2-2011

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Wanner, Greg A.; Pegg, Mark A.; Schainost, Steven; Klumb, Robert A.; and Shuman, Dane A., "River geomorphology and fish barriers affect on spatial and temporal patterns of fish assemblages in the Niobrara River, Nebraska" (2011). *Papers in Natural Resources*. 337.
https://digitalcommons.unl.edu/natrespapers/337

River geomorphology and fish barriers affect on spatial and temporal patterns of fish assemblages in the Niobrara River, Nebraska

February 2011

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Abstract. — The Niobrara River in northern Nebraska traverses the heart of the Great Plains with portions of the river protected under the National Wild and Scenic River system managed by the National Park Service. The Niobrara River changes from a narrow, entrenched stream to a wide, highly braided river with four fish barriers and 36 distinct geomorphic segments in the lower 531 river kilometers (rkm). Our objectives were to examine the spatial and temporal patterns of fish assemblages in the Niobrara River related to environmental variables, fish barriers, and river geomorphology. Tote-barge electrofishing occurred monthly from June to September in 2009 at 17 sites downstream of Dunlap Diversion Dam near Hemingford, Nebraska (river kilometer [rkm] 531) to the mouth (rkm 0) where the Niobrara River meets the Missouri River. In all, we collected 33,888 fish from 42 species and 11 families. Species richness was greatest near the mouth (rkm 4) and subsequently declined sharply upstream of the first fish barrier (Spencer Dam; rkm 63). Monthly changes in the fish assemblages were generally low with most differences due to young of the year, large-bodied fish recruiting to the electrofishing gear. Fish barriers, both anthropomorphic and natural, had significant impacts on the fish community by blocking fish migration, creating high abundances downstream of the structures, and species absent above the barriers. Bray-Curtis dissimilarity values between sample sites ranged from 45.4 to 96.5, which indicated high variation in the fish assemblage as river geomorphic features changed. Norden Chute (rkm 193), a natural fish barrier, marked a sharp change in geomorphic structure from a highly braided river with heterogeneous diversity of habitats downstream to a single river channel with a reduced floodplain upstream. Above the chute, the fish assemblage was dominated by insectivores fish species, while downstream occurrence of piscivores increased. Based on our results, fish barriers affected the diversity and abundances of fish both upstream and downstream.

Introduction

The Niobrara River traverses the heart of the Great Plains and extends approximately 900 km from its headwaters in eastern Wyoming to its confluence with the Missouri River, near Niobrara, Nebraska (Figure 1). The Niobrara River is considered a relatively undisturbed river from anthropomorphic influences with over 150 river kilometers (rkm) of the river under the protection of the National Wild and Scenic River System managed by the National Park Service. Human induced alterations to the continuity of the mainstem river include Spencer Dam (rkm 63), Cornell Dam (rkm 242), and Dunlap Diversion Dam (rkm 531) (Figure 1). Both Spencer and Cornell dams are flow through reservoirs with no influence on the natural hydrograph. The most significant alteration to the hydrograph is found immediately downstream of the Dunlap Diversion Dam where up to 90% of the annual streamflow, relative to upstream of the diversion, is diverted for agricultural irrigation (Shaffer 1975). However, the river regains significant flow within a few kilometers downstream of the diversion, mainly from groundwater seepage (Bentall and Shaffer 1975). These three dams are complete barriers to the upstream migration of fish. Additionally, Norden Chute (rkm 193) is a natural fish barrier where the river narrows and the channel cuts through a bedrock formation (Figure 1). The effects of barriers on rivers and ecosystems are well documented with mostly negative impacts on the native fish community. Low-head dams are responsible for altering the natural cycle of flow, physical characteristics of the river channel and floodplain, transforms the biological characteristics, and fragments the continuity of rivers (Petts 1984; Ligon et al. 1995; Ward and Stanford 1995; Poff et al. 1997).

The geomorphology of the Niobrara River changes dramatically from the mouth upstream to the Dunlap Diversion Dam. The Niobrara River physically changes multiple times by the degree of confinement of the river channel, degree of sinuosity, channel width variation, and by various sand bar configurations. Alexander et al. (2009) reported 36 distinct geomorphic segments from the mouth to the Dunlap Diversion Dam. Differences in physical habitats along the longitudinal gradient of the river would likely affect the fish assemblage present. At any given location, the fish community is influenced by historical, evolutionary, and biogeographical processes as well as species interactions and environmental variation that influence their abundance and distributions (Ricklefs 1987).

Fish community data within the Niobrara River were limited both spatially and temporally. Fish investigations in the Niobrara River thus far were for basic inventories, miscellaneous collections, random surveys with low sample size, and research studies that were focused over short time periods or sampling areas (Schainost 2008). Many of these past fish surveys focused on tributaries to the Niobrara River. Seventy species of fish have been collected within the Niobrara River basin from 1893 to 2005 (Schainost 2008). However, information regarding how fish barriers and river geomorphology affect fish assemblages was unknown. Therefore the three objectives of this study were 1) to describe the monthly fish community from the mouth (rkm 0) upstream to the Dunlap Diversion Dam (rkm 531); 2) compare fish assemblages upstream and downstream of barriers and among river geomorphology segments; and 3) identify environmental variables that influence the fish community.

Study Area

The Niobrara River watershed is approximately 34,913 km^2. Land use in the basin is predominately livestock ranching with row-crop agriculture in the eastern region (Dappen et al. 2007). The river has a relatively steep gradient of 1.5 m/km or a mean slope of 0.15% from the Dunlap Diversion Dam to its mouth. In comparison, the Missouri River on the border of South

Dakota and Nebraska falls at 0.2 m/km, and the central Platte River in Nebraska is 1.2 m/km (Bentall 1991). The average annual precipitation in the basin ranges from 40 cm in the west to over 60 cm in the eastern basin. Around Valentine, Nebraska, 80-90% of the base flow is derived by ground water, while approximately 15% of base flow originates from ground water near the mouth (USDA 1973). Mean annual discharge of the Niobrara River is 0.8 m^3/s near Hay Springs (rkm 505), 3.1 m^3/s near Cody (rkm 327), 23.1 m^3/s near Norden (rkm 193), 43.5 m^3/s at Spencer Dam (rkm 63), and 48.8 m^3/s at the mouth (rkm 0) (Figure 1) (Schainost 2008; Alexander et al. 2009). The Niobrara River has a naturally high sediment load and transports an estimated 300 metric tons of sediment per day at the mouth (Hotchkiss et al. 1993).

Our study area was from the mouth (rkm 0) near Niobrara, Nebraska to the Dunlap Diversion Dam (rkm 531) (Figure 1). The study area was divided into four reaches based on indentified fish migration barriers. The first river reach was the mouth to Spencer Dam (rkm 0 to 63), a functioning hydropower dam built in 1927 with a hydraulic height of 8 m. The second reach was from Spencer Dam to Norden Chute (rkm 63 to 193). Norden Chute is a natural barrier where the river narrows and is cutting into a Tertiary-age bedrock formation consisting of easily erodible fine silt and clay and resistant gravel and sand (Condra and Reed 1943) with a hydraulic height of 1 to 2 m depending on river discharge. High water velocity through the narrow chute may additionally impede upstream movement of fish. The river is persistently braided or island-dominated and with high variation in channel width from 550 m at the mouth to 30 m at Norden Chute. The third reach was from Norden Chute to Cornell Dam (rkm 193 to 242), a decommissioned hydropower dam built in 1915 with a hydraulic height of 3 m. The fourth reach was from Cornell Dam to the Dunlap Diversion Dam, built in 1945 to divert water for agricultural irrigation with a hydraulic height of 4 m. Reaches three and four are restricted by an entrenched canyon with consistent channel widths that progressively decrease to <2 m downstream of Dunlap Diversion.

Methods

Fish sampling

Sample site selection was based on 36 distinct geomorphic segments along the Niobrara River identified by Alexander et al. (2009). Geomorphic segmentation was based on degree of confinement of the river channel, channel planview pattern (degree of sinuosity), channel width variation, and sand bar configurations. Seventeen fixed sample sites were selected for sampling representing 12 of the 36 geomorphic segments (Figure 1). A fixed sampling strategy was used opposed to random or stratified-random sampling design due to the remoteness and lack of access to most of the Niobrara River. Two sample sites were selected in each geomorphic segment downstream of Spencer Dam due to the size of the wetted width in this reach. Sample sites were also located immediately downstream and upstream of Spencer Dam, Norden Chute, and Cornell Dam.

The seventeen fixed sites were sampled each month from June to September 2009 using a tote-barge electrofisher. The tote-barge was outfitted with a Smith and Root 2.5 GPP (Smith-Root, Inc., Vancouver, Washington) electrofishing system rated at 2,500 watts of output power, using pulsed DC at 1-3 amps and 60 pulses per second. The electrofishing operation required three people for sampling, a person pushing the barge, one operating the anode ring, and one person netting fish. The dip net had a 2 m handle with a D-frame that was 45 cm wide and 45 cm in length with a 30 cm deep bag that had 6-mm “Atlas” mesh with a breaking strength of 32 kg (Duraframe Dipnet, Viola, Wisconsin). Four “transects” were sampled monthly from June to

September in each site and electrofished for 5 – 10 min for a total sampling time of 20 – 40 min per site. Maximum sampling time for a transect was 10 min to reduce stress to captured fish. Each electrofishing transect was recorded in seconds. All identified microhabitats (e.g., pools, open water, vegetated shoreline, etc.) in each site were sampled with the tote-barge electrofisher. The entire microhabitat was sampled if the electrofished transect was < 10 min. A single-pass through a habitat with an electrofisher can effectively be used to detect spatial and temporal trends in relative abundance and species richness (Bertrand et al. 2006). An effort was made to collect all stunned fish. Captured fish were identified to species, counted, and released alive. At each electrofishing transect, water temperature (°C), dissolved oxygen (DO) (mg/L), and conductivity (µS/cm) were measured with a Hach HQ40D multimeter, (Hach Company, Loveland, Colorado), water velocity (m/s) was measured using a Marsh-McBirney Flo-Mate portable flow meter, model 2000 (Marsh-McBirney Inc., Frederick, Maryland), turbidity (nephelometric turbidity unit [NTU]) was measured using a Hach Turbidimeter, model 2100P (Hach Company, Loveland, Colorado), a Garmin GPSMAP 76S global positioning system (GPS) (Garmin International, Inc., Olathe, Kansas) was used to quantify distance sampled, depth was measured with a ruler, and substrate (percent silt, sand, and gravel), and vegetation (submerged coverage along transect) was visually estimated as percent composition.

Data analysis

Fish assemblage richness, Shannon's diversity index (H'), and evenness (J') were calculated for each sample site. Richness is the number of species represented in an assemblage. Shannon's (H') was calculated as:

$$H' = - \sum^{s} (p_i)(\log_e p_i)$$

$i = 1$

where s = the number of species, and p_i = the proportion of the total sample represented by the ith species. Evenness (J') was calculated from Shannon's diversity index as:

$$J' = H'/H'\text{max} = H'/\log_e s$$

where $H'\text{max} = \log_e s$ = maximum possible value of Shannon's index, and s = number of species (Kwak and Peterson 2007). Shannon's (H') is sensitive to changes in rare species in the fish assemblage. Evenness (J') ranges from 0 (low evenness indicated by single-species dominance) to 1 (equal abundance of all species).

