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Spatial and temporal patterns and the influence of abiotic factors on larval fish catches in the lower Niobrara River, Nebraska



February 2011

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Abstract

The Niobrara River has a natural hydrograph and temperature regime with the lower 32 km protected under the National Wild and Scenic River system managed by the National Park Service. The largest threat to this river is decreased instream flows due to water withdrawals for agriculture. The Niobrara River a large tributary to the Missouri River may positively influence fish production. However, no information exists regarding phenology of fish spawning or what abiotic factors may influence spawning. Our objectives were to examine the taxonomic composition and the spatial and temporal patterns of the larval fish assemblage in relation to environmental variables in the lower Niobrara River. Larval fish sampling occurred weekly from April to August in 2008 and May to August 2009 with drift nets set in the Niobrara River at two sites: the mouth and 63 kilometers upstream. Each year, larval fish first appeared in the drift during the second week of May and were collected until the third week of August. Larval river carpsuckers *Carpiodes carpio* were the most abundant species in the drift during early-June, followed by red shiners *Notropis lutrensis* and sand shiners *Notropis stramineus* in late-June to mid-August, with *Lepomis* spp. appearing during late-June to late-July. No diel cycle in occurrence of larval fish in the drift was observed and likely resulted from the naturally high turbidity (mean nephelometric turbidity unit [NTU] > 74). Larval fish densities were 24% higher in 2009 compared to 2008. Spatially, the greatest numbers of larval fish for most fish species were collected at our upstream site located immediately downstream of Spencer Dam. Differences in environmental variables were found among sites and years as mean water temperature, velocity, and turbidity were higher and dissolved oxygen was lowest at the mouth site in 2009. The results of canonical correspondence analysis found red shiners and sand shiners were associated with high water temperatures with low stable flows found late summer.

Larval flathead chubs *Platygobio gracilis* and common carp *Cyprinus carpio* abundance was positively related to dissolved oxygen and water velocity and negatively with water temperature. River carpsuckers were associated with high water velocities and moderate water temperatures while *Lepomis* spp. were positively associated with high conductivity and high water temperatures. Fish species that successfully spawned in the lower Niobrara River are adapted to extreme temperatures, high variability in discharge, turbidity, and sediment load. Based on the importance of abiotic factors affecting larval fish abundances, a reduction in in-stream flows would likely jeopardize native fish populations and eliminate some productivity of fish in this river.

Introduction

The Niobrara River in Nebraska is principally groundwater fed with the lower 32 km designated in 1991 as a National Recreational River, managed by the National Park Service (NPS). This designation preserves free-flowing rivers that have exceptional natural and recreational values. The Niobrara River currently retains a natural hydrograph and temperature regime which provides important seasonal habitats for 54 species of native fishes (Schainost 2008). The largest threat to the Niobrara River is reduced flows due to increased water diversion for agricultural irrigation development within the basin (Zuerlein 2007). The Niobrara River is the only major tributary to an inter-reservoir reach of the Missouri River between Fort Randall and Gavins Point dams (Figure 1). Since the closure of Gavins Point Dam in 1955, a 24 km delta has formed from deposition of sediment delivered from the Niobrara River (Graeb et al 2009).

Numerous studies have reported the importance of the Niobrara River to the Missouri River downstream of their confluence. Reduced flows could jeopardize native fish populations and reduce productivity of fish and invertebrates in the Niobrara River and areas downstream of the Missouri/Niobrara rivers confluence. The natural flow regime of the Niobrara River, such as magnitude, rate of change, periodicity, and duration of the spring high flow period positively influenced paddlefish *Polyodon spathula* recruitment in the Missouri River (Pracheil et al. 2009). Sauger *Sander canadense* populations demonstrated an affinity to the delta formed with warmer, more turbid discharge, and actively meandering and complex riverine habitats found downstream of the Niobrara River confluence compared to the cold, clear water upstream of the confluence (Graeb et al. 2009). The benthic fish community in the Missouri River downstream of Fort Randall Dam has been monitored since 2003 and Shuman et al. (2010) reported that the relative abundance of native fish, including the endangered pallid sturgeon *Scaphirhynchus albus* and shovelnose sturgeon *S. platyrhynchus*, was highest downstream of the confluence. Additionally, shovelnose sturgeon condition (Wanner 2006) and the relative abundance of macroinvertebrates (Grohs 2008) increased downstream of the confluence. Increasing evidence supports the hypothesis that discharges from the Niobrara River positively influence the native fish community in the Missouri River. However, fish community data within the Niobrara River is limited (Schainost 2008) and knowledge of the larval fish assemblage was non-existent. Native fish, such as pallid sturgeon, shovelnose sturgeon, paddlefish, and sauger may move upstream into the Niobrara River to initiate spawning; however, their migration upstream is blocked 63.3 river kilometers (rkm) upstream from the mouth because of Spencer Dam.

