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## Determinants of Fish Assemblage Structure in Northwestern Great Plains Streams

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### Abstract

Prairie streams are known for their harsh and stochastic physical conditions, and the fish assemblages therein have been shown to be temporally variable. We assessed the spatial and temporal variation in fish assemblage structure in five intermittent, adventitious northwestern Great Plains streams representing a gradient of watershed areas. Fish assemblages and abiotic conditions varied more spatially than temporally. The most important variables explaining fish assemblage structure were longitudinal position and the proportion of fine substrates. The proportion of fine substrates increased proceeding upstream, approaching 100% in all five streams, and species richness declined upstream with increasing fine substrates. High levels of fine substrate in the upper reaches appeared to limit the distribution of obligate lithophilic fish species to reaches further downstream. Species richness and substrates were similar among all five streams at the lowermost and uppermost sites. However, in the middle reaches, species richness increased, the amount of fine substrate decreased, and connectivity increased as watershed area increased. Season and some dimensions of habitat (including thalweg depth, absolute distance to the main-stem river, and watershed size) were not essential in explaining the variation in fish assemblages. Fish species richness varied more temporally than overall fish assemblage structure did because common species were consistently abundant across seasons, whereas rare species were sometimes absent or perhaps not detected by sampling. The similarity in our results among five streams varying in watershed size and those from other studies supports the generalization that spatial variation exceeds temporal variation in the fish assemblages of prairie and warmwater streams. Furthermore, given longitudinal position, substrate, and stream size, general predictions regarding fish assemblage structure and function in prairie streams are possible.

Prairie ecosystems are one of the most endangered on the continent (Samson and Knopf 1994), and few naturally functioning watersheds remain because of fragmentation (Dodds et al. 2004). Increased interest in the conservation and management of small and nongame fishes and prairie stream habitats has intensified sampling efforts in prairie streams. However,

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prairie streams are little understood compared to their forested counterparts, and understanding how prairie fish assemblages vary across time and space is important in understanding inference from fish collections in monitoring programs or species inventories.

Prairie stream fish assemblages are reported to have high temporal variability (Harrell 1978; Ross et al. 1985; Bramblett and Fausch 1991; Dodds et al. 2004) because abiotic conditions in these streams are harsh and stochastic (Matthews 1988; Fausch and Bestgen 1997; Adams et al. 2004; Dodds et al. 2004). In addition, the spatial position within a drainage can greatly influence fish assemblages (Horwitz 1978; Evans and Noble 1979; Matthews 1986; Schlosser 1987; Bhat 2004). The spatiotemporal variation of fish assemblages has been evaluated in warmwater streams in the Midwest (Schlosser 1987), the coastal plains (Adams et al. 2004), and the central and southern Great Plains (Fausch and Bramblett 1991; Meador and Matthews 1992; Williams et al. 1996; Tripe and Guy 1999; Ostrand and Wilde 2002; Thornbrugh and Gido 2010), and large rivers in the Great Plains (Barko et al. 2004; Pegg and McClelland 2004). However, no attempts have been made to describe how fish assemblages in northwestern Great Plains streams vary spatially and temporally or to determine which abiotic factors are important in explaining this spatiotemporal variation.

Most studies on the spatiotemporal variation of stream fish assemblages have focused on one stream, one stream and a few of its tributaries, or multiple sites within a stream network (Schlosser 1987; Meador and Matthews 1992; Williams et al. 1996; Tripe and Guy 1999; Ostrand and Wilde 2002). However, we are aware of no studies that have assessed the role of watershed size on the spatiotemporal variation of fish assemblages in multiple streams that flow directly into the same river. Our goal was to determine the relative influence of spatial, temporal, and abiotic factors in structuring prairie stream fish assemblages in five streams across a gradient of watershed sizes in the northwestern Great Plains.

## METHODS

*Study area.*—The study area consisted of tributaries to the Yellowstone River between river kilometer (rkm) 147 (measuring from its confluence with the Missouri River) and rkm 379 in Montana. All of the tributaries in this area share characteristics in common with typical prairie streams, including relatively frequent and stochastic flooding and drying events, intermittency in at least the headwater to middle reaches, temporally variable turbidity, and low gradients (Rabeni and Jacobson 1999; Dodds et al. 2004). All of the streams are located in the northwestern Great Plains ecoregion (Woods et al. 1999), where grazing and row crop agriculture are the dominant land use activities and oil extraction is prevalent within some drainages. The potential fish species pool is the same for all streams in the study area (White and Bramblett 1993; Holton and Johnson 2003).

*Study design.*—We studied fish assemblages in five streams that represented a gradient of watershed areas. The sampling frame was populated based on the following criteria: (1) each stream was a tributary connected directly to the Yellowstone River between rkm 147 and 379; (2) there were minimal anthropogenic hydrological influences (e.g., irrigation withdrawal or return or reservoirs); (3) each stream was large enough to maintain water in some portion of it; and (4) each stream was wadeable in its lower reaches near the Yellowstone River confluence. The sampling frame was stratified by watershed area in 500-km² increments, and study streams were randomly selected. The streams selected were O'Fallon (4,080 km²), North Sunday (1,937 km²), Cabin (1,026 km²), Cedar (553 km²), and Sweeney (264 km²) creeks (Figure 1). All five streams were adventitious tributaries to the much larger Yellowstone River.