Mean catch per unit effort (CPUE) was calculated as number of fish/hr electrofishing. Mean CPUE was compared among sample sites along the Niobrara River and among months. The mean CPUE data was checked for independent and normal distributions. The data were not normally distributed; therefore, we $\log_{10}$(CPUE+1) transformed the data and normality improved based on residual and normal probability plots of the residuals (Neter at al. 1996). Mean CPUE was compared among months and sample sites for the most abundant species with a two-way analysis of variance (ANOVA). When differences in mean CPUE were significant ($P \leq 0.05$), a Bonferroni multiple range test was used to determine which means varied significantly ($P \leq 0.10$). When the interaction term was significant, a one-way ANOVA test was performed. All ANOVAs were performed with Number Cruncher Statistical Software (Hintz 2006).

Spatial and temporal differences in the fish community were tested using analysis of similarity (ANOSIM). Species structure was compared among months, sample sites, and reaches defined by fish barriers using a Bray-Curtis dissimilarity matrix calculated from relative abundance data (Bray and Curtis 1957). Relative abundance data were square-root transformed to better meet analysis assumptions of multivariate normality. A Bray-Curtis post-hoc test was used to compare fish communities among months, sample sites, and reaches. Fish community patterns in structural changes were identified using SAS (SAS institute Inc. 1999) and Primer v5 (Primer-E Ltd 2001).

Nonparametric multidimensional scaling (NMDS) plots were additionally used to map the relative association among months, sample sites, and river reaches with the electrofishing relative abundance data. The NMDS plots were used to graphically illustrate the differences in the fish community structure temporally and spatially.

The "BEST" procedure, using "BIOENV" in Primer and a permutation process was used to identify habitat variables that explained patterns in the fish community. We used 999 permutations that led to a set of Spearman rank correlations that best identified the variables that explained abiotic factors affecting the fish community. Analysis was between samples and the resemblance measure was Euclidean distances. Environmental variables used in the analysis were temperature, turbidity, conductivity, mean depth of transect, dissolved oxygen, water velocity, proportion of cobble, proportion of vegetation, percent silt, percent sand, and percent gravel. Once the best model was identified (highest correlation), a principal components analysis (PCA) was performed using the environmental variables in that model to identify key environmental variables and determine whether abiotic factors differed among sample sites. Variables were examined for normality and were $\log_{10}(X+1)$ transformed to linearize the relationships. Principal components that were retained for interpretation were those with an eigenvalue greater than 1.0 that follows the Kaiser-Guttman criterion (Guttman 1954; Cliff 1988). Abiotic factors with eigenvectors (correlations) greater than 0.40 were qualitatively designated as "high" and considered biologically important (Hair et al. 1987). A one-way ANOVA was applied to the factor scores of the retained principal components to assess differences among sample sites each year. When significant differences were found, a Bonferroni multiple range test was used to identify which means were different.

Results

We conducted 272 electrofishing subsamples at 17 sites along the Niobrara River for a total effort of 37 h and 31.5 km from June to September 2009 (Table 1). Mean turbidity ranged from 5 (SE = 0) at the furthest upstream site to 124 (SE = 11) at the mouth. Conductivity and dissolved oxygen had low variability from the mouth to rkm 374 but conductivity substantially increased and dissolved oxygen decreased at the most upstream site (rkm 505). The lowest water velocities were encountered at the sample site immediately downstream of Spencer Dam (mean mid-column velocity = 0.28 m/s, SE = 0.06) and the highest water velocities were found downstream of Cornell Dam (mean mid-column velocity = 0.75 m/s, SE = 0.05). Mean sampling depths ranged from 29 to 51 cm with the shallowest areas downstream of Cornell Dam and the deepest at the most upstream site (rkm 505). The entire study area was dominated by sand substrate (range 56% to 100%) with an increase in gravel upstream of Norden Chute, with the exception of the area immediately upstream of Cornell Dam where fine sand is trapped behind the structure (Table 1).

Temperature, turbidity, conductivity, and percent gravel had the highest correlation (r = 0.382) from the BEST procedure that helped to explain patterns in the fish community due to environmental variables. These four environmental variables were then used in a principal component analysis (PCA), which yielded two principal components (PC) with eigenvalues greater than 1.0. These two principle components explained 77% (PCA axis 1 = 41% and PCA axis 2 = 36%) of the variance in the data. In relation to PCA1, positive correlations were found for temperature and turbidity while percent gravel was negatively correlated. Temperature, conductivity, and percent gravel were negatively correlated with PC2 (Table 2). Significant differences were found among sample sites for both principal components (*P* <0.001) (Figure 2). These differences were found in the temperatures and turbidity among sample sites as these two variables were generally highest near the mouth of the river and both gradually decreased upstream, while conductivity and percent gravel substrate increased at sites furthest upstream.

From June to September 2009, we collected 33,888 fish from 42 species and 11 families (Table 3). Total catch at each site ranged from 816 to 4,467 fish with an average catch rate of 1,028 fish/h. Sand shiners *Notropis stramineus* (39%) were the most abundant species followed by red shiners *Cyprinella lutrensis* (25%), white suckers *Catostomus commersoni* (8%), creek chubs *Semotilus atromaculatus* (5%), river carpsuckers *Carpiodes carpio* (4%), bigmouth shiners *Notropis dorsalis* (3%) and channel catfish *Ictalurus punctatus* (3%). Sand shiners, red shiners, shorthead redhorse *Moxostoma macrolepidotum*, and largemouth bass *Micropterus salmoides* were the only species collected at all sample sites. Plains topminnow *Fundulus sciadicus* was the only state imperiled fish species collected and was only found at two sites (rkm 310 and 374) upstream of Cornell Dam. Five species of nonnative fish were collected including common carp *Cyprinus carpio*, spotfin shiner *Cyprinella spiloptera*, rainbow trout *Oncorhynchus mykiss*, rock bass *Ambloplites rupestris*, and yellow perch *Perca flavescens*. Although native to Nebraska, northern pike *Esox lucius*, bluegill *Lepomis macrochirus*, largemouth bass, black crappie *Pomoxis nigromaculatus*, and white crappie *Pomoxis annularis* were introduced into the Niobrara River basin as sport fish.

Fourteen species of fish were found only in the Niobrara River reach downstream of Spencer Dam which included: shortnose gar *Lepisosteus platostomus*, Gizzard shad *Dorosoma* *cepedianum*, spotfin shiner, silver chub *Macryhybopsis storeriana*, emerald shiner *Notropis atherinoides*, suckermouth minnow *Phenacobius mirabilis*, bluntnose minnow *Pimephales notatus*, quillback *Carpiodes cyprinus*, flathead catfish *Pylodictis olivaris*, orange-spotted sunfish *Lepomis humilis*, white crappie, johnny darter *Etheostoma nigrum*, sauger, and freshwater drum *Aplodinotus grunniens* (Table 5). River carpsucker and flathead chubs *Platygobio gracilis* were only found from the mouth to Norden Chute. Channel catfish were found in high abundances from the mouth to Norden Chute with only two young of the year collected upstream of the chute. Rainbow trout were exclusively found at the sampling site downstream of Cornell Dam. Brook stickleback *Culea inconstans*, central stoneroller *Campostoma anomalum*, and plains topminnows were only found upstream of Cornell Dam.

In the Niobrara River, species richness generally decreased moving upstream. From the mouth to Spencer Dam, richness averaged 21 while from Norden Chute to Cornell Dam and from Cornell Dam to Dunlap Diversion Dam species richness averaged 13. Species richness comparisons above and below fish barriers were substantially different. At all three barriers, more species were found downstream of the barrier compared to upstream (Figure 3). Shannon's diversity index (*H*') and evenness (*J*') substantially declined from the mouth to Spencer Dam, increased upstream of Spencer Dam and subsequently declined downstream of Norden Chute. Upstream of Norden Chute to Dunlap Diversion Dam, diversity (*H*') and evenness (*J*') was high with the exception of the site downstream of Cornell Dam (Figure 3). Diversity (*H*') and evenness (*J*') were low due to the dominance of sand shiners and red shiners in the fish assemblage downstream of the barriers.

The ANOSIM tests revealed significant differences in the fish communities among months ($R = 0.049$; $P = 0.001$); however, the low Global R values suggest differences were not large (Table 4). June and July had weak differences compared to August and September in the fish assemblage and abundances. Graphically, NMDS plots suggested high overlap in the fish communities among months. Significant differences in the fish communities were found among sample sites (*R* = 0.59; *P* =0.001) and reaches (*R* = 0.498; *P* = 0.001). Bray-Curtis post-hoc pairwise comparisons indicated significant differences in fish assemblage and abundance for nearly all sample sites and all reaches. Most similarities between sample sites were found in the highly braided reaches of the Niobrara River from the mouth to rkm 106 (sample sites 1 - 8) (Table 4). Graphically, NMDS suggested high overlap in the fish communities among sample sites 1 through 8 (Figure 4). Sample sites 9 through 17 had more variability with less overlap in the fish communities. Differences in the fish communities among the four river reaches were clearly defined with Norden Chute being a significant division (Figure 5).

The Bray-Curtis dissimilarity values were generally lowest between adjacent sample sites with a few exceptions demonstrating an increase in dissimilarities with distance among sites and changes in river geomorphology (Table 5). Contributions to dissimilarities between sites were largely driven by the relative abundance of sand shiners, red shiners, white suckers, creek chubs, river carpsuckers, and bigmouth shiners. The Bray-Curtis dissimilarity values between sample sites ranged from 45.4 to 96.5 (Table 5). Sample sites 3 through 9 (highly braided river) had moderate dissimilarities. Surprisingly, species structure between site 13 (entrenched river site downstream of Cornell Dam) and sites 4 through 8 (braided river) were generally more similar (dissimilarly score <66) driven by a species structure dominated by sand shiners, red shiners, and bigmouth shiners. Species structure at site 15 was moderately dissimilar to sites 4 through 7 (braided river) and 11 through 13 (entrenched river). Site 15 is characterized by a width restricted river, sinuous, irregular channel width variation, and alternating sand bars. Lower dissimilarly scores were attributed to the relative abundances of sand shiners, red shiners, and white suckers within these river habitats at each sampling site. Average dissimilarities between river reaches defined by fish barriers were generally high and ranged from 68.9 to 83.5 with the lowest dissimilarity in the fish communities between the wide highly braided river reaches downstream of Norden Chute from the more entrenched channel upstream (Table 6).

Significant interactions ($P \leq 0.030$) were found for all two-way ANOVAs comparing mean CPUE of sand shiners, red shiners, white suckers, creek chubs, river carpsuckers, bigmouth shiners, and channel catfish among months and sample sites. Therefore, a one-way ANOVA was performed to compare mean CPUE among months. Temporal differences in relative abundance were low for most fish species and the differences that were found were essentially from the early to late summer months. Significant monthly differences in relative abundance were found for sand shiners ($P < 0.001$) and red shiners ($P = 0.037$) with a similar trend of increasing from June to July then a decrease each month in August and again in September (Figure 6). Channel catfish mean CPUE significantly differed among months ($P = 0.040$) as relative abundance increased each month from June to August where it stabilized through September. No significant differences in relative abundances were found among months for white suckers, creek chubs, river carpsucker, and bigmouth shiners ($P \geq 0.056$). Similar to monthly channel catfish relative abundances, white sucker, creek chub, and river carpsucker mean CPUE gradually increased each month from June to August where it remained in September. Bigmouth shiner abundance slowly declined from June to August with a small increase in September (Figure 6).