Spencer Dam was constructed in 1927 and has since functioned as a complete barrier to upstream fish migration. Although Spencer Dam is a barrier, it is operated as a run of river dam

with little adverse affects to the natural hydrograph and temperature regime. Hesse and Newcomb (1982) recommended a fish bypass at Spencer Dam to provide upstream access for spawning sauger, walleye *S. vitreus*, and channel catfish *Ictalurus punctatus*. The Niobrara River, including sites upstream of Spencer Dam, may also provide critical sturgeon spawning sites, increased distance necessary for larval sturgeon drift (Braaten et al 2008), as well as nursery habitat for young of the year sturgeon. Pallid sturgeon and shovelnose sturgeon have been found in the Niobrara River downstream of Spencer Dam (Wanner et al. 2009; Wanner, unpublished data), although it is unknown if these species are spawning there.

For many riverine fishes, successful spawning is associated with a combination of abiotic factors including discharge (Hynes 1970; Robinson et al. 1998; Mathews 1998; Koel and Sparks 2002; Bednarski 2008), turbidity (Faushch and Bestgen 1997), temperature (Wolf et al. 1996; Wolter 2007), photoperiod (Bye 1989), and dissolved oxygen (Schiemer et al. 2002). Currently, there is no information on the larval fish assemblage in the Niobrara River. To gain an understanding of the larval fish assemblage and what environmental variables determined the reproductive success for native fish in the lower Niobrara River our objectives of this study were to: 1) describe the larval fish assemblage of the lower Niobrara River downstream of Spencer Dam; 2) determine the temporal and spatial relative abundance of the larval fish community in the Niobrara River; and 3) determine what environmental variables influence successful spawning in this river.

Study Area

The Niobrara River watershed is approximately 34,913 km² and extends approximately 900 km from its headwaters in Wyoming to its confluence with the Missouri River near

Niobrara, Nebraska (Alexander et al. 2009). Land use in the basin is predominately livestock ranching with row-crop agriculture in the eastern region (Dappen et al. 2007). The Niobrara River has a relatively steep gradient of 1.4 m/km (i.e., mean slope of 0.14%) from the Keya Paha River confluence (rkm 95) to its mouth. In comparison, the Missouri River on the border of South Dakota and Nebraska falls at 0.2 m/km, the central Platte River gradient is 1.2 m/km, and the Middle Loup River gradient is 1.3 m/km (Bentall 1991). The average annual precipitation in the Niobrara River basin ranges from 40 cm in the west to over 60 cm in the eastern basin. A high proportion of flow in the Niobrara River is derived from ground water. Around Valentine, Nebraska, 80-90% of the base flow is derived by ground water, while near the mouth approximately 15% of base flow originates from ground water (USDA 1973). Mean annual discharge of the Niobrara River is 43.5 m³/s at Spencer Dam, 48.3 m³/s at the Pischelville Bridge (Alexander et al. 2009), and 48.8 m³/s at the mouth (Schainost 2008).

The lower Niobrara River downstream of Spencer Dam (Figure 1) is characterized as highly braided with multiple river channels and transports an estimated 300 metric tons of sediment per day (Hotchkiss et al. 1993). The river downstream of Spencer Dam has three distinct geomorphic reaches (Alexander et al. 2009). Immediately downstream of Spencer Dam is the “single thread” reach (rkm 54.7 to 62.8). This reach is characterized predominantly by a single river channel with depths from 0.3 to 2.0 m that meanders from bank to bank with alternating sand bars that may be covered by immature vegetation. The “braided” reach (rkm 19.3 to 54.7) is characterized by several relatively shallow (0.1 – 0.3 m) channels that migrate between complexes of emergent and submergent sandbars. The “delta” reach (rkm 0.0 rkm to 19.3) is characterized with several thalwegs that flow between sandbars with mature vegetation and whose dimensions generally are proportional to the active channel width. The thalwegs

between the vegetated sandbars are relatively deep (0.5 – 3.0 m) with high water velocity (0.8 – 1.8 m/s) (Wanner et al. 2009).