We measured the spatiotemporal variation in fish assemblages in these streams at three sites on each stream. These sites, selected from the lower, middle, and upper longitudinal reaches of each stream (Figure 1), were surveyed during two summers (July 2005, 2006), two autumns (October 2005, 2006), two winters (February 2006, 2007), and two springs (April 2006, 2007). The lower sites were established in a reach from 1 to 5 rkm from the confluence with the Yellowstone River, resulting in approximately equal connectivity (in terms of distance) to the same main-stem fish species pool. The upper sites were established at the estimated uppermost location of permanent water. The middle sites were established about midway between the upper and lower sites.

We investigated the fine-scale longitudinal variation in fish assemblages at 9–10 summer longitudinal sites on each stream, arrayed over the entire stream lengths from mouth to headwaters. 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. Nine or 10 sites on each stream were established depending on access and grants of permission. These sites were sampled from 1 June to 18 August in 2004 and from 22 May to 5 August in 2005. Summer longitudinal sites also served as spatiotemporal sites where the sites overlapped.

*Fish sampling.*—In an effort to capture all fish species present at each site, 300-m reaches were sampled (Patton et al. 2000) with a seine (6.1 m × 1.8 m with 0.6-cm-bar mesh). Seining began upstream and progressed downstream within a reach. Individual seine hauls were no longer than 60 m and typically were 30 m or less, depending on the physical characteristics 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, in which one person would hold the seine against the current in a U shape while another disturbed the substrate immediately upstream of the seine (Rabeni et al. 2009). A dip net (0.30 m × 0.15 m × 0.6-cm bar mesh) was used to sample fish if the stream was too shallow or narrow for effective seining.
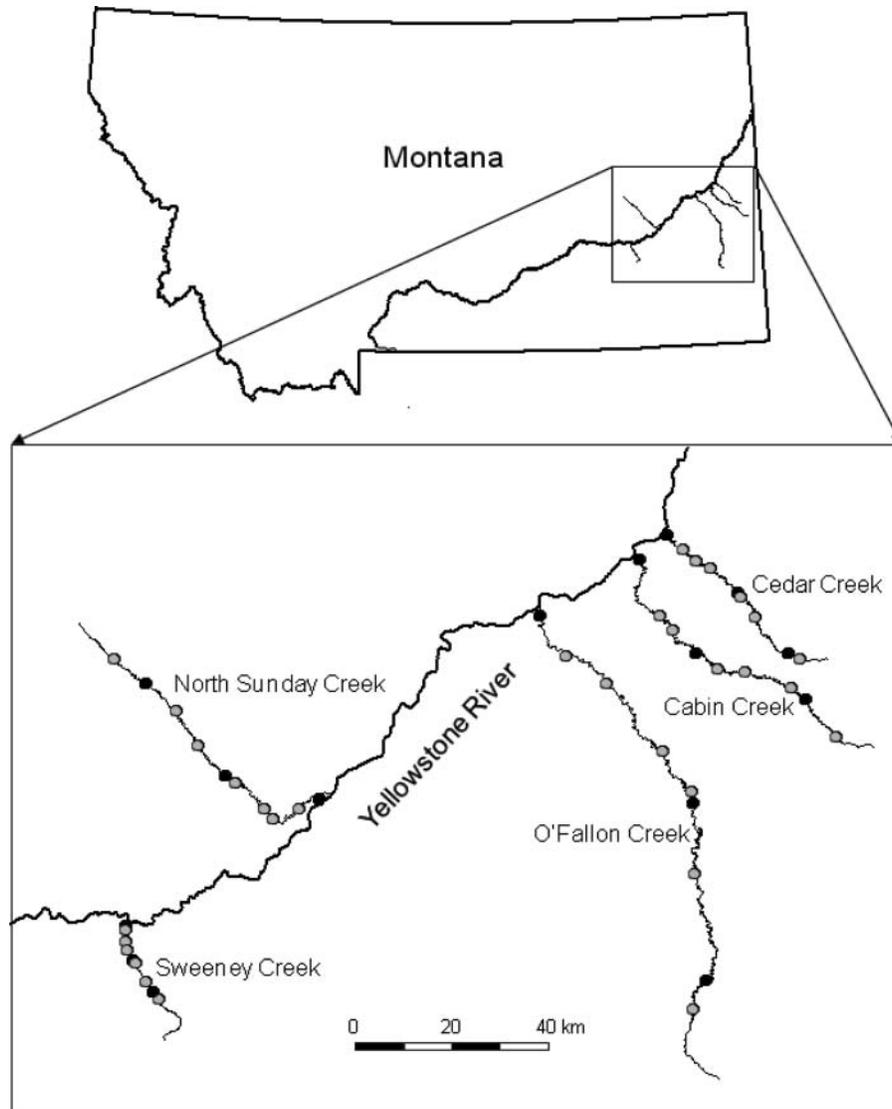
FIGURE 1. Map of the study area showing the locations of the spatiotemporal (black circles) and longitudinal (gray circles) sites on five Montana prairie streams during 2005–2007.

Fish were anesthetized with tricaine methanesulfonate (MS-222) to facilitate processing, identified to species (*Hybognathus* spp. <55 mm were classified as juvenile *Hybognathus* spp. because identification to species is difficult in the field), and enumerated. All fish except up to 10 voucher specimens of each species per sample were returned to the stream after processing.