Monthly differences in fish abundances were most evident downstream of Norden Chute and Cornell Dam. The highest abundances of sand shiners were found at the sample site downstream of Norden Chute in June (4,169 fish/hr; SE = 2,472) and declined to < 3 fish/hr in September. Red shiners followed a similar trend with 1,319 fish/hr (SE = 383) in July and declined to < 9 fish/hr in September downstream of Norden Chute. Adult channel catfish were likely targeting the abundance of prey downstream of this barrier as they were found in their highest abundance at this site during July with 138 fish/hr (SE = 138) and also declined to < 9 fish/hr in September. In a reverse trend, adult river carpsucker downstream of Norden Chute went from 0 fish/hr in June to 252 fish/hr in September. Throughout the study area, the highest relative abundance of bigmouth shiner (371 fish/hr; SE = 116) was found in June and creek chub (789 fish/hr; SE = 189) in September at the sample site immediately downstream of Cornell Dam. In all other months, relative abundance declined by >52% for bigmouth shiners and >82% for creek chubs at this site.

Spatial differences in relative abundances were significant ($P < 0.001$) for all seven fish species tested. Sand shiners were found in high relative abundances across the entire 531 rkm study area; however, mean CPUE was significantly higher at sites immediately downstream of fish barriers and relative abundance was lowest near the mouth of the river (Figure 7). Red shiners were also found in high relative abundances from the mouth to rkm 310, where mean CPUE was significantly lower at the two most upstream sites (rkm 374 and 505) (Figure 7). White suckers were rarely detected in the lower braided reaches of the Niobrara River. White sucker mean CPUE significantly increased at rkm 167 and was the highest immediately upstream of Norden Chute (rkm 201). White sucker relative abundance then significantly decreased at rkm 224 then gradually increased at each sample site upstream for the next 304 rkm (Figure 7). Creek chub relative abundance nearly followed the same pattern of white suckers. Creek chub relative abundance gradually began increasing from rkm 167 to 242 at Cornell Dam. The population of creek chubs immediately upstream of Cornell Dam were either extirpated or at such low abundances that they were not detected. From rkm 310 to 505, creek chub mean CPUE significantly increased to the highest abundances found throughout the study area (Figure 7). River carpsucker were found in the highest relative abundances near the mouth (rkm 3 and rkm 25) then significantly declined moving upstream to Norden Chute (Figure 7). Bigmouth shiners were found in the highest relative abundances immediately downstream and upstream of Cornell Dam. Other notable areas of high abundance were the middle sections of the mouth to Spencer Dam reach and the Spencer Dam to Norden Chute reach (Figure 7). Channel catfish relative abundance followed a similar trend as river carpsucker with significantly higher mean CPUE in the mouth to Spencer Dam reach. Channel catfish mean CPUE significantly declined in the reach upstream of Spencer Dam and only two young of the year channel catfish were collected at the next sample site upstream of Norden Chute (Figure 7).

Discussion

Our study covered the entire free-flowing reach of the mainstem Niobrara River and sampled monthly from June to September 2009. This was the first study to assess the seasonal attributes of the fish community and largest in geographic scope of the mainstem river (Schainost 2008). This study did expand or filled gaps in the identified range for seven species, two species contracted in range, while some species appear to be extirpated from reaches or at such low abundance that they were not detected where they have been reported from earlier sampling events. Schainost (2008) organized data from fish collections in the Niobrara River basin from 1893 to 2005. Data from that report were generally from basic inventories before 1950's, from 1950 to 1970 data was collected for university studies in the tributaries to the Niobrara River, and sampling increased from the 1970's to 2005 through the Nebraska Game and Parks Commission and Nebraska Department of Environmental Quality. These past surveys were over short periods of time (once a year) or were concentrated only in tributaries or short reaches of the mainstem river. Golden shiner *Notemigonus crysoleucas* was the only new species found in the mainstem Niobrara River in 2009 although this species has been collected in numerous tributaries within the basin (Schainost 2008). Grass pickerel *Esox americanus* were found from the mouth to rkm 310 an expansion upstream and downstream compared to earlier reports (Schainost 2008). Gizzard shad, shortnose gar, and spotfin shiner were collected for the first time immediately downstream of Spencer Dam compared to earlier reports that these species only strayed from the Missouri River near the mouth of the Niobrara River (Schainost 2008). In a previous study using tote-barge electrofishing downstream of Spencer Dam in 2008, gizzard shad young of the year comprised >31% of the catch (Wanner et al. 2009). However, gizzard were nearly absent in 2009 and was likely due to low spawning success or recruitment in the Missouri River as no larval gizzard shad were collected during a larval fish study in the lower Niobrara River in 2008 and 2009 (Wanner et al. 2010). Stonecats and white suckers range expanded downstream of Spencer Dam, although these species are common to the tributaries of the lower Niobrara River (Schainost 2008). In our study, central stonerollers were confined to immediately downstream of the Dunlap Diversion Dam even though they have been found in the middle Niobrara River near Cornell Dam, the lower river near Spencer Dam and most tributaries. Blacknose shiner *Notropis heterolepis* (Nebraska state critically imperiled species), and blacknose dace *Rhinichthys obtusus*, finescale dace *Phoxinus neogaeus*, pearl dace *Margariscus margarita* (all three Nebraska state imperiled species) have previously been collected in the Niobrara River (Schainost 2008) but none were collected during this study lending support for their status. Additionally, all four of these fish are considered headwater species and are more likely to be found sparsely distributed in cool-water tributaries to the Niobrara River (Schainost 2008). Goldeye were historically abundant in the Niobrara River downstream of Spencer Dam prior to 1970 (Schainost 2008) with a few collected during the late 1970's (Hesse and Newcomb 1982). However, dam construction on the Missouri River has substantially reduced the goldeye population in that river (Shuman et al. 2010) and has likely extirpated this fish from the Niobrara River as none were collected during this study or any other study in the Niobrara River since the 1970's. Plains minnow *Hybognathus placitus*, western silvery minnow *Hybognathus argyritis*, and river shiner *Notropis blennius* have been previously collected throughout the length of the Niobrara River but none were collected during this study. Previous fish investigators in the Niobrara Rive may have misidentified the brassy minnow *Hybognathus hankinsoni* for a plains minnow or western silvery minnow and the sand shiner for a river shiner. However, we can not exclude the possibility that these fish have been extirpated or are now at such low abundances that we were not able to detect them.

Norden Chute may have recently become a fish barrier. Channel catfish and flathead chubs were regularly collected upstream of Norden Chute (Schainost 2008) and a popular channel catfish fishery became established downstream of Cornell Dam during the 20th century (M. Lindvall, U.S. Fish and Wildlife Service, personal communication). A bridge across the Niobrara River at the Norden Chute was constructed in 1963 in a constricted section. The additional constriction of the river at this point may have created a steeper notch in the bedrock in recent years (Alexander et al. 2009). Erosional processes of the bedrock are slowly moving the notch upstream increasing the hydraulic drop. Upstream migration of fish through the chute has likely been blocked for only the last 10 - 20 years. However, backed up water due to flooding from ice jams downstream of the chute may temporarily eliminate the fish barrier. Due to constant erosion, occasionally the bedrock notch has deteriorated, reducing the hydraulic drop and may temporarily provide fish passage for some fish species. Erosion of the bedrock notch continues to migrate upstream where it will meet an area of sand and gravel alluvium subsequently eliminating this natural fish barrier in approximately 25 to 40 years depending on river discharge (J. Alexander, U.S. Geological Survey, personal communication).

Along the longitudinal gradient, fish species diversity generally increases downstream with species addition rather than replacement (Schlosser 1987; Matthews 1998; Jackson et al. 2001). As with previous studies, species richness in the Niobrara River did increase moving from upstream to the mouth. Multiple mechanisms that can explain longitudinal gradients of increasing fish diversity such as resource availability, as well as diversity, and quality of habitats (Schlosser 1987; Oberdorff et al. 2001; Ibanez et al. 2007; McGarvey and Ward 2008; Muneepeerakul et al. 2008). Habitats in the braided reach (downstream of Norden Chute to the mouth) of the Niobrara River are diverse with shallow and deep pools with, variable water velocities, vegetated shorelines, and wide expanses of emerged and submerged sandbars that creates multiple river channels. Upstream of Norden Chute the Niobrara River is characterized by more homogenous habitats resulting from a single river channel that lacks a large floodplain and has low variability in depths and water velocities (Alexander et al. 2009). Reductions in habitat diversity in streams have been reported to reduce the number of species (Gorman and Karr 1978). Additionally, a positive relationship has been reported between species richness and discharge (Oberdorff et al. 1995; Xenopoulos and Lodge 2006; McGarvey and Ward 2008), while a negative effect on species richness was found with discharge variability (Horwitz 1978; Poff and Allan 1995). Species richness was found to decline with discharge in this study.

Environmental variables did influence the fish community in the Niobrara River. Abiotic factors such as water temperature, turbidity, conductivity, and percent gravel influenced species structure. Physical factors such as temperature, salinity, pH, and dissolved oxygen can limit stream fish distribution (Matthews 1998; Ostrand and Wilde 2001). Only the most upstream site in this study near Dunlap Diversion Dam had a coldwater designation (i.e., water temperatures remain <22 °C) (www.deq.state.ne.us), which likely influenced the fish community and diversity. Consequently, the Niobrara River fish community during this study was dominated by warm-water species with only one cool-water (northern pike) and cold-water (rainbow trout) species collected during this study. Water temperature and percent gravel were important factors in both principle components of the PCA. Water temperatures generally increased from the Dunlap Diversion Dam downstream to the mouth. Temperature is well known to structure fish communities (Matthews 1998; Ostrand and Wilde 2001). Temperature also affects the timing of spawning and growth of fishes. The timing of larval fish in the lower Niobrara River was highly correlated with water temperatures (Wanner et al. 2010). Gravel was nearly absent downstream of Norden Chute and also likely influenced the species structure. In another Great Plains river, it was reported that substrate influenced the fish and macroinvertebrate communities in the Neosho River in Kansas (Tiemann et al. 2004).

Monthly differences were found in the fish communities although these differences in species structure were generally low. The seasonality in the fish community was most likely explained by young of the year fish of large-bodied species appearing and recruiting to the electrofishing gear. Although not significant, a trend was observed as river carpsucker, white sucker, and creek chubs all increased in abundance in the August and September sampling periods compared to the earlier months due in a large part to young of the year of those species appearing. Many of the small-bodied fish (i.e., sand shiners and red shiners) declined in abundance in August and September likely from natural mortality. Young of the year small-bodied fish were observed in extremely high abundances during August and September. However, most of these fish were not effectively collected through the 6-mm mesh of the dip net though temporarily stunned by the electric field in the water but escaped. This mesh size appeared to be more effective at collecting fish >30 mm while some larval channel catfish were collected due to their pectoral and dorsal spines snagging on the mesh.