Methods

Larval fish sampling

Larval fish were sampled from 23 April to 20 August 2008 and 5 May to 18 August 2009 nearly every week at two sample sites. One sample site was 0.6 km above the confluence of the Missouri and Niobrara rivers. This site was immediately downstream of the railroad bridge that crosses the Niobrara River on the west shoreline where most of the river flows, and is referred herein as the “mouth site”. The second site was 0.4 km downstream of Spencer Dam. This site was immediately downstream of the U.S. Highway 281 bridge on the south shore where most of the river flow occurs and herein is referred to as the “Spencer Dam site”. Larval fish drift can vary throughout the day, therefore, each site was sampled once in the morning (0600 to 1200 hours) and once in the afternoon (1500 to 2200 hours) each week to address diel patterns in the drift. A target of eight sub-samples was conducted at each site per diel period. Larval nets were fished on the bottom of the river for a maximum of 10 min per sub-sample, depending on detrital loads. Because of high detritus, each subsample at the mouth site was generally sampled for 0.5 to 1 min while low detritus allowed the Spencer Dam site to be sampled from 5 to 10 min for each sub-sample. The larval drift net had a mouth opening that was 0.5 m high, 1 m wide, and the net was 5 m long with 500 µm Nitex nylon mesh. The drift net was held stationary on the bottom of the river. River depths at the sampling sites varied with the continuous shifting sand bars, but ranged in depths of 0.5 to 0.7; therefore, the entire water column was sampled. Each net was outfitted with a mechanical flow meter (General Oceanics Inc., Miami, Florida) to

determine the water velocity (m/s) at the mouth opening to calculate the volume (m³) of water filtered. Turbidity (nephelometric turbidity unit [NTU]) was measured using a Hach Turbidimeter, model 2100P (Hach Company, Loveland, Colorado), while 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), and depth was measured at each larval net sub-sample.

All larval fish samples were preserved in a 10% buffered formalin solution containing “Rose Bengal” dye. In the laboratory larval fish were then sorted from detritus and stored in 95% ethyl alcohol. All larval fish were identified at a minimum to family and enumerated. Larval fish were identified using keys from McGuire (1981), Auer (1982), Fuiman et al. (1983), Wallus et al. (1990), Kay et al. (1994), Simon and Wallus (2003), and Wallus and Simon (2008). Specific keys were used to differentiate sturgeons in the genus *Scaphirhynchus* (Snyder 2002) and among Asian carp species (Soin and Sukhanova 1972). Because of the difficulty to reliably identifying some larval cyprinids, red shiner *Cyprinella lutrensis* and sand shiner *Notropis stramineus* data were combined. The three early development phases of fish, yolk-sac larvae, larvae, and juvenile were distinguished using the definitions in Auer (1982). The yolk-sac phase lasts from hatching to complete yolk absorption; the larval phase begins after absorption of the yolk and lasts until complete formation of all fin rays. All larval fish were measured to total length (TL) under a microscope at 6 to 12X magnification.

Water temperature was monitored downstream of Spencer Dam with HOBO waterproof temperature loggers (Onset Computer Corporation, Bourne, Massachusetts). Temperature was recorded every 0.5 h at three sites in 2008 (Spencer Dam [rkm 63], Redbird Bridge [rkm 43], and

the Railroad Bridge [rkm 0.6]) and two sites in 2009 (Redbird Bridge and the Railroad Bridge) (Figure 1). River discharge data was recorded by the U.S. Geological Survey (USGS) gage station (USGS 06465500 Niobrara River near Verdel, Nebraska) located at the Pischelville Bridge (Figure 1) (http://waterdata.usgs.gov/usa/nwis/uv?site_no=06465500).

Data analysis

Mean catch per unit effort (CPUE) for each larval fish drift subsample was calculated as number of larval fish/100 m³ of water filtered. The mean CPUE data were checked for normality and log₁₀(CPUE+1) transformed; normality improved based on residual and normal probability plots of the residuals (Neter et al. 1996). The larval fish data were analyzed to compare diel relative abundance at each site (mouth and Spencer Dam) each year using paired *t*-tests for overall fish CPUE and for five abundant taxa: red/sand shiners, common carp *Cyprinus carpio*, flathead chub *Platygobio gracilis*, river carpsuckers *Carpionodes carpio*, and *Lepomis* spp. Average diel sample times were 0917 hours in the morning and 1601 hours in the afternoon in 2008 and 0907 hours in the morning and 1831 hours in the afternoon in 2009. If relatively few differences in relative abundance were found between diel periods, then that data was combined to investigate differences in the mean log₁₀(CPUE+1) data between years and sample sites using a two-way analysis of variance (ANOVA). When differences in mean log₁₀(CPUE+1) 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. A Kolmogorov-Smirnov (KS) test was used to compare length frequency distributions of the most abundant larval fish taxa between sampling sites and years. To control our family-wise error rate for multiple *t*-tests and KS tests, we adjusted the probability levels

using Bonferroni corrections by dividing α by the number of comparisons (Sokal and Rohlf 1995).