*Abiotic variable measurements.*—Abiotic variables (wetted width, depth, substrate composition, and discharge) were measured following Environmental Monitoring and Assessment Program methods (Lazorchak et al. 1998) at all sites. Transect measurements ($N = 11$) were collected at 30-m intervals. Wetted width was measured at each transect. Depth and substrate size-class were measured at five equally spaced points along each transect between the wetted edges of the stream. Substrate was initially classified into seven size classes (Kaufmann and Robison 1998); however, we simplified substrate data into the proportion of fine substrate (<2 mm) in the sampled reach for data analysis. Depth and substrate of the thalweg were measured at 3-m intervals along the entire length of the site. Discharge was calculated for all flowing sites using the velocity–area procedure (Kaufmann 1998). Current velocity was measured with a Marsh-McBirney Model 2000 flowmeter.

*Winter sampling.*—Spatiotemporal sites were surveyed in February 2006 and 2007 for the presence or absence of ice. To determine whether pools froze completely, we drilled holes in the ice with an ice auger at some sites and measured ice thickness and liquid water depth underneath the ice. Fish collections

were not made at these times because ice usually made seining impossible.

*Analysis of spatiotemporal data.*—Spatiotemporal patterns in species richness and abiotic variables (i.e., wetted area, mean thalweg depth, mean wetted width, and proportion of fine substrates) were examined graphically. The relationships between fish species richness and abiotic variables were assessed with correlation analysis using SAS version 9.1.3 (SAS 2003). The wetted area, wetted width, and proportion of fine substrates 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 when transformed. Dry sites were excluded from correlation analyses. Each relationship was examined graphically for nonlinear relationships.

The spatial, temporal, and abiotic variables that best explained fish assemblage structure (i.e., the variation in the identity and abundance of fish species) were identified using canonical correspondence analysis (CCA; vegan package version 1.8–3 in R version 2.4.0; R Development Core Team 2006). First, to determine the relative importance of each variable alone, we assessed all explanatory variables separately with data pooled from all streams. Second, to determine which variables in combination explained fish assemblage structure in all five streams pooled, we used a stepwise model-building approach. Third, to determine how much additional variability could be explained if stream identity were known, and to determine whether the variables that were important in each stream were the same as for all streams pooled, we developed stepwise individual-stream models.

Analyses were performed on $\log_{10}(x + 1)$ transformed species abundance data (Ter Braak 1986). Abiotic variables were not transformed before analyses because the significance of CCA results does not depend on parametric distribution assumptions (Palmer 1993) and because 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). Variables examined were longitudinal position (i.e., lower, middle, and upper), season (i.e., spring, summer, and autumn), rank watershed area, wetted width, mean thalweg depth, wetted area, proportion of fine substrates, and discharge.

The goodness of fit was determined for each ordination by dividing the amount of variation explained by the abiotic variables by the total amount of variation (Ter Braak 1986), resulting in a value analogous to the coefficient of determination ($r^2$; Williams et al. 1996). Significance was determined by running 999 permutations with the predictor variable of interest randomized to calculate a *P*-value that we compared with $\alpha = 0.05$ for statistical significance.

We used a forward stepwise selection approach to build pooled-stream and individual-stream CCA models (Ter Braak

and Verdonschot 1995; Jaworski and Ragnarsson 2006). The significant ($P < 0.05$) single-variable model that explained the most variation was used as the start model and all remaining variables were added to the CCA model independently. The significant two-variable model that explained the most variation was then used as a starting model and the same process was repeated. The final multiple-variable model was selected by examining a 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 5% of additional variation.

Our graphical interpretation of the pooled-stream stepwise CCA ordination focused on interpretation of species associations with abiotic variables. Only the first two CCA axes were examined because little variation was explained by additional axes.

*Analysis of summer longitudinal data.*—The relationships between species richness and the proportion of fine substrates with distance from the stream mouth during summer were assessed graphically for each stream. We used regression to fit lines to the relationships to facilitate graphical interpretation; however, given the potential lack of independence among sites on the same stream, we do not report statistical significance or coefficients of determination. Linear and quadratic regression lines were fit for straight and curvilinear relationships, respectively (Littell et al. 1991). We graphically assessed the effect of watershed size on the relationship between species richness and relative distance from the stream mouth. We calculated relative distance as distance from the mouth to the site in question divided by the distance from the mouth to the uppermost site on the stream.

## RESULTS

### Spatiotemporal

*Fish assemblage characteristics.*—Twenty-four species and 34,867 individuals were collected in 90 spatiotemporal samples. Nineteen species were native (94% of the individuals) and five were nonnative (6% of the individuals). Fathead minnow *Pimephales promelas* (29%), sand shiner *Notropis stramineus* (13%), flathead chub *Platygobio gracilis* (9%), lake chub *Couesius plumbeus* (6%), and plains minnow *Hybognathus placitus* (5%) were the most abundant species and made up about 62% of all the individuals collected. Fish were collected from each spatiotemporal site during at least one sampling event; however, fish were absent during some samplings at middle and upper North Sunday Creek and at middle Sweeney Creek.