Monthly differences due to fish movements were most evident downstream of two barriers on the river: Norden Chute and Cornell Dam. The highest abundances (>1,300 fish/hr) of sand shiners and red shiners were in June and July downstream of Norden Chute while mean CPUE declined for both species to <9 fish/hr by September. The high density of prey fish during the early summer months likely attracted adult channel catfish to the downstream area of this barrier as they were found in their highest abundance during the same time period with a similar decline in September. Bigmouth shiners (June) and creek chubs (September) were found in their highest abundance downstream of Cornell Dam with substantial declines in relative abundance during the other three months of sampling. The occurrence of high abundance directly downstream of barriers is likely due to migrations in search of spawning or feeding areas. Adult creek chubs are opportunistic feeders (Quist et al. 2006) and were likely preying on the high abundance of small shiners downstream of Cornell Dam.

In general, the geomorphic segmentation by Alexander et al. (2009), which described the basic physical characteristics of the Niobrara River, helped to define boundaries of where differences in the fish community should be expected. The fish community, at any given location, is influenced by historical, evolutionary, and biogeographical processes as well as species interactions and environmental variation that influence their abundance and distribution (Ricklefs 1987). Differences in the fish communities were found at most sampling sites, which indicated that river geomorphology likely influenced the presence and abundances of fish species. There was overlap in species structure from one sample site to the next; however, abundances, richness, diversity, and evenness generally changed from upstream or downstream of any given site. The most similar fish communities between sites were found in the highly braided section of the Niobrara River downstream of Norden Chute (rkm 0 to 193). The fish communities at sample sites 4 and 5 (rkm 25 and 45) were the most ubiquitous being similar to sites as far upstream as site 8 (rkm 106). Between sites 8 (rkm 106) and 9 (rkm 167) appeared to be a transitional area in the fish community where white sucker and creek chub began to appear in substantial numbers while these two species were nearly absent downstream. Between these two sites, the geomorphology changes from a river that is redirected at the valley walls to a river that is intermittently entrenched upstream. From the PCA, this section of the Niobrara River was a transitional area in environmental factors with much clearer water and gravel substrate upstream and substantially more turbid and 100 % sand substrate downstream. The fish community generally changed at each subsequent sampling site upstream of Norden Chute which indicated that the degree of confinement, sinuosity, channel-width variation, and sand bar configuration likely affected the fish assemblage and abundances in the Niobrara River.

The effects of fish barriers on species richness was especially pronounced in the Niobrara River as there were substantial declines in species richness above the three barriers during this study. Many species downstream of Spencer Dam collected during this study are considered “Missouri River strays” such as flathead catfish, freshwater drum, gizzard shad, shortnose gar and large river fishes such as silver chubs *Macrhybopsis storeriana* and sauger (Schainost 2008).

Pallid sturgeon, shovelnose sturgeon, bigmouth buffalo *Ictiobus cyprinellus*, smallmouth buffalo *Ictiobus bubalus*, blue sucker *Cycleptus elongatus*, and walleye *Sander vitreum* have also been collected in the Niobrara River downstream of Spencer Dam and likely do not occur above the dam (Wanner et al. 2009; Wanner et al. 2010). The ability of these migratory species that use the lower Niobrara River likely enhances the Missouri River fish populations. Accessibility for fish to immigrate (Taylor 1997; Robinson and Rand 2005) and proximity to an external migrant source can also influence species diversity (Gorman 1986; Osborne and Wiley 1992). Upstream of Spencer Dam to the Dunlap Diversion Dam are species that are tolerant of extreme river conditions and are often pioneer species (e.g., bigmouth shiner, creek chub, grass pickerel, green sunfish *Lepomis cyanellus*, longnose dace *Rhinichthys cararactae*, red shiner, sand shiner, stonecat *Noturus flavus*, and white sucker) (Schainost 2008). Unfortunately, the barriers (Spencer Dam, Norden Chute, Cornell Dam, Dunlap Diversion Dam, Box Butte Dam, and 15 unnamed low-head dams upstream of Box Butte Reservoir) prohibit the free dispersal of Great Plains stream fishes. The importance of the free dispersal of Great Plains stream fish is well documented (Smith and Hubert 1989; Fausch and Bramblett 1991; Fausch and Bestgen 1997; Labbe and Fausch 2000; Scheurer et al. 2003; and Hoagstrom et al. 2006). Due to the dynamic nature of Great Plains streams, fishes need a diversity of free-flowing habits to disperse to under periodic harsh conditions (i.e., droughts and floods) (Hoagstrom et al. 2006; Grossman et al. 2010). The restriction of movements is detrimental during droughts and flood events (Ward and Stanford 1995; Hoagstrom et al. 2006; Grossman et al. 2010). There is a preponderance of evidence that on-going climate change will have irreversible affects on natural species around the world (Hughes 2000; Salo et al. 2000; McCarthy 2001; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Fragmentation of the Niobrara River will limit the dispersal of native fish, and obstruct fish displacement to newly suitable sites (Buisson et al. 2010) such as the cool, groundwater tributaries. Low-head dams are also responsible for altering the natural cycle of flow, physical characteristics of the river channel and floodplain, transforms the biological characteristics, and fragments the continuity of rivers (Petts 1984; Ligon et al. 1995; Ward and Stanford 1995; Poff et al. 1997). Fish in the Niobrara River are likely drifting over the barriers without a means of returning upstream. Most fish species in the Niobrara River that were found downstream of a barrier were also found upstream. However, it has been reported that fish species can eventually be completely extirpated above low-head dams (Winston et al. 1991). Although some barriers on the Niobrara River are natural, anthropogenic structures have created unnatural areas where prey fishes are likely more susceptible to predation with potentially increased density dependent mortality. The highest densities of sand shiners and red shiners were found immediately downstream of Norden Chute and marked the most upstream site for river carpsuckers and flathead chubs. At the sample site downstream of Cornell Dam had the second highest densities of red shiners and creek chubs. The barriers on the Niobrara River did evidently restrict the movements and eliminated upstream habitats that may be important to the life histories of native fishes.

The fish community in the Niobrara River did follow the predicted patterns identified in the well known hypothesis of the river continuum concept (Vannote et al. 1980), but more closely resembled the niche diversity model (Lowe-McConnell 1975; Schlosser 1982), where the increase in stream volume increased the volume of habitats that led to an increase in the number of species in the most downstream reaches. Stream fish communities are spatially and temporally dynamic and fish migration or barriers to migration along with environmental variation plays fundamental roles in organizing the fish community (Roberts and Hitt 2010).

The niche diversity model has been reported to be one of the best models for characterizing community structure in fine-grain habitats (Pringle et al. 1988; Roberts and Hitt 2010) like those habitats found in the Niobrara River. Barriers to fish migration are well known to affect the diversity and abundances of fish both upstream and downstream as we observed in the Niobrara River. We also observed that changes in the river geomorphology, even over short distances, can affect fish species structure. Based on our results, not only is Norden Chute an upstream fish migration barrier, it additionally marked a sharp physical change in geomorphology that dramatically affected the fish community. The sharp contrast from a highly braided river with heterogeneous diversity of habitats downstream of the chute to a single river channel lacking much of a floodplain upstream of this barrier, had led to extensive species replacement and community "zonation". These sharp contrasts are typical over large spatial extents where rivers cross geographic boundaries (Rahel and Hubert 1991; Matthews 1998). Above the chute, the fish community was dominated by insectivores while downstream there was an additive effect with the increase of piscivorous fish. Currently, the largest threat to the native fish community in the Niobrara River is the reduction of instream flows due to water withdrawals in the basin. Future studies are needed to help explain how changes in instream flows might impact the native fish community. These studies should provide hydromorphologic models that describe the spatial mosaic of physical features that are relevant to fish, models that describe habitat use by fish, and models that quantify the amounts useable habits related to flow (Parasiewicz 2007). These environmental instream flow models could then be used by fishery managers to ensure that adequate amounts of high quality water are flowing for all life stages of native fish in the Niobrara River.

Acknowledgements

We thank the National Park Service (NPS), Nebraska Game and Parks Commission (NGPC), Nebraska Public Power District, U.S. Fish and Wildlife Service (USFWS) - Region 6 Water Resources Division, USFWS - Region 6 Aquatic Nuisance Species Coordinator, Missouri Department of Conservation, and U.S. Army Corps of Engineers for funding. We also thank field technicians from the USFWS - Great Plains Fish and Wildlife Conservation Office, NPS - Missouri National Recreational River Office, and NGPC. In addition, we thank the landowners that gave access to sample sites along the river.

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Table 1. Total effort, average time ofday, and means with standard error in parentheses of environmental variables measured at each sampling site on the Niobrara River from June to September 2009.

Site	Total effort (s)	Total effort (m)	Time of day (hhmm)	Temp. (°C)	Turb. (NTU)	Cond. (µS/cm)	DO (mg/L)	Bottom velocity (m/s)	Mid-column velocity (m/s)	Depth (cm)	% silt	% sand	% gravel
Mouth to Spencer Dam (rkm 0 to 63)													
Site 1 (rkm 3)	8,723	2,087	1053 (0305)	25.4 (0.7)	124 (11)	271 (4)	9.2 (0.2)	0.38 (0.05)	0.40 (0.05)	39 (6)	0	100 (0)	0
Site 2 (rkm 4)	9,162	2,934	1245 (0301)	26.0 (0.6)	121 (10)	272 (3)	9.4 (0.2)	0.45 (0.03)	0.49 (0.03)	36 (4)	0	100 (0)	0
Site 3 (rkm 25)	8,119	2,126	1157 (0205)	24.0 (1.7)	80 (7)	270 (9)	9.1 (0.4)	0.35 (0.05)	0.37 (0.05)	36 (5)	4 (3)	96 (3)	0
Site 4 (rkm 45)	8,859	2,100	1510 (0336)	26.6 (1.0)	86 (7)	274 (7)	9.3 (0.2)	0.47 (0.03)	0.51 (0.03)	37 (5)	0	100 (0)	0
Site 5 (rkm 57)	8,096	2,196	1136 (0301)	23.9 (0.7)	61 (7)	257 (4)	9.3 (0.2)	0.43 (0.04)	0.47 (0.04)	31 (3)	1 (1)	98 (1)	1 (1)
Site 6 (rkm 62)	5,389	1,583	1537 (0352)	23.1 (1.2)	55 (5)	250 (6)	9.0 (0.2)	0.25 (0.06)	0.28 (0.06)	35 (3)	4 (2)	94 (2)	2 (2)
Spencer Dam to Norden Chute (rkm 63 to 193)													
Site 7 (rkm 81)	8,401	1,610	1427 (0249)	25.0 (0.7)	66 (7)	260 (5)	9.2 (0.1)	0.49 (0.05)	0.53 (0.05)	32 (5)	0	100 (0)	0
Site 8 (rkm 106)	8,072	1,962	1348 (0330)	25.0 (1.5)	144 (34)	254 (17)	9.3 (0.1)	0.31 (0.05)	0.35 (0.05)	37 (5)	0	100 (0)	0
Site 9 (rkm 167)	8,302	1,825	1151 (0323)	22.5 (0.6)	32 (6)	229 (3)	8.9 (0.1)	0.45 (0.04)	0.49 (0.04)	28 (2)	0	100 (0)	0
Site 10 (rkm 192)	4,820	1,300	1245 (0059)	23.6 (1.0)	24 (2)	232 (4)	9.1 (0.1)	0.36 (0.08)	0.43 (0.08)	48 (4)	0	97 (2)	3 (2)
Norden Chute to Cornell Dam (rkm 193 to 242)													
Site 11 (rkm 201)	7,767	1,834	1529 (0101)	24.2 (0.9)	22 (1)	229 (4)	9.9 (0.1)	0.52 (0.07)	0.56 (0.07)	45 (7)	0	87 (6)	13 (6)
Site 12 (rkm 224)	8,400	1,714	1814 (0102)	25.1 (1.0)	19 (1)	232 (5)	9.7 (0.1)	0.47 (0.07)	0.56 (0.06)	39 (3)	0	56 (9)	44 (9)
Site 13 (rkm 242)	8,078	1,918	1025 (0119)	20.8 (1.0)	20 (1)	217 (8)	9.1 (0.2)	0.69 (0.08)	0.75 (0.05)	29 (1)	0	85 (4)	15 (4)
Cornell Dam to Dunlap Diversion (rkm 242 to 531)													
Site 14 (rkm 244)	8,400	2,416	0855 (0055)	19.8 (0.8)	19 (1)	206 (3)	8.9 (0.1)	0.44 (0.04)	0.49 (0.04)	32 (3)	0	100 (0)	0
Site 15 (rkm 310)	6,520	1,315	1223 (0032)	22.6 (0.6)	38 (9)	226 (3)	8.8 (0.2)	0.36 (0.04)	0.46 (0.05)	46 (4)	3 (2)	87 (4)	11 (3)
Site 16 (rkm 374)	8,319	1,782	1501 (0154)	23.6 (0.5)	21 (4)	259 (2)	9.6 (0.4)	0.41 (0.03)	0.57 (0.04)	42 (4)	1 (1)	68 (7)	31 (7)
Site 17 (rkm 505)	7,829	787	1323 (0325)	21.6 (0.8)	5 (0)	429 (7)	8.4 (0.1)	0.40 (0.03)	0.49 (0.03)	51 (4)	0	70 (4)	30 (4)