Principal component analysis (PCA) was used to determine whether abiotic factors differed among sample sites each year. Abiotic variables measured at each site for the PCA were turbidity, conductivity, dissolved oxygen, water velocity, and mean daily temperature. Cumulative degree days were calculated from the mean daily temperatures (Pawiroredjo et al. 2008). 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 which 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). Two-sample t -tests were applied to the factor scores of the retained principal components to assess differences in abiotic factors between sample sites each year. Probability levels were adjusted for repeated analyses using a Bonferroni correction.

Variations in the fish communities at each sampling site and year were evaluated with detrended correspondence analysis (DCA). The DCA is an unconstrained ordination technique that produces simultaneous ordination of samples and species (ter Braak and Prentice 1988). Only abundant species ($\geq 1\%$ of total catch) were used in the DCA: flathead chubs, common carp, red/sand shiners, river carpsuckers, and *Lepomis* spp. Relative abundance data were $\log_{10}(\text{CPUE}+1)$ transformed for the DCA. Axes retained for interpretation were those with an eigenvalue ≥ 0.2 (Matthews 1998). Two-sample t -tests were applied to the DCA axes scores to assess differences in species composition between sample sites each year. Probability levels were adjusted for repeated analyses using a Bonferroni correction. The influence of abiotic

factors on larval fish density was then tested with a Pearson correlation between the axes that were retained for interpretation in the PCA and DCA. The influence of abiotic factors on larval fish density would be indicated by significant correlations.

Associations of larval fish species with environmental variables were also evaluated with canonical correspondence analysis (CCA). This constrained ordination technique is a direct gradient multivariate analysis that creates species gradients relative to environmental gradients. $\text{Log}_{10}(\text{CPUE}+1)$ transformed relative abundance data for abundant species ($\geq 1\%$ of total catch) were included in the analysis. Environmental variables were $\text{log}_{10}(X+1)$ transformed that included: Julian date, daily mean temperature, cumulative degree days, turbidity, conductivity, dissolved oxygen, mean daily discharge, and water velocity. The CCA was performed in a forward selection mode with each environmental variable tested sequentially using Monte Carlo permutation tests ($P < 0.05$) before inclusion to the final model. A CCA ordination or “biplot” was created to illustrate the distribution of species and sample points that jointly represent the dominant ecological relationships (McGarigal et al. 2000). Vectors or arrows emanate from the grand mean of all explanatory variables. Direction of the arrows in the ordination space are relative to the axes and indicated ecologically what the multivariate axes represent and the length of the arrow indicates the importance of an environmental variable (ter Braak 1986). The position of the species points relative to the arrows indicates how optimum the environmental conditions are for each species (Palmer 1993). All ANOVA’s, KS tests, PCA, and Pearson correlations were performed with Number Cruncher Statistical Software (NCSS; Hintze 2007). The DCA and CCA were performed using the statistical package CANOCO version 4.5 (ter Braak and Smilauer 2002).

Results

We sampled for larval fish every 3 to 13 days from 23 April to 20 August in 2008 and every 5 to 7 days 5 May to 18 August 2009. In 2008, 600 sub-samples were collected on 40 dates while 468 sub-samples were collected on 32 dates in 2009 (Table 1). Total volume of water filtered through drift nets was 22,509 m³ in 2008 and 25,146 m³ in 2009 (Table 1). During the study water temperature ranged from 14 to 30 °C, turbidity from 23 to 670 NTU's, conductivity from 206 to 360 µS/cm, DO from 6.4 to 11.3 mg/L, and water velocity from 0.02 to 1.77 m/s (Table 2).

The Principal Component Analysis (PCA) yielded two principal components (PC) with eigenvalues greater than 1.0, which explained 77% (PCA axis 1 = 48% and PCA axis 2 = 29%) of the variance in the environmental data. In relation to PCA1, positive correlations were found for conductivity, mean daily temperature, and cumulative degree days while dissolved oxygen was negatively correlated. Turbidity and water velocity were positively correlated with PC2 (Table 3). Significant differences were found between sites and years for both principal components (Figure 2). The mouth site each year had significantly higher water conductivity, temperature, cumulative degree days and lower dissolved oxygen compared to the Spencer Dam site ($t \geq 4.65$; $P < 0.001$). No differences were found between years at the mouth ($t = -1.31$; $P = 0.190$) or at Spencer Dam ($t = -0.48$; $P = 0.635$). Turbidity and water velocity was significantly higher at the mouth site compared to Spencer Dam site each year ($t \geq 8.11$; $P < 0.001$). No significant differences in turbidity and water velocity were found between years for the Spencer Dam site ($t = 0.43$; $P = 0.667$) while these variables were significantly higher in 2008 compared to 2009 at the mouth ($t = 8.73$; $P < 0.001$).