*Species richness.*—Graphical examination indicated that, in general, species richness declined with changes in location from downstream to upstream and with decreasing watershed area (Figure 2). Deviations from these trends were largely associated with Sweeney and North Sunday creeks. The upstream site on Sweeney Creek sometimes had higher species richness than the
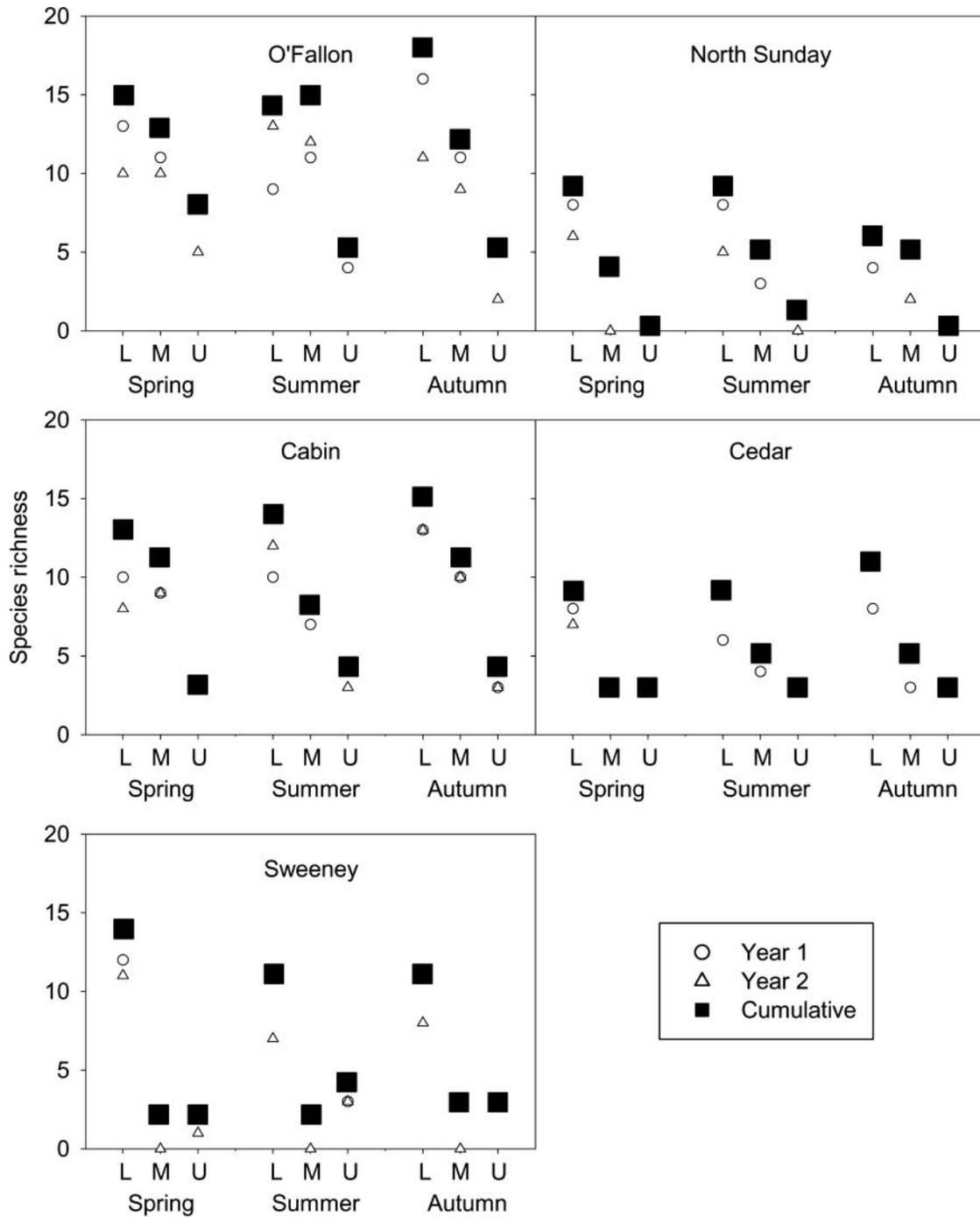
FIGURE 2. Species richness at the lower (L), middle (M), and upper (U) spatiotemporal sites by stream and season for five Montana prairie streams during 2005–2007. Cumulative species richness is calculated from pooled data from years 1 and 2.

middle site did, and species richness was often lower in North Sunday Creek than in the smaller streams even though it was the second largest stream by watershed area (Figure 2).

Species richness was not consistent among seasons. For example, species richness in lower O'Fallon Creek was highest in autumn in the first year of sampling (16 species) but highest in

summer in the second year (13 species; Figure 2). Cumulative species richness (i.e., all samples pooled) generally exceeded the species richness of single samples (Figure 2).

*Abiotic characteristics.*—In general, wetted width, wetted area, and discharge decreased from downstream to upstream and with decreasing watershed area. The proportion of fine

substrates increased from downstream to upstream in all five streams, generally increasing with decreasing watershed area. We saw no consistent spatial pattern in mean thalweg depth. For example, the deepest habitats in the largest stream were at the lowermost site, whereas in the other streams the deepest habitats were usually at the middle or uppermost sites. The extent to which no stream discharge occurred ranged from 0% (Cabin Creek) to 61% (Sweeney Creek). Abiotic characteristics varied less among seasons than among longitudinal positions. The proportion of fine substrates remained relatively constant among seasons, rarely varying by more than 0.15. In general, wetted width, thalweg depth, and discharge decreased from spring through summer; however, these metrics sometimes increased in autumn.

Ice cover was prevalent during winter. Eighty-one percent (22 of 27) of winter sites surveyed had surface ice; however, liquid water existed beneath the ice at all accessible sites except at the upper sites of O'Fallon and North Sunday creeks in February 2007. Ice thickness ranged from 0.1 to 1.0 m, and water depth below the ice ranged from 0.05 to 0.70 m. Anchor ice occurred at two of the five sites where surface ice was not present.