Table 2. Results of the Principal Component Analysis (PCA) for the axes retained for interpretation. Eigen vectors (correlations) for each abiotic factors (values greater than 0.4 are in bold; Hair et al. 1987), eigenvalues and percentage of explanation are given.

Variables	PC1	PC2
Temperature	**0.55**	**-0.44**
Turbidity	**0.66**	0.28
Conductivity	0.30	**-0.63**
% gravel	**-0.42**	**-0.58**
Eigenvalues (λ)	1.64	1.45
% of explanation	41.07	36.31

Table 3. Total number of fish by species captured at each sampling site with a tote-barge electrofisher in the Niobrara River from June to September 2009. Total effort in seconds presented in parentheses.

		Mouth to Spencer Dam (rkm 0 to 63)						Spencer Dam to Norden Chute (rkm 63 to 193)				Norden Chute to Cornell Dam (rkm 193 to 242)			Cornell Dam to Dunlap Diversion (rkm 242 to 531)			
Species	N	Site 1 rkm 3 (8,723)	Site 2 rkm 4 (9,162)	Site 3 rkm 25 (8,119)	Site 4 rkm 45 (8,859)	Site 5 rkm 57 (8,096)	Site 6 rkm 62 (5,389)	Site 7 rkm 81 (8,401)	Site 8 rkm 106 (8,072)	Site 9 rkm 167 (8,302)	Site 10 rkm 192 (4,820)	Site 11 rkm 201 (7,767)	Site 12 rkm 224 (8,400)	Site 13 rkm 242 (8,078)	Site 14 rkm 244 (8,400)	Site 15 rkm 310 (6,520)	Site 16 rkm 374 (8,319)	Site 17 rkm 505 (7,829)
Lepistosteidae - gars																		
Shortnose gar *Lepisosteus platostomus*	8	5	1	2														
Clupeidae - herrings																		
Gizzard shad *Dorosoma cepedianum*	1						1											
Cyprinidae - carps and minnows																		
Central stoneroller *Campostoma anomalum*	425																	425
Red shiner *Cyprinella lutrensis*	8,544	264	347	545	511	835	461	663	349	756	920	705	556	994	290	319	27	2
Spotfin shiner *Cyprinella spiloptera*	140	41	91	1	1	6												
Common carp *Cyprinus carpio*	53	3	4	11	5	14	7	8								1		
Brassy minnow *Hybognathus hankinsoni*	101				46	2	1		3	18	21			1				9
Silver chub *Macryhybopsis storeriana*	29	2	3	2	9	12	1											
Golden shiner *Notemigonus crysoleucas*	11			2		5					4							
Emerald shiner *Notropis atherinoides*	2	1	1															
Bigmouth shiner *Notropis dorsalis*	1,036	4		122	45	7	3		17	125	16	61	4	446	177	4		5
Sand shiner *Notropis stramineus*	13,078	43	78	429	898	1,524	672	815	441	2,532	2,893	230	122	1,242	163	238	367	391
Suckermouth minnow *Phenacobius mirabilis*	1				1													
Bluntnose minnow *Pimephales notatus*	1		1															
Fathead minnow *Pimephales promelas*	171			2	7		7	2	5	3	5	104	3	15	11		7	
Flathead chub *Platygobio gracilis*	702	98	103	182	115	50	16	87	34	11	6							
Longnose dace *Rhinichthys cataractae*	524									1	18	57	213	13		23	97	102
Creek chub *Semotilus atromaculatus*	1,826				7			2	1	62	41	86	131	362		57	195	882

Table 3 continued.

Species	N	Mouth to Spencer Dam (rkm 0 to 63)						Spencer Dam to Norden Chute (rkm 63 to 193)				Norden Chute to Cornell Dam (rkm 193 to 242)			Cornell Dam to Dunlap Diversion (rkm 242 to 531)			
		Site 1 rkm 3 (8,723)	Site 2 rkm 4 (9,162)	Site 3 rkm 25 (8,119)	Site 4 rkm 45 (8,859)	Site 5 rkm 57 (8,096)	Site 6 rkm 62 (5,389)	Site 7 rkm 81 (8,401)	Site 8 rkm 106 (8,072)	Site 9 rkm 167 (8,302)	Site 10 rkm 192 (4,820)	Site 11 rkm 201 (7,767)	Site 12 rkm 224 (8,400)	Site 13 rkm 242 (8,078)	Site 14 rkm 244 (8,400)	Site 15 rkm 310 (6,520)	Site 16 rkm 374 (8,319)	Site 17 rkm 505 (7,829)
Catostomidae - Suckers																		
River carpsucker *Carpiodes carpio*	1,311	155	99	513	64	53	24	104	156	23	120							
Quillback *Carpiodes cyprinus*	1	1																
White sucker *Catostomus commersoni*	2,607				2	2			1	105	114	935	43	84	189	186	612	334
Shorthead redhorse *Moxostoma macrolepidotum*	560	29	49	88	39	15	6	5	7	24	18	16	4	2	9	16	162	71
Ictaluridae - bullhead catfishes																		
Black bullhead *Ameiurus melas*	23		4	2		4					10			1	1	1		
Channel catfish *Ictalurus punctatus*	961	101	423	121	80	28	72	43	12	13	66	2						
Stonecat *Noturus flavus*	90		3						1			12	5	6		13	5	45
Flathead catfish *Pylodictis olivaris*	13	4	6	1	1	1												
Esocidae - pikes																		
Grass pickerel *Esox americanus vermiculatus*	54	5	17	4	2	7		3	1		1	2			1	11		
Northern pike *Esox lucius*	2																	2
Salmonidae - trouts																		
Rainbow trout *Oncorhynchus mykiss*	2													2				
Cyprinodontidae - killifishes																		
Plains topminnow *Fundulus sciadicus*	36															5	31	
Gasterosteidae - sticklebacks																		
Brook stickleback *Culea inconstans*	18															16	2	

Table 3 continued.

Species	N	Mouth to Spencer Dam (rkm 0 to 63)						Spencer Dam to Norden Chute (rkm 63 to 193)				Norden Chute to Cornell Dam (rkm 193 to 242)			Cornell Dam to Dunlap Diversion (rkm 242 to 531)			
		Site 1 rkm 3 (8,723)	Site 2 rkm 4 (9,162)	Site 3 rkm 25 (8,119)	Site 4 rkm 45 (8,859)	Site 5 rkm 57 (8,096)	Site 6 rkm 62 (5,389)	Site 7 rkm 81 (8,401)	Site 8 rkm 106 (8,072)	Site 9 rkm 167 (8,302)	Site 10 rkm 192 (4,820)	Site 11 rkm 201 (7,767)	Site 12 rkm 224 (8,400)	Site 13 rkm 242 (8,078)	Site 14 rkm 244 (8,400)	Site 15 rkm 310 (6,520)	Site 16 rkm 374 (8,319)	Site 17 rkm 505 (7,829)
Centrarchidae - sunfishes																		
Rock bass *Ambloplites rupestris*	6										1							5
Green sunfish *Lepomis cyanellus*	488	29	136	20	14	52	26	42	14	2	44	17		1		49	42	
Orange-spotted sunfish *Lepomis humilis*	18	5	13															
Bluegill *Lepomis macrochirus*	194	3	6	19	13	38	17		29	1	63			1		4		
Largemouth bass *Micropterus salmoides*	522	5	13	29	42	38	28	66	49	51	98	42	2	12	8	12	24	3
White crappie *Pomoxis annularis*	16		1	8	1	2	4											
Black crappie *Pomoxis nigromaculatus*	5								3		2							
Percidae - perches																		
Johnny darter *Etheostoma nigrum*	20	7	13															
Yellow perch *Perca flavescens*	249				1	1			1		6			3	1	53	183	
Sauger *Sander canadense*	27	5	5	4		3	10											
Sciaenidae - drums																		
Freshwater drum *Aplodinotus grunniens*	11	6	5															
Total fish	33,888	816	1,422	2,107	1,904	2,699	1,356	1,840	1,124	3,727	4,467	2,269	1,083	3,186	850	1,008	1,754	2,276

Table 4. Bray-Curtis post-hoc pairwise comparisons of the fish community in the Niobrara River. N = number of pairwise comparisons among months (June to September), 17 sample sites, and four reaches separated by fish barriers. Pairwise comparisons were significant if "significance level percent" was **<0.5** at α = 0.05.

Group	N	*R*	*P*	Significance level (%)
Month	6	0.049	<0.001	
June and July		0.004		25.7
August and September		0.002		32.7
All other monthly comparisons		≥0.044		≤0.4*
Sample site	136	0.590	<0.001	
1 and 2		-0.025		70.0
4 and 5		0.125		1.4
4 and 6		0.133		1.0
4 and 7		0.147		1.5
4 and 8		0.106		1.4
5 and 6		0.093		3.4
5 and 7		0.161		1.0
7 and 8		0.072		4.5
All other site comparisons		≥0.171		≤0.3*
Reach	6	0.395	<0.001	
All reaches		≥0.120		≤0.1*

Table 5. Bray-Curtis dissimilarity comparisons providing information corresponding to differences in species abundance among the groups that described a minimum cumulative total of 90% of variation between sample sites along the Niobrara River from June to September 2009. Scale is 0 to 100, where 0 means there is no difference in the species structure between the two sites and 100 indicates completely different species structure. An average dissimilarity score < 70 (highlighted in bold) indicates moderate differences in the fish communities between sample sites.

