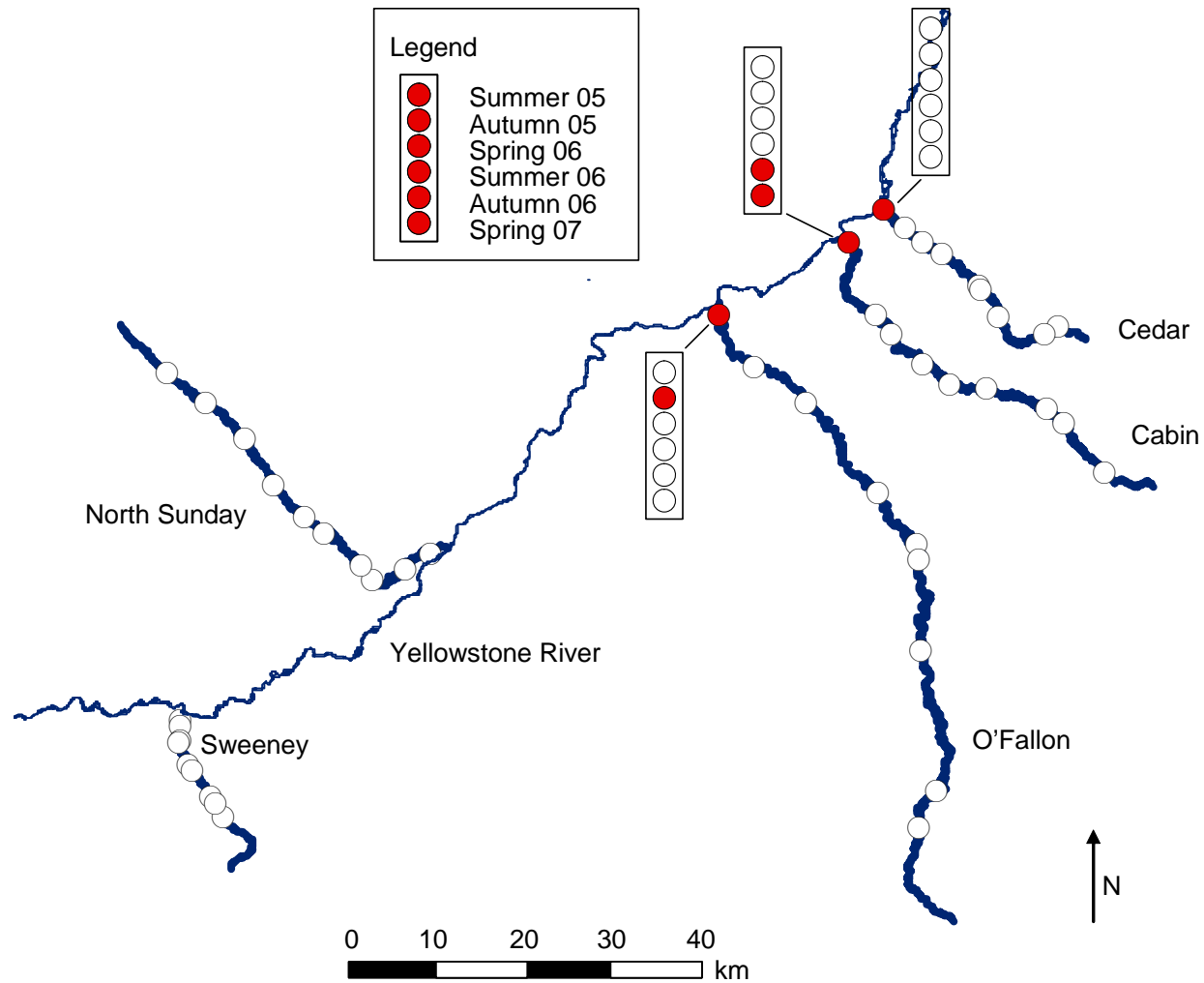


Figure 23. Map of smallmouth buffalo presence in longitudinal and spatiotemporal sites, sampled from June 2005 through April 2007. Dots along stream indicate presence (shaded) and absence from all samples. Dots in boxes represent presence (shaded) and absence of smallmouth buffalo during spatiotemporal sampling (summer 2005 to spring 2007, from top to bottom).