*Fish assemblage and abiotic associations.*—Species richness was significantly negatively correlated with the proportion of fine substrates and positively correlated with wetted area and wetted width. The strongest correlation was with the proportion of fine substrates (Table 1).

All variables used in single-variable pooled-stream CCA models except season were significantly related to ($P < 0.05$) and explained moderate to low amounts of the variability in the composition of the fish assemblage (Table 2). Longitudinal position explained the greatest amount of the variation in the fish assemblage (18.5%), followed by the proportion of fine substrates (13.9%). The remaining single-variable models explained less than 10% of the variation (Table 2).

All four stepwise pooled-stream models were significant (Table 3). Beginning with longitudinal position (18.5% variation explained), adding proportion of fine substrates to the model explained an additional 6.7% of variation in the fish assemblage. Rank watershed area and wetted area explained an additional 4.7% and 3.4% of the variation, respectively. However, the two-variable model was selected as the best stepwise model because no inflection point was detected in the variation-explained plot

TABLE 1. Correlation coefficients and *P*-values for the significant relationships between species richness and abiotic variables for five Montana prairie streams during 2005–2007. All correlations are for linear relationships, with $N = 89$; all variables were $\log_{10}(x + 1)$ transformed.

| Statistic | Proportion fines | Wetted area | Wetted width |
|---|---|---|---|
| Correlation coefficient ($r^2$) | –0.71 | 0.44 | 0.34 |
| *P*-value | <0.01 | <0.01 | <0.01 |

TABLE 2. Single-variable canonical correspondence model results, including the percentage of the variation in fish assemblage explained and *P*-values for five Montana prairie streams during 2005–2007.

| Model variable | Percent variation explained | *P*-value |
|---|---|---|
| Longitudinal position | 18.5 | 0.001 |
| Proportion of fine substrates | 13.9 | 0.001 |
| Wetted area | 7.3 | 0.001 |
| Wetted width | 6.9 | 0.001 |
| Thalweg depth | 4.4 | 0.002 |
| Rank watershed area | 4.3 | 0.002 |
| Discharge | 4.3 | 0.002 |
| Season | 2.1 | 0.717 |

and subsequent additional variables explained less than 5% additional variation (Table 3).

Longitudinal position and the proportion of fine substrates explained 25.2% of the overall variation in the fish assemblage (Table 3), and CCA axes 1 and 2 represented 92% of this variation. Four primary groups of fish species were revealed by the CCA ordination plot and all but one species was placed within one of four groups (Figure 3). Group 1 fishes were associated with upper longitudinal positions (i.e., near the headwaters) and higher amounts of fine substrates (green sunfish *Lepomis cyanellus*, black bullhead *Ameiurus melas*, brassy minnow *H. hankinsoni*, and fathead minnow). Group 2 fishes were associated with lower longitudinal positions (i.e., near the confluence with the Yellowstone River) and lower amounts of fine substrates (western silvery minnow *H. argyritis*, river carpsucker *Carpiodes carpio*, common carp *Cyprinus carpio*, stonecat *Noturus flavus*,

TABLE 3. Stepwise multivariable pooled-stream canonical correspondence model results, including the percentage of the variation in fish assemblage explained and *P*-values for five Montana prairie streams during 2005–2007. The model that explained the most variation is presented for each model type. The two-variable model was selected as the multivariable model for further assessment.

| Model type | Model variable(s) | Percent variation explained | *P*-value |
|---|---|---|---|
| One variable | Longitudinal position | 18.5 | 0.001 |
| Two variable | Longitudinal position + fines | 25.2 | 0.001 |
| Three variable | Longitudinal position + fines + rank watershed area | 29.9 | 0.001 |
| Four variable | Longitudinal position + fines + rank watershed area + wetted area | 33.3 | 0.002 |
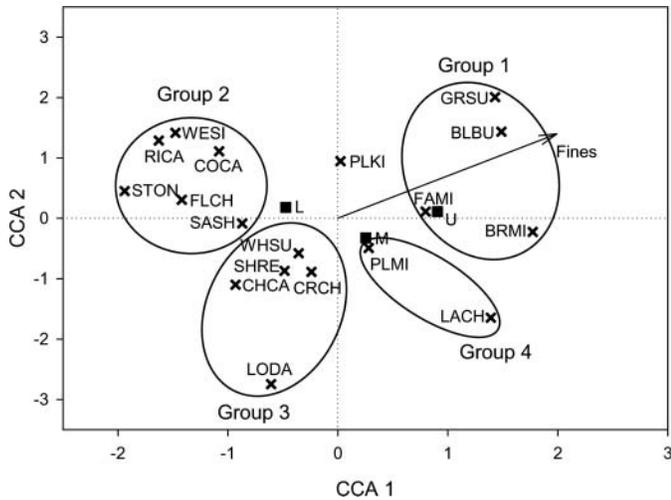
FIGURE 3. Canonical correspondence analysis (CCA) ordination plot of fish species (× symbols), longitudinal position (squares), and proportion of fine substrates (arrow) for five Montana prairie streams during 2005–2007. The explanatory variables are the proportion of fine substrates (fines) and the lower, middle, and upper longitudinal positions (L, M, and U, respectively). Groups 1, 2, 3, and 4 represent our interpretation of the ordination. Abbreviations for fish species are as follows: 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).

flathead chub, and sand shiner). Group 3 fishes were weakly associated with lower and middle longitudinal positions and moderate amounts of fine substrates (white sucker *Catostomus commersonii*, shorthead redhorse *Moxostoma macrolepidotum*, channel catfish *Ictalurus punctatus*, creek chub *Semotilus atromaculatus*, and longnose dace *Rhinichthys cataractae*). Group 4 fishes were weakly associated with middle and upper longitudinal positions and moderate amounts of fine substrates (plains minnow and lake chub). The northern plains killifish *Fundulus kansae* was not strongly associated with any longitudinal position, although it was associated with moderate amounts of fine substrates (Figure 3). Species associations with middle sites and moderate amounts of fine substrates may alternatively be interpreted as being unrelated to these variables (Ter Braak 1987).