Sample site	Site 2 (rkm 4)	Site 3 (rkm 25)	Site 4 (rkm 45)	Site 5 (rkm 57)	Site 6 (rkm 62)	Site 7 (rkm 81)	Site 8 (rkm 106)	Site 9 (rkm 167)	Site 10 (rkm 192)	Site 11 (rkm 201)	Site 12 (rkm 224)	Site 13 (rkm 242)	Site 14 (rkm 244)	Site 15 (rkm 310)	Site 16 (rkm 374)	Site 17 (rkm 505)
Site 1 (rkm 3)	**67.13**	71.80	72.88	80.50	74.73	71.77	75.71	87.60	90.71	85.07	82.78	84.46	84.80	80.80	93.37	96.47
Site 2 (rkm 4)		74.33	74.88	80.81	76.04	73.21	78.37	87.76	90.24	86.69	85.38	85.18	85.73	82.31	92.45	95.44
Site 3 (rkm 25)			**62.95**	**65.89**	**64.10**	**59.97**	**65.51**	73.17	82.32	82.73	81.57	71.45	82.17	77.32	86.43	88.12
Site 4 (rkm 45)				**54.36**	**53.20**	**52.70**	**61.11**	**57.54**	76.21	76.56	76.22	**61.10**	75.50	**69.68**	82.29	83.98
Site 5 (rkm 57)					**48.10**	**51.82**	**64.69**	**45.37**	**67.41**	79.12	77.61	**53.36**	81.47	71.94	83.61	84.74
Site 6 (rkm 62)						**51.60**	**62.50**	**52.99**	71.61	76.56	74.63	**57.98**	78.20	**69.30**	83.55	85.38
Site 7 (rkm 81)							**56.66**	**59.05**	76.56	77.14	76.31	**60.79**	76.56	**69.62**	81.71	84.27
Site 8 (rkm 106)								70.90	82.90	79.08	79.93	**68.98**	77.40	73.08	83.30	86.09
Site 9 (rkm 167)									**61.66**	79.92	82.12	**55.93**	81.51	74.69	80.75	79.80
Site 10 (rkm 192)										81.75	85.75	70.83	87.01	79.04	84.98	85.78
Site 11 (rkm 201)											74.61	73.53	73.92	**65.36**	72.23	77.47
Site 12 (rkm 224)												70.37	80.16	**69.16**	79.14	81.36
Site 13 (rkm 242)													71.26	**67.28**	79.98	73.98
Site 14 (rkm 244)														70.84	81.80	85.21
Site 15 (rkm 310)															**66.54**	73.11
Site 16 (rkm 374)																**66.72**
Site 17 (rkm 505)																

Table 6. Species specific contributions to differences among assemblage groups. Bray-Curtis dissimilarity comparisons providing information corresponding to differences in species abundance among groups that described a minimum cumulative total of 90% of the dissimilarity among the reaches along the Niobrara River from June to September 2009. Average dissimilarity scale is 0 to 100, where 0 means there is no difference in the species structure between the two river reaches and 100 indicates completely different species structure. An average dissimilarity score < 70 (highlighted in bold) indicates moderate differences in the fish communities between river reaches.

	Mean relative abundance (fish/h)				Mean dissimilarity and contribution (%)					
Species	Mouth to Spencer Dam (Group 1)	Spencer Dam to Norden Chute (Group 2)	Norden Chute to Cornell Dam (Group 3)	Cornell Dam to Dunlap Diversion Group 4)	1 versus 2	1 versus 3	1 versus 4	2 versus 3	2 versus 4	3 versus 4
Bigmouth shiner	19.07 (13.54)	17.31 (8.61)	82.53 (21.15)	25.31 (9.41)	1.4 (2)	4.1 (5)	2.8 (3)	3.7 (5)	2.5 (3)	5.3 (7)
Central stoneroller	0	0	0	55.36 (15.97)	-	-	2.8 (3)	-	2.4 (3)	2.8 (4)
Channel catfish	68.98 (16.25)	20.58 (9.05)	0.24 (0.24)	0	3.5 (5)	4.1 (5)	4.3 (5)	-	-	-
Creek chub	0.48 (0.43)	15.19 (4.22)	111.30 (33.38)	144.90 (28.60)	-	5.1 (7)	8.1 (10)	4.5 (6)	7.1 (9)	10.3 (14)
Flathead chub	43.46 (8.50)	15.43 (2.94)	0	0	2.9 (4)	3.4 (4)	3.5 (4)	-	-	-
Green sunfish	24.79 (5.95)	14.70 (4.28)	2.85 (1.24)	11.58 (2.38)	1.6 (2)	1.5 (2)	2.0 (2)	-	-	-
Largemouth bass	12.93 (2.33)	37.98 (7.96)	8.47 (2.53)	5.34 (1.33)	2.5 (4)	-	-	2.5 (3)	2.5 (3)	-
Longnose dace	0	3.50 (1.55)	41.68 (7.83)	29.66 (5.22)	-	3.4 (5)	2.1 (2)	2.9 (4)	1.8 (2)	3.9 (5)
Red shiner	235.91 (24.82)	362.20 (56.40)	364.70 (93.99)	69.43 (17.04)	15.1 (22)	16.9 (22)	14.9 (18)	16.3 (22)	14.2 (18)	17.3 (23)
River carpsucker	78.33 (23.21)	59.76 (18.92)	0	0	6.0 (9)	4.5 (6)	4.7 (6)	3.8 (5)	4.0 (5)	-
Sand shiner	286.34 (36.54)	955.27 (220.05)	273.54 (69.97)	129.12 (17.67)	29.0 (42)	18.8 (25)	17.2 (21)	28.7 (38)	28.2 (35)	13.5 (18)
Shorthead redhorse	20.00 (4.24)	8.05 (2.19)	3.92 (1.59)	36.03 (12.52)	-	-	2.6 (3)	-	1.9 (2)	2.1 (3)
White sucker	0.33 (0.20)	32.87 (6.70)	172.07 (58.84)	166.16 (25.41)	1.4 (2)	7.8 (10)	10.7 (13)	7.0 (9)	8.7 (11)	13.0 (17)
Average dissimilarity					**68.9**	76.7	83.5	74.6	80.6	74.6

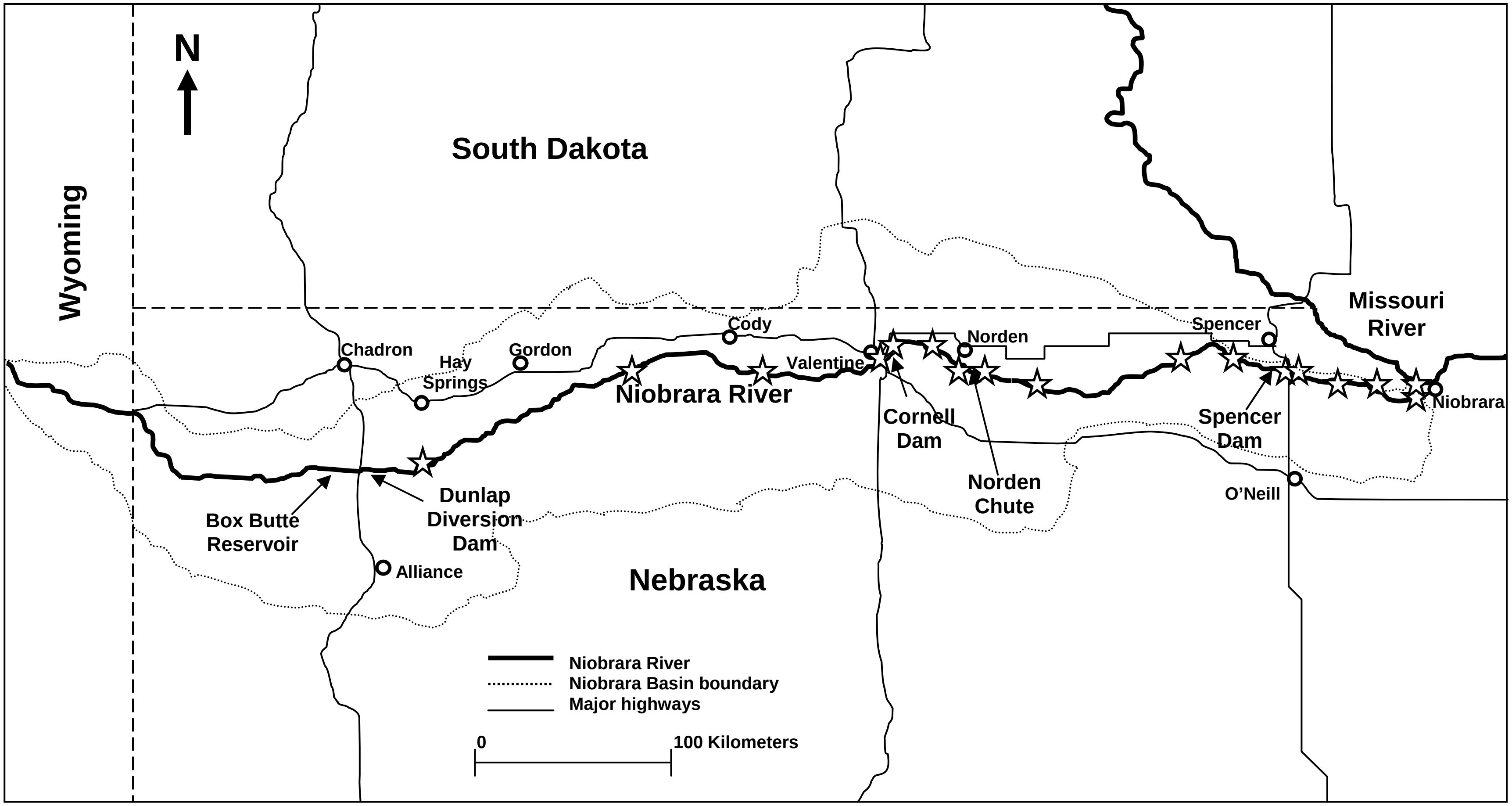

Figure 1. Study area of the Niobrara River from the mouth at the confluence with the Missouri River upstream to the Dunlap Diversion Dam near Alliance, Nebraska. Seventeen sites, indicated by stars, were sampled with a tote-barge electrofisher each month from June to September 2009.