In total, 2,517 larval fish from 11 species and six families were collected in 2008 and 4,065 larval fish from 13 species and seven families were collected in 2009. In 2008 and 2009, 66% fewer larval fish were collected at the mouth of the Niobrara (Table 4) compared to the site downstream of Spencer Dam (Table 5). In both years, the majority of larval fish captured were red/sand shiners (57% in 2008; 79% in 2009), river carpsucker (36% in 2008; 8% in 2009), common carp (<1% in 2008; 3% in 2009), flathead chubs (1% in 2008 and 2009), and centrarchids (3% in 2008; 7% in 2009) of which most were *Lepomis* spp. (2% in 2008; 4% in 2009).

Larval fish and eggs began to appear in our samples during the second week of May in each year. Changes in larval fish abundance at both sample sites generally coincided temporally but peaks in abundance at the mouth site generally lagged about one week behind the Spencer Dam site for both years (Figures 3-7). Larval common carp (Figure 3) and flathead chubs (Figure 4) appeared earlier in the sampling season when temperatures were between 15 - 25 °C. In 2008 and 2009, common carp appeared after the descending limb of the hydrograph in late May and early June. Flathead chub larvae abundance generally peaked at both sample sites with a subsequent protracted spawning over two months. Larval river carpsucker abundances peaked when water temperatures were between 20 - 25 °C. Multiple modes of larval river carpsucker relative abundance were evident with peak abundances in early June in both years during an increase in river discharge with a second peak in abundance in late June 2008 that followed a major flood event (Figure 5) while in 2009 the second mode was weaker with consistent larval production for six weeks. Increases in red/sand shiner larvae generally occurred following a period of stable river discharges when mean daily temperatures exceeded 25 °C, early July in 2008 and late June in 2009 (Figure 6). Red/sand shiners spawned over a protracted period as fry

were sampled for two months in both years. Larval *Lepomis* spp. relative abundance peaked during early July in 2008 and fry persisted through an extended period throughout the month of July in 2009 when mean daily temperatures were approximately 26 °C (Figure 7). A total of 2,850 unidentified fish eggs were collected in 2008 (32%) and 2009 (68%) and their relative abundance (Figure 8) generally followed that of river carpsucker (Figure 5) and *Lepomis* spp. (Figure 7).

The majority of larval fish collected during this study were yolk-sac larvae. Yolk-sac larvae constituted 97% of common carp catch (100% in 2008; 97% in 2009), 94% of flathead chub (92% in 2008; 94% in 2009), 97% of river carpsuckers (97% in 2008; 96% in 2009), 52% of red/sand shiner (61% in 2008; 49% in 2009), and of 57% *Lepomis* spp. (53% in 2008; 58% in 2009). Mean lengths of yolk-sac larvae were similar between sites and years for all fish species (Figure 9). Red/sand shiner and *Lepomis* spp. larvae mean lengths were greatest at the Spencer Dam site while river carpsucker mean length was longer at the mouth in 2008. In 2009, all fish taxa except red/sand shiners had greater mean lengths at the mouth site. There were relatively few differences in length frequency distributions (all larval stages) between sample sites and years (Table 6). No significant differences were found in length frequency distributions of fry between sample sites and years for common carp ($D = 0.23$ to 0.40 ; $P \geq 0.103$), flathead chubs ($D = 0.18$ to 1.00 ; $P \geq 0.105$), or *Lepomis* spp. ($D = 0.18$ to 0.31 ; $P \geq 0.026$). However, significant differences in river carpsucker and red/sand shiner length frequency distributions were found between nearly all site and year comparisons (Table 6).

There were no significant differences ($P \geq 0.013$) in the relative abundance of total larval fish and the most common taxa collected between diel periods after Bonferroni corrections ($P \leq 0.008$) at either sample site in both years (Table 7). Because no significant differences were

found between diel periods, relative abundance data was combined in further analyses. Significant differences were found in the relative abundance of larval fish collected in the Niobrara River between sample sites and years for all taxa tested (Table 8; Figures 3-7). Relative abundance was higher ($P < 0.001$) in 2009 for total larval fish, red/sand shiners, common carp, flathead chubs, and *Lepomis* spp. compared to 2008. River carpsucker was the only taxa with higher abundances ($P < 0.001$) in 2008 compared to 2009. Relative abundance of total larval fish, red/sand shiners, flathead chubs, and river carpsuckers was highest at the Spencer Dam site compared to the mouth ($P \leq 0.011$). Only common carp ($P = 0.005$) and *Lepomis* spp. ($P = 0.003$) larval abundances were significantly higher at the mouth.