In stepwise single-stream CCA models, the variable that explained the most variation in the fish assemblage was longitudinal position for all five streams (Table 4). The proportion of fine substrates was not included in any of the single-stream CCA models, season was included in the Cabin Creek model, and season and wetted area were included in the Cedar Creek model. The models for O'Fallon, North Sunday, and Sweeney creeks included only longitudinal position. Stream identity was an important factor because single-stream models explained 51.5–79.4% of the variation, whereas the pooled-stream model explained just 25.2% of the variation in fish assemblages (Tables 3, 4).

TABLE 4. Stepwise multivariable single-stream canonical correspondence model results, including the percentage of the variation in fish assemblage explained and *P*-values for five Montana prairie streams during 2005–2007. Streams are ordered by watershed area from largest to smallest.

| Stream | Model variable(s) | Percent variation explained | *P*-value |
|---|---|---|---|
| O'Fallon | Longitudinal position | 51.5 | 0.001 |
| North Sunday | Longitudinal position | 51.7 | 0.001 |
| Cabin[a] | Longitudinal position + season | 65.2 (55.7) | 0.049 (0.001) |
| Cedar[a] | Longitudinal position + season + wetted area | 79.4 (61.7) | 0.046 (0.001) |
| Sweeney | Longitudinal position | 62.4 | 0.001 |

[a]The values in parentheses are for the model with longitudinal position as the only variable.

## Summer Longitudinal

*Fish assemblage characteristics.*—Twenty-five species and 52,449 individuals were collected from the 178 summer longitudinal samples. Eighteen species were native (96% of the individuals) and seven were nonnative (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 69% of the total fish assemblage. At least one fish was sampled at each longitudinal site except for the uppermost sites on North Sunday and Cedar creeks, where no fish were sampled in 2005 and 2006.

*Longitudinal variation in species richness.*—Species richness declined with distance from the mouth in all streams (Figures 4A–4E). Species richness near the mouth and in the headwaters was similar among all streams (Figure 4F). Species richness declined more rapidly moving upstream in terms of both absolute (Figures 4A–E) and relative distance (Figure 4F) as watershed area decreased. However, species richness in North Sunday Creek (with the second largest watershed) declined more rapidly than in Cabin Creek (with the third largest watershed).

*Abiotic characteristics.*—We examined the relationship between the proportion of fine substrates and distance from the mouth because the proportion of fine substrates was most strongly correlated with species richness in the spatiotemporal analysis. The proportion of fine substrates was positively related to distance from the mouth for all streams (Figures 4A–E).