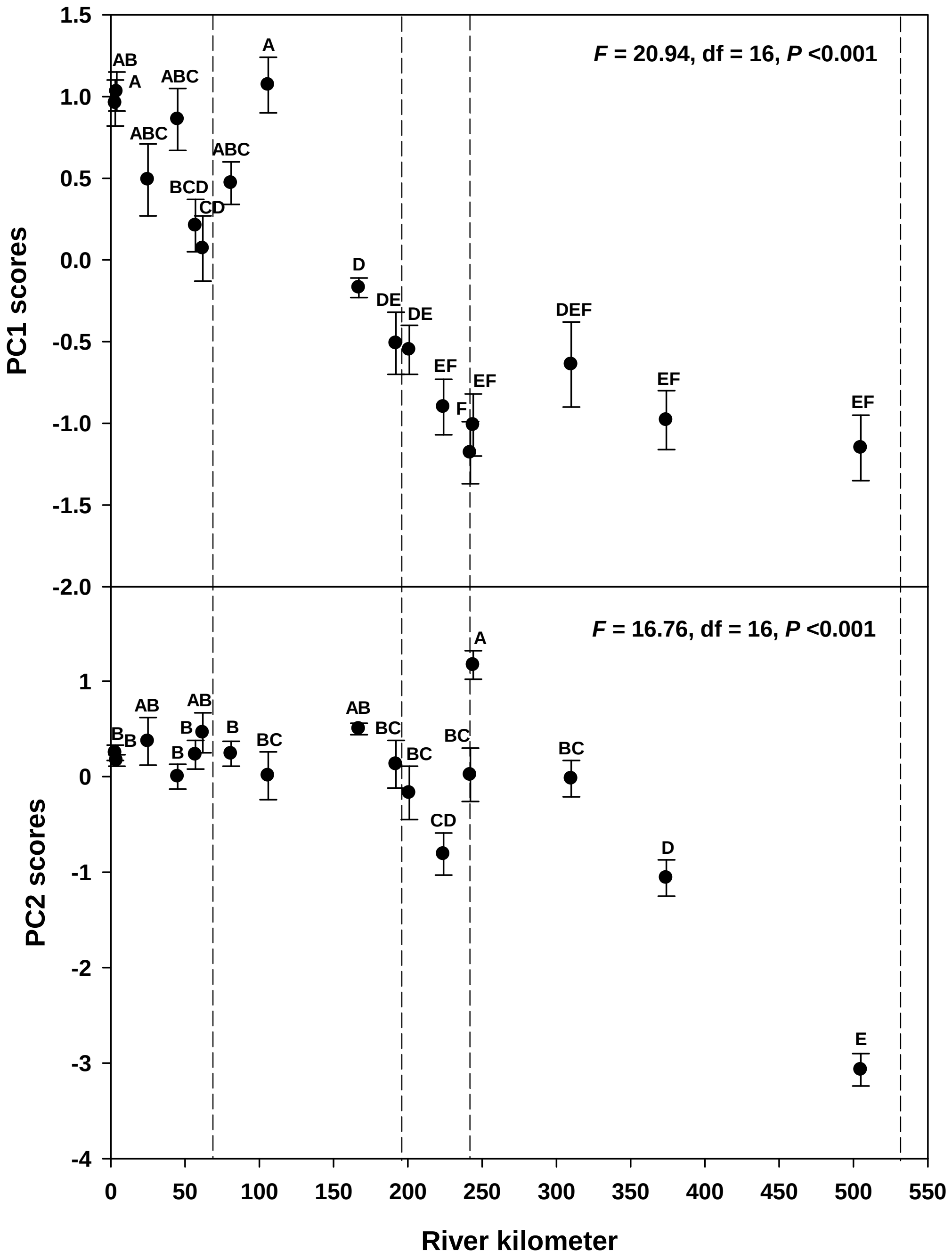

Figure 2. Mean principle component analysis (PCA) scores and standard error bars for Axis 1 (top) and Axis 2 (bottom) for each sampling site derived from the abiotic factors matrix. Analysis of variance (ANOVA) was applied to the factor scores of the retained principal components to compare differences among sample sites. Sample sites that share a common letter were not significantly different at α = 0.10. Hatch lines indicate fish barriers: Spencer Dam (rkm 63), Norden Chute (rkm 193), Cornell Dam (rkm 242), and Dunlap Diversion Dam (rkm 531).

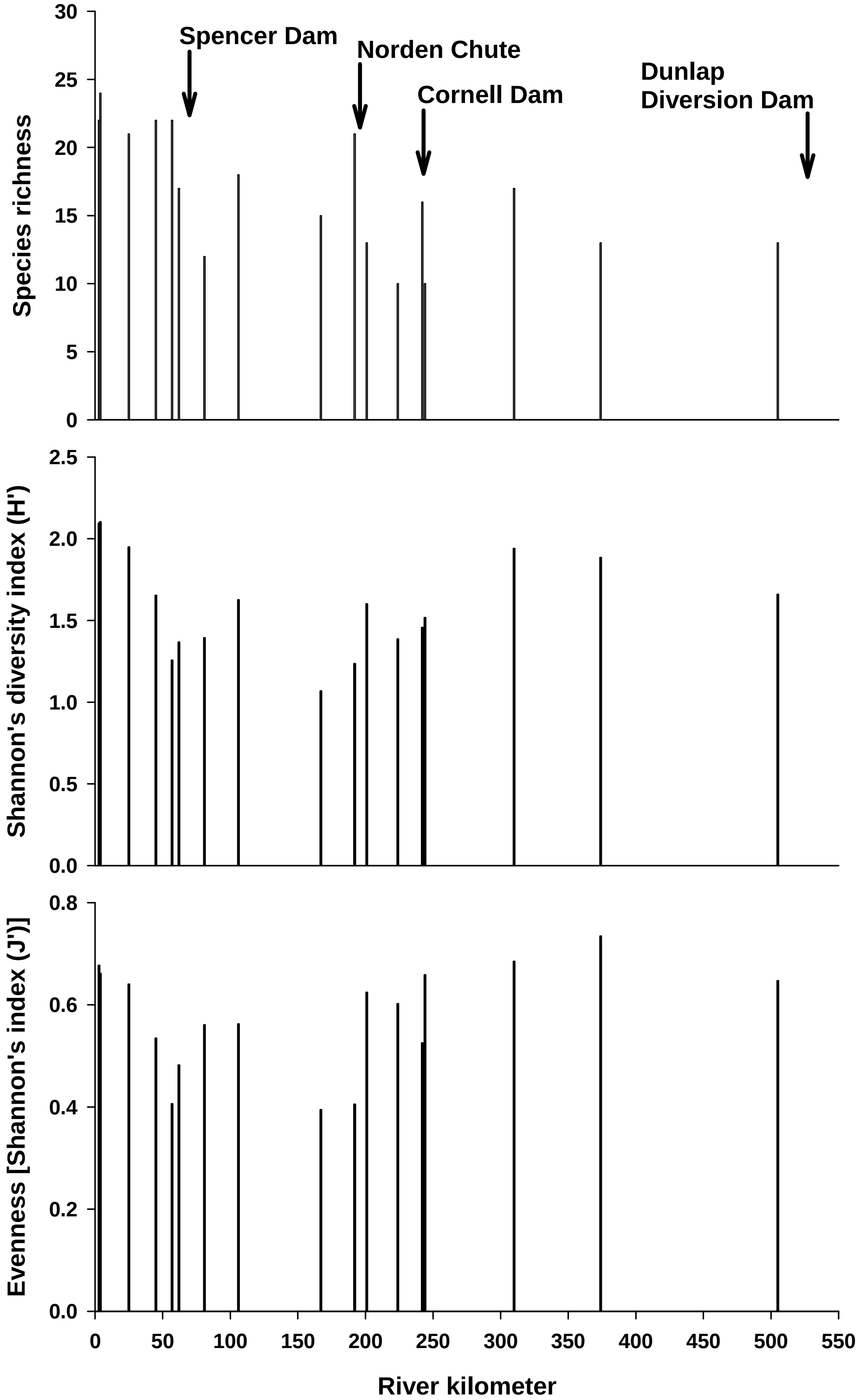

Figure 3. Species richness, diversity, and evenness at seventeen sites sampled monthly from June to September 2009 within four reaches delineated by fish barriers along the Niobrara River, Nebraska from the mouth (rkm 0) to the Dunlap Diversion Dam (rkm 531).

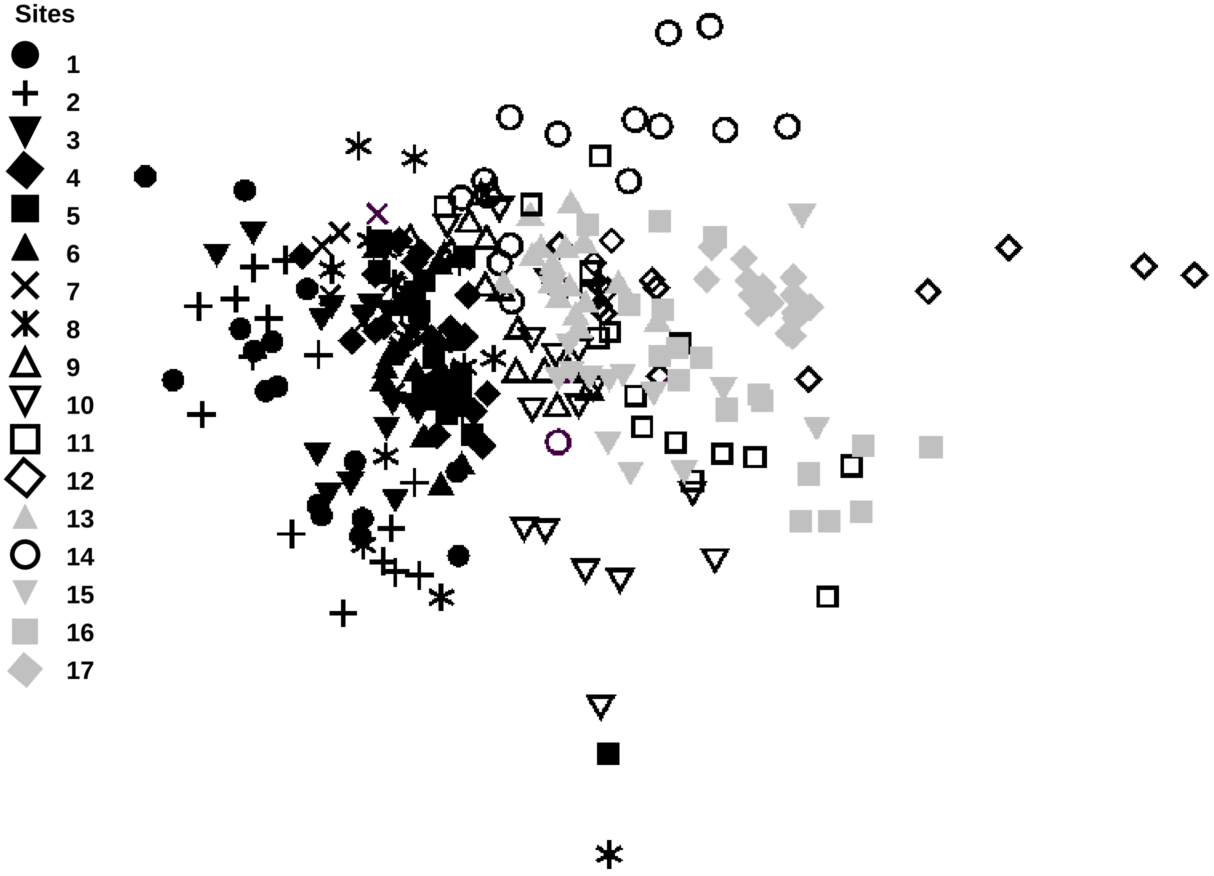

Figure 4. Nonparametric multidimensional scaling (NMDS) ordination based on species abundance in the Niobrara River comparing the fish community among sample sites from June to September 2009.