The first two Detrended Correspondence Analysis axes explained 53% (DCA1 = 32%, eigenvalue = 0.53 and DCA2 = 21%; eigenvalue = 0.34) of variance within the larval fish assemblage and both axes were retained for interpretation. Common carp and flathead chub loaded most positively with DCA1. Common carp and flathead chubs were more predominant in the fish community at the mouth site in 2009 compared to the mouth in 2008 ($t = -9.07$; $P < 0.001$) and to the Spencer Dam site in 2008 ($t = 8.45$; $P < 0.001$) and 2009 ($t = 5.06$; $P < 0.001$). Common carp and flathead chubs were also more predominant at the Spencer Dam site in 2009 compared to both sites in 2008 ($t = -6.15$ and -7.87 ; $P < 0.001$) (Figure 10). *Lepomis* spp., red/sand shiner, and river carpsucker had most positive scores on the DCA2 axis indicating the larval fish community differed significantly spatially and temporally (Figure 10). The larval fish community at the mouth site in 2008 significantly differed from the Spencer Dam site in 2008 ($t = 2.71$; $P = 0.007$) and 2009 ($t = 2.65$; $P = 0.008$), but not to the mouth site in 2009 (DCA2; $t = 1.04$; $P = 0.299$). No significant differences in the larval fish community were found between years at the Spencer Dam site ($t = 0.26$; $P = 0.792$).

Pearson correlations between DCA1 and both principle components were negative and significant (PC1; $r = -0.28$; $P < 0.001$; PC2; $r = -0.17$; $P < 0.001$). Therefore, abundance of larval common carp and flathead chubs was associated with low mean daily water temperatures, cumulative degree days, conductivity, turbidity, and water velocity and higher dissolved oxygen (Figure 11a). The correlations between DCA2 and both principal component axes were positive; but, only was significant for PCA1 ($r = 0.38$; $P < 0.001$) and not PCA2 ($r = 0.05$; $P = 0.196$). Therefore, DCA2 axis explained that abundances of larval *Lepomis* spp., red/sand shiners, and river carpsucker were associated with higher mean daily water temperatures, cumulative degree days, and conductivity (Figure 11b). Variability in the abundances of *Lepomis* spp., red/sand shiners, and river carpsucker lacked an association with turbidity and water velocity.

Results of the CCA retained all environmental variables ($P \leq 0.050$) except turbidity ($P = 0.066$). The first two axes explained 94% (CCA1 = 75%, eigenvalue = 0.23 and CCA2 = 19%, eigenvalue = 0.05) of the species-environment relations contained in the data. Julian date, cumulative degree days, and mean daily temperature loaded negatively and mean daily discharge loaded positively along the first axis (Figure 12). Conductivity and water velocity loaded positively and dissolved oxygen loaded negatively on the second axis (Figure 12). A strong positive relationship was found between the abundances of larval flathead chubs and common carp with dissolved oxygen and both were generally found earlier in the sampling year as abundance was also negatively related to water temperatures, cumulative degree days, and Julian date. Larval river carpsucker were also found earlier in the sampling year with a strong positive association with high water discharge and water velocity but abundance was negatively related to higher cumulative degree days and Julian date. Larval *Lepomis* spp. were associated with high conductivity and mean daily temperatures and negatively to dissolved oxygen. Larval red/sand

shiners were found later in the sampling season; they were positively associated with a late Julian date and high cumulative degree days but negatively to high discharge (Figure 12).

Discussion

Most fish collected during this study were in the yolk-sac larval stage. Therefore, larvae in this study were collected shortly after being produced and habitat conditions measured were close to those needed for successful spawning. Additionally, successful spawning conditions throughout the study area and upstream of Spencer Dam was evident as yolk-sac fry were ubiquitous and supported by the lack of differences in length frequency distributions between sample sites. Additionally, variation in larval fish lengths between sample sites and years was likely low since habitat quality and food availability were likely similar. Some caution should be used when interpreting the length data during this study as it has been well documented that larval fish preserved in formalin and to a greater extent in alcohol undergo considerable shrinkage from its original live length (Fowler and Smith 1983; Leslie and Moore 1986; Jennings 1991; Fisher et al 1998; Paradis et al. 2007). Additionally, differences in the amount of shrinkage from preservation techniques have been found to vary among fish species (Jennings 1991). However, all larval fish in this study were preserved in a consistent manner; therefore, length data analyses in this study would not be affected by shrinkage.