## DISCUSSION

Prairie streams are often characterized as harsh and stochastic environments (Matthews 1988; Fausch and Bestgen 1997; Dodds et al. 2004) with temporally variable fish assemblages (Harrell 1978; Ross et al. 1985; Bramblett and Fausch 1991; Dodds et al. 2004). However, in our study of five
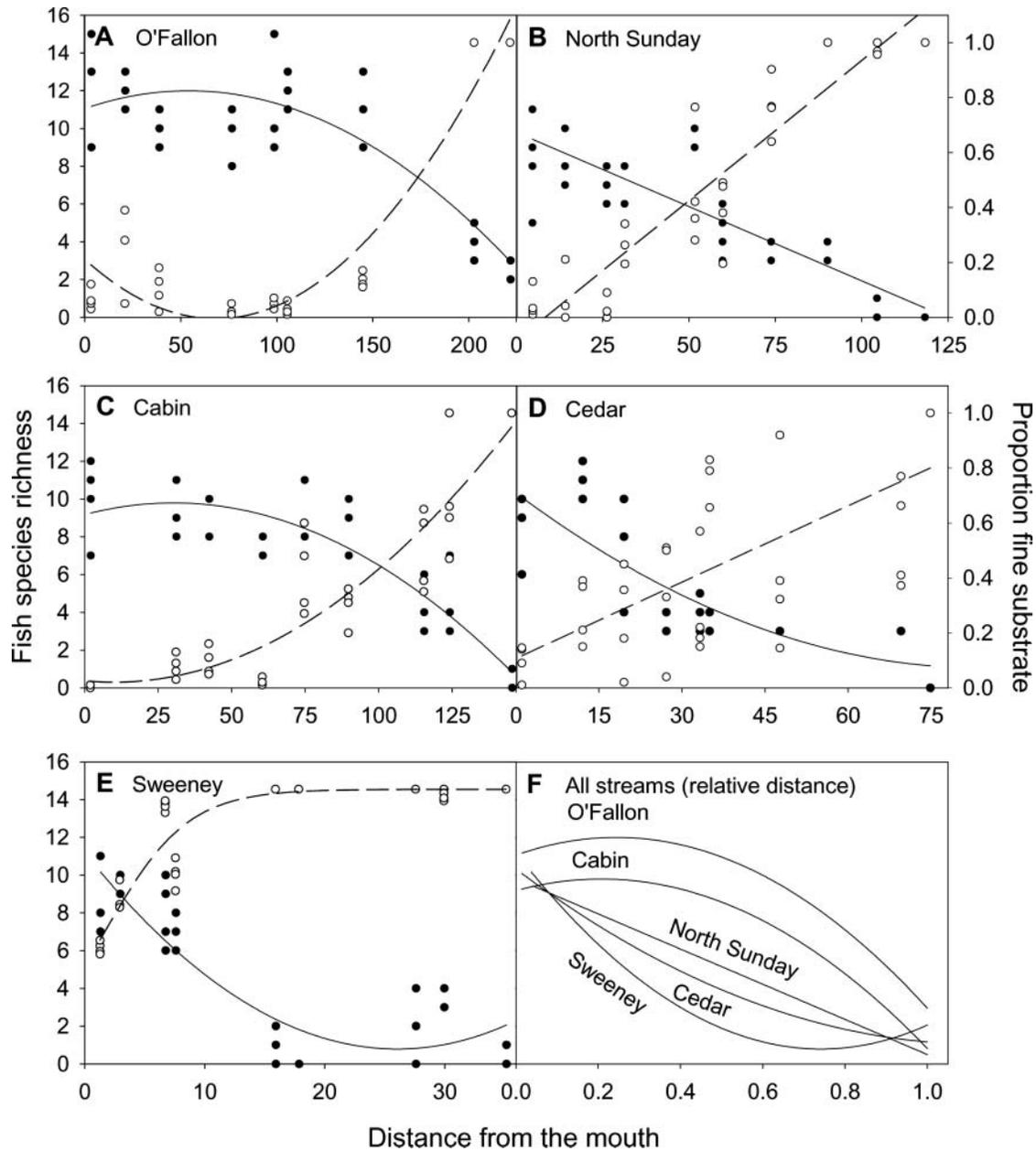
FIGURE 4.    Panels **(A–E)** depict the relationships between species richness (filled circles; solid lines) and the proportion of fine substrates (open circles; dashed lines) with the distance from the stream's mouth for five Montana prairie streams during 2005–2007. Panel **(F)** depicts the relationship between species richness and the relative distance from the mouth for the five streams.

northwestern Great Plains streams, fish species richness and assemblage structure varied more spatially than temporally. Furthermore, the variables that explained the most variation in species richness and assemblage structure were deterministic factors (longitudinal position, proportion of fine substrate, and rank watershed size), which did not vary or varied little temporally. We observed the well-known trend of longitudinal declines in species richness from mouth to headwaters (Harrel et al. 1967; Horwitz 1978; Rahel and Hubert 1991). However,

our results indicate that in addition to relative longitudinal position, the composition of substrate is important in determining fish assemblage structure in prairie streams.

Integration of several lines of evidence supported our conclusion that longitudinal position, the proportion of fine substrate, and watershed size were the most important factors in determining fish assemblage structure. First, fish species richness declined with increasing distance from the stream mouth and increasing proportion of fine substrates. Second, fish species

richness declined with watershed area. Third, longitudinal position, substrate composition, and rank watershed area explained significant amounts of variability in the structure of fish assemblages, whereas season was not a significant explanatory variable in our pooled-stream model.

Fish assemblage function also appeared to be related to longitudinal position and the proportion of fine substrates. Seven of 11 fish species that were associated with lower or middle longitudinal positions and lower proportions of fine substrates are obligate lithophilic spawners (Bramblett et al. 2005). Although it is known that fish species richness and diversity may decline with anthropogenic sedimentation (Berkman and Rabeni 1987; Rabeni and Jacobson 1999), we observed that seemingly natural longitudinal gradients of substrate composition also influence fish assemblages. Fish species associated with lower and middle sites also tended to have larger adult body sizes (Brown 1971) than the species associated with upper sites, probably because of the proximity and connectivity of lower sites to the main-stem Yellowstone River.

The location of the transition between fine and coarse substrates on the longitudinal profile varied with watershed area. As watershed area increased, the upstream extent of gravel substrates increased. The frequency and magnitude of flow events capable of flushing fine substrates probably increase with watershed area. Therefore, in our study area, larger watersheds had coarser substrates farther upstream, in terms of absolute and relative distance, than did smaller watersheds. Notably, the longitudinal gradient we observed of increasing substrate size proceeding downstream was the opposite of the trend predicted at larger whole-river scales (Leopold et al. 1964; Allan 1995). This pattern of smaller substrates in headwaters and larger substrates in downstream reaches may be unique to streams with relatively low gradients and erodible soil types.

In contrast to our findings, the proportion of fine substrates increased and fish assemblage structure varied only slightly with increasing distance from the main-stem river in three Kansas River tributaries (Thornbrugh and Gido 2010). This seeming disparity probably reflects differences in sampling scale and local geomorphology between the two studies. Whereas we sampled tributaries from their headwaters (from 35 to over 200 stream km from the Yellowstone River, depending on watershed size) to their lower reaches, Thornbrugh and Gido (2010) concentrated on confluence zones and sampled only the lower 20 km of their study tributaries, probably not far enough to document strong longitudinal shifts in assemblage structure. Our lowermost sites were located from 1 to 5 km upstream from the Yellowstone River and were not on the Yellowstone River floodplain, whereas Thornbrugh and Gido (2010) sampled floodplain sites less than 1 km from the Kansas River. Tributary sites located on the Kansas River floodplain probably had lower gradient and less sediment transport than our lowermost sites, which may explain the increases in fine substrates with proximity to the Kansas River (Thornbrugh and Gido 2010).