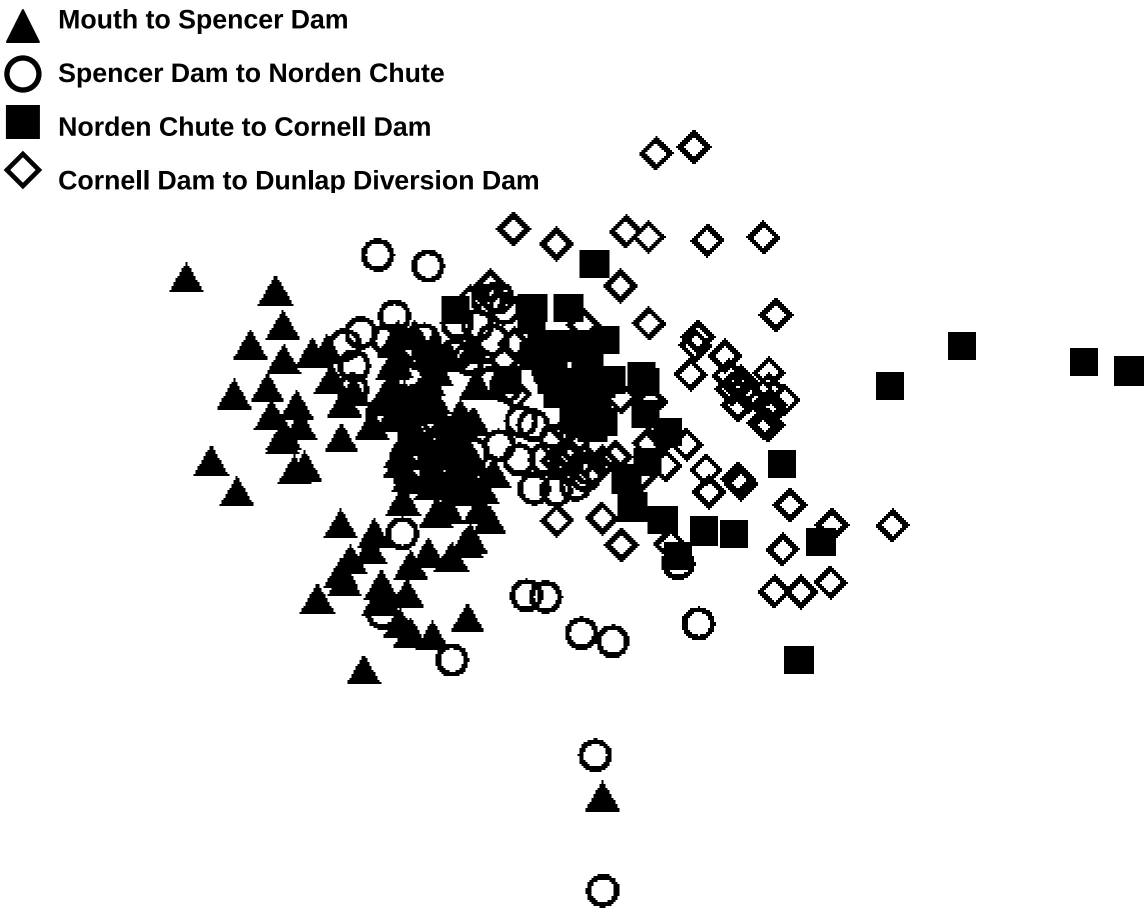

Figure 5. Nonparametric multidimensional scaling (NMDS) ordination based on species abundance in the Niobrara River comparing the fish community among river reaches separated by fish barriers from June to September 2009.

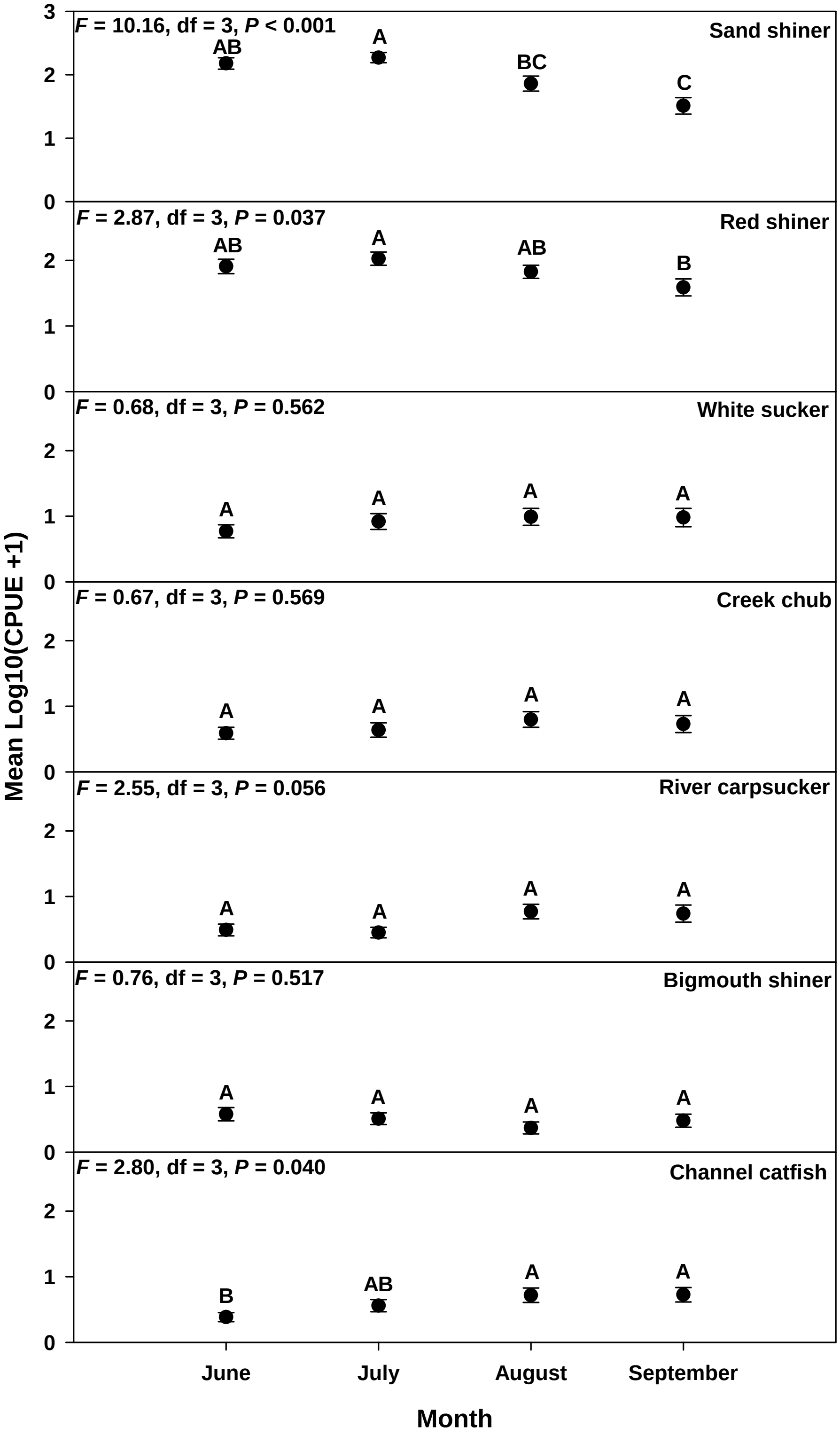

Figure 6. Monthly mean catch per unit effort (CPUE) and standard error bars for the seven most abundant species captured with a tote-barge electrofisher in the Niobrara River from June to September 2009. Months with the same letter are not significantly different ($P \geq 0.10$) using analysis of variance (ANOVA) with a Bonferroni multiple comparison test.

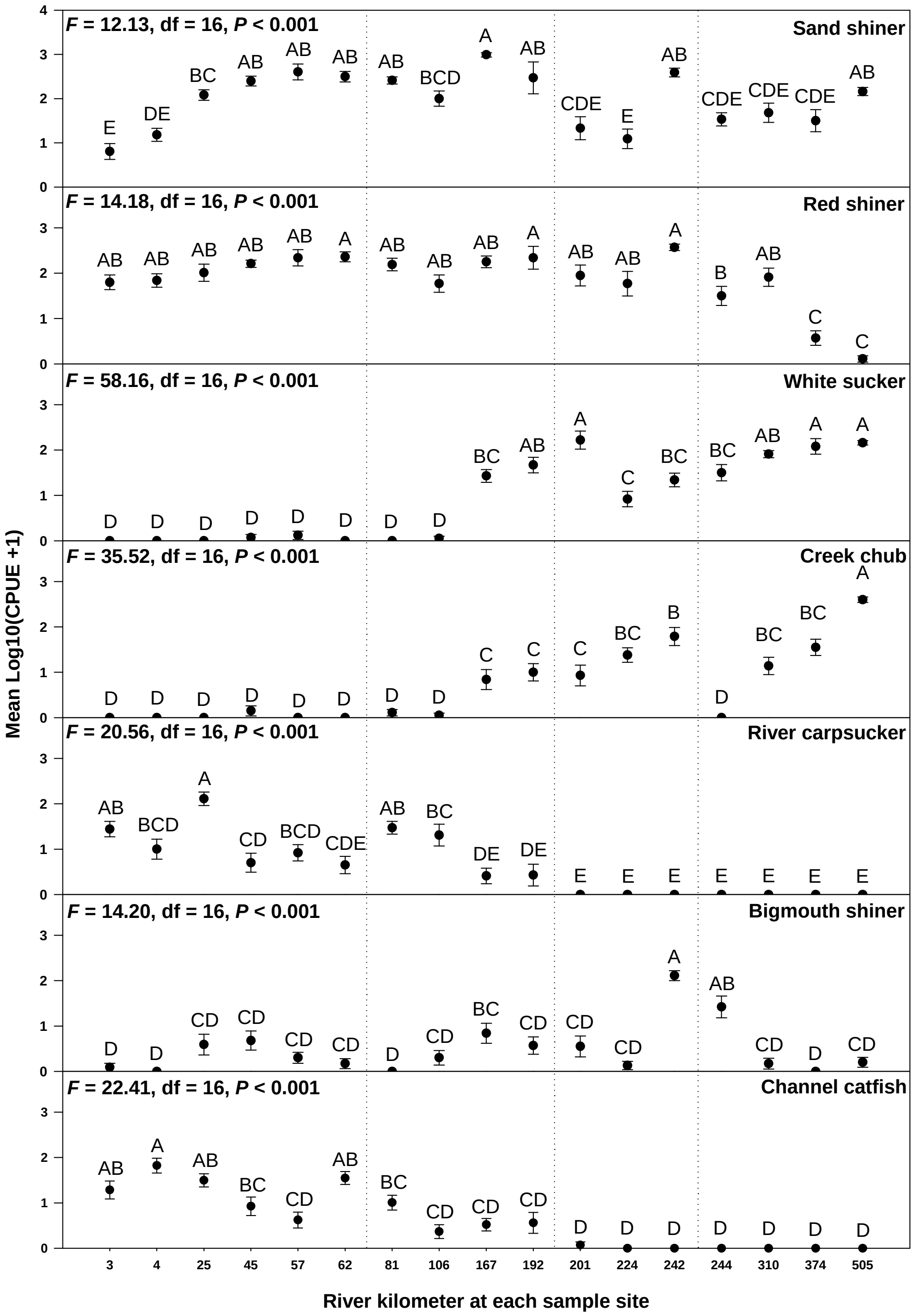

Figure 7. Mean catch per unit effort (CPUE) and standard error bars for the seven most abundant species captured with a tote-barge electrofisher in the Niobrara River from June to September 2009. Sample sites with the same letter are not significantly different ($P \geq 0.10$) using analysis of variance (ANOVA) with a Bonferroni multiple comparison test. Dotted lines indicate breaks in river reaches separated by fish barriers. Hatch lines indicate fish barriers: Spencer Dam (rkm 63), Norden Chute (rkm 193), Cornell Dam (rkm 242), and Dunlap Diversion Dam (rkm 531).