During this study we attempted to identify and separate red shiner and sand shiner larvae because of the dominance of these two species in the Niobrara River fish assemblage (Wanner et al. 2009). Reliably distinguishing between cyprinid species at the larval stage is generally difficult due to the high number of species, high morphological similarity, and lack of comparative literature (Fuiman et al 1983). This was the case for red shiners and sand shiners as

both species have preanal myomere counts that commonly range from 21 to 23. “State-of-the-art” methods to separate the two species characterized the sand shiner as having a flattened eye and red shiners having an outlined gut (Fuiman et al. 1983). However, fixation of larval fish in formalin and storage in alcohol made the eye appear flattened for most larval specimens. Red shiners and sand shiners are “pioneer” species that occur in harsh environmental conditions where most other species can not persist (Pflieger 1997). Red shiners have been reported to spawn at water temperatures of 15.6 - 29.4 °C in Kansas, Oklahoma, and Texas (Cross 1967; Farringer et al. 1979) and as high as 34 °C (Gale 1986) and sand shiners at 21 - 37 °C in Kansas (Summerfelt and Minckley 1969). Both species peak in spawning activity that coincided with maximal thermal temperatures and minimal discharge. Because of the almost complete overlap of spawning conditions for red shiners and sand shiners, the timing and abundance of larvae of these two species in the drift likely had high overlap and further limited our ability to distinguish between the two species.

The results from our study showed that water temperature was a major factor influencing the timing and abundance of larval fish in the Niobrara River. Larval red/sand shiners and *Lepomis* spp. abundance was highly correlated with water temperature and these species were first found when daily average water temperatures approached 25 °C and peak abundances occurred after 27 °C. Stable flows during the high temperature period may have also supported these high abundances of shiners and centrarchids (Summerfelt and Minckley 1969). River carpsucker, common carp, and flathead chub abundance was correlated with lower water temperatures and high dissolved oxygen in the Niobrara River compared to the other fish species. During late May and early June when average daily temperatures approached 18 °C, these species began to appear and abundances declined sharply when average daily temperatures

reached 25 °C. Common carp fry appeared in the drift after the descending limb of the hydrograph. Common carp are likely taking advantage of the flooded vegetation during high water events, successfully spawn, and fry enter the drift when water began to recede. River carpsuckers in the Niobrara River appeared to be associated with river discharge with bimodal peaks in relative abundance following large changes in discharge. Bednarski et al. (2008) reported that native catostomids (river carpsucker, shorthead redhorse *Moxostoma macrolepidotum*, and *Ictiobus* spp.) in the Milk River, a large tributary to the Missouri River in Montana, had a protracted spawning period with bimodal peaks in larval abundance compared to most other fish species. Native fish in the Northern Great Plains are adapted to a predictable spring rise from snowmelt that likely triggers these fish to begin migrations in preparation to spawn and then initiate spawning during later high discharge events from rainfall (Galat et al. 2005). Bednarski et al. (2008) reported that higher abundances of native catostomids were found when the timing of high discharge events coincided with warmer water (mean water temperature = 20.3 and 21.7 °C), which coincided with temperatures and high abundances of larval river carpsuckers observed during this study. For many riverine fishes, successful spawning is associated with a combination of abiotic factors including discharge (Hynes 1970; Robinson et al. 1998; Mathews 1998; Koel and Sparks 2002; Bednarski 2008), turbidity (Faushch and Bestgen 1997), temperature (Wolf et al. 1996; Wolter 2007), photoperiod (Bye 1989), pH (Baumgartner et al. 2008), conductivity (Baumgartner et al. 2008), and dissolved oxygen (Schiemer et al. 2002).

Our results support Pavlov (1994) and Reeves and Galat (2010) hypothesis that turbid rivers generally lack a diel cycle of larval drift. In the Niobrara River, differences in larval abundances were lacking between morning and afternoon sampling periods at both of our sample

sites each year. However, no samples were taken during the night period during this study, when larval fish drift may have been significantly different. Larval fish abundance in drift has been shown to vary between diel periods in the Upper Colorado River, Colorado (Carter et al. 1986), tropical rivers in Peru (Pavlov et al. 1995), River Sieg, Germany (Bischoff and Scholten 1996) Putta Creek, California (Marchetti and Moyle 2000) Elbe River, Germany (Oesmann 2003), and Missouri River, Missouri (Reeves and Galat 2010). Explanations for variation in diel drift include avoiding predation, searching for feeding or nursery habitats, or disorientation after dark and being swept into high current due to high discharge following storm events (Brown and Armstrong 1985; Pavlov 1994; Pavlov et al. 1995). The lower Niobrara River has naturally high turbidity and carries a daily sediment load >300 metric tons (Hotchkiss et al. 1993). The mouth site consistently had turbidity values > 62 NTU and the Spencer Dam site was \geq 25 NTU. Turbidities around 25 NTU are considered by Pavlov (1994), Pavlov et al. (1995), and Reeves and Galat (2010) high (secchi depth < 30 cm) and were attributed to the lack of a diel cycle for larval fish drift in rivers in Peru and the Missouri River.

Relative abundance of larval fish was higher downstream of Spencer Dam compared to the mouth. The mouth site had warmer water temperatures, higher water velocity, and increased turbidity compared to the Spencer Dam site; however, differences in larval fish abundance between sampling sites were likely attributed to the adult relative abundances of each species. Adult sand shiners, red shiners, and river carpsuckers are more abundant just upstream of Spencer Dam while adult centrarchids (green sunfish and largemouth bass) are more abundant immediately upstream of the mouth (Wanner et al. 2009; Wanner, unpublished data).

Relative abundance of larval fish was higher in 2009 compared to 2008. Major differences were found between water years as 2009 had significantly higher water conductivity,

temperature, cumulative degree days, water velocity, and turbidity and lower dissolved oxygen compared to 2008. Compared to 2008, mean daily discharge was higher from April to August with the exception of May during 2009. The consistently higher discharge in 2009 inundated more habitats that may have led to increased spawning success and larval fish survival. No major flood events occurred during the study in 2009, while there was a major flood event in early June 2008 that could have contributed to the higher abundance of river carpsucker that year. However, the flood event could have also rapidly flushed fry from the Niobrara River depressing larval densities. Following the flood in 2008, common carp production was low, while production was high over a two month period in 2009. In 2009 the average water temperature warmed earlier resulting in higher cumulative degree days throughout the study, which may have contributed to increased abundances of cyprinids and centrarchids compared to 2008. Increased water temperatures may have also increased the densities of zooplankton and macroinvertebrates and therefore increased prey for larval fish and increased survival.

Larval fish catches in the lower Niobrara River generally reflected the fish community present in that reach (Wanner et al. 2009; Wanner, unpublished data). Shiners (red and sand), river carpsucker, and centrarchids were the most abundant larval fish collected which is similar to the juvenile and adult fish community surveyed there with electrofishing gear. Major differences between larval and adult fish catches were the general lack of channel catfish and the absence of gizzard shad *Dorosoma cepedianum* larvae compared to the adult fish community present (Wanner et al. 2009). Channel catfish young-of-the-year (YOY) were sampled with electrofishing gear in high numbers in both 2008 and 2009 with YOY gizzard shad the predominant species caught in 2008 (Wanner et al. 2009) but rare in 2009 (Wanner, unpublished data). Channel catfish were one of the most abundant fish captured by trawls and seines in the

Platte River, Nebraska; however, few larval channel catfish were collected in their drift nets (Peters and Parham 2008). Post-hatch channel catfish likely have low drift rates, potentially being entrained in near shore eddies with low water velocity. Additionally, larval channel catfish may transition to a benthic behavior early post-hatch (within two weeks) to initiate exogenous feeding as seen in other benthic fish (Braaten et al. 2008). Larval gizzard shad have been reported in high abundances in the Missouri River immediately downstream of the Niobrara River confluence with a few ($n = 2$) collected in the Niobrara River near the mouth (Graeb 2006; Wuellner et al. 2008). Sporadic gizzard shad recruitment was evident in those Missouri River studies. Most gizzard shad likely spawned in the Missouri River and used the Niobrara River as a nursery and foraging area based on high YOY catches in 2008 (Wanner et al. 2009). Gizzard shad larval recruitment was evidently low in 2009 (Wanner, unpublished data). Sauger larvae were the first larval fish collected during sampling, but numbers were few. Our sampling likely occurred too late to capture sauger larvae. In the Missouri River immediately downstream of the Niobrara River confluence, sauger spawn in April (Nelson 1968; Graeb 2006; Graeb et al. 2009).

Fish assemblages in the lower Niobrara River are similar to those in the Platte River that crosses central Nebraska and enters the Missouri River near Plattsmouth, Nebraska (Hoagstrom and Berry 2006). The habitats and geomorphology of the lower Niobrara River are very similar to those of the lower Platte River. Both rivers are characterized as having a wide channel, shifting sandbars, discharge highly influenced by ground water, steep gradient, and monthly average temperatures of 0 °C in January and 25 °C in July (Peters et al. 1989; Alexander et al. 2009). From 1998 to 2004, the Platte River was sampled for larval fish that used drift nets with identical dimensions used in this study but with a larger 600 μm mesh (Peters and Parham 2008). The amount of water sampled per year in their study (22,303 to 29,156 m^3) was similar to this

study (22,509 and 25,146 m³). Overall, the proportions of various fish species were quite similar between studies especially for cyprinids (Platte River 63% to 90%; Niobrara River 58% to 83%), catostomids (Platte River 2% to 33%; Niobrara River 8% to 36%), and ictalurids (< 1% in both rivers). Major differences in larval catches between the rivers were the high proportion of centrarchids