The longitudinal changes in fish assemblages that we observed are probably also related to a longitudinal gradient in connectivity. Intermittent streams lose connectivity spatially and temporally as surface flow ceases and fish are unable to colonize from more perennial reaches (Labbe and Fausch 2000; Dodds et al. 2004). Species richness declined markedly in two of our study creeks where continuous flow ended and intermittency began. Anthropogenic factors may also have limited connectivity in two other creeks because declines in species richness corresponded to potential fish movement barriers created by culverts and spreader dikes.

Watershed area influenced several aspects of fish assemblages and habitat. Total species richness, discharge, wetted width, and the upstream extents of some fish species and gravel substrates all increased as watershed area increased. Individual stream models were more explanatory than models with streams pooled, presumably because the five study streams varied substantially in watershed area. Moreover, the addition of rank watershed area to our model with streams pooled was significant. Many studies have noted the influence of stream size on species richness; however, these studies often focus on the changes in stream size within a single watershed (Harrel et al. 1967; Lotrich 1973; Evans and Noble 1979; Rahel and Hubert 1991) and rarely among watersheds (Fausch et al. 1984; Hitt and Angermeier 2008; Thornbrugh and Gido 2010). Here, we demonstrate the importance of watershed area on fish assemblage structure among five watersheds that are tributaries to the same main-stem river.

In all five streams, species richness was similar among lower sites (mean = 9–11 species) and upper sites (mean = 1–2 species), despite large differences in watershed area. However, the absolute distance from the stream mouth was not a good predictor of species richness. Species richness at middle sites was generally positively related to watershed area, as was the proportion of gravel substrate and connectivity (i.e., discharge). High species richness at lower sites was supported by gravel substrate and adequate connectivity and proximity to the main-stem river, whereas species richness at upper sites was probably limited by the lack of gravel substrate and lack of connectivity to lower reaches.

Although spatial variation exceeded temporal variation in the fish assemblages in our study, there was substantial temporal variation in species richness. Cumulative species richness at a site was generally greater than in individual samples, indicating that multiple sampling events are necessary to fully characterize fish assemblages. Temporal variation in species identity and abundance also occurred but was less substantial than the variation in species richness. Season was not a significant explanatory variable in our pooled-stream model and explained only moderate amounts of variation in the fish assemblages in just two of five individual-stream CCA models. This suggests that temporal variability in the overall fish assemblage was moderate because common species were consistently abundant across time, as has been observed elsewhere (Matthews et al. 1988).

Spates, drying, and spawning events may have accounted for some of the temporal variability we observed. Some cyprinids make upstream spring and autumn migrations into tributaries or synchronize spawning with turbid storm events (Mendelson 1975; Gorman 1986; Cross and Moss 1987) and spates in intermittent streams may increase connectivity. Episodic appearances of emerald shiners and western silvery minnows in some of our study streams may have been associated with spates or spawning events. Substantial drying at one sampling site probably explained the decline from 5 species and 211 individuals in a summer sample to only 2 species and 9 individuals in the subsequent autumn sample. Local extirpations can be caused by drought and drying (Harrel et al. 1967; Mundahl 1990; Ostrand and Wilde 2001, 2004), and the extirpation of fish that we observed at one sampling site was probably caused by drying. Although freezing of intermittent pools has been reported to reduce overwinter survival of fish (Labbe and Fausch 2000), it did not appear to cause local extirpations in our study. Liquid water was generally present beneath surface ice, and fish assemblages were similar in autumn and subsequent spring sampling events.

The greater spatial variation than temporal variation detected in this study may be partially attributed to the study design, which was conducted over a fairly large spatial scale and a moderate (2-year) temporal scale. The probability of a major disturbance increases with the duration of the study. However, several floods and seasonal drying occurred during our study. Eastern Montana was in a drought from at least 2000 through 2006 (MDAC 2005). Wetter conditions would increase connectivity in intermittent reaches, allowing for greater dispersal opportunities, and thus would potentially reduce the spatial variation in fish assemblages. In addition, temporal variation probably was underestimated because we did not include rare species or sites with no fish present in the CCA due to their strong influence on models. Including rare species, however, would also increase spatial variation, because these species generally occurred at only a few sites.

Spatial variation exceeded temporal variation in fish assemblages in five northwestern Great Plains streams across a gradient of watershed areas, suggesting that the deterministic factors of longitudinal position, substrate, watershed area, and connectivity were more important than stochastic factors such as spates or drying in explaining the variation in the fish assemblages in the northwestern Great Plains. Similar findings in the Great Plains and Midwest (Schlosser 1987; Meador and Matthews 1992; Williams et al. 1996; Tripe and Guy 1999; Ostrand and Wilde 2002) suggest that the generalization that spatial variation exceeds temporal variation in the fish assemblages of prairie and Midwestern streams is appropriate. Moreover, given longitudinal position, substrate composition, watershed size, and connectivity, general predictions regarding fish assemblage structure (i.e., species richness, identity, and abundance) and function (i.e., lithophilic spawners) in prairie streams are possible.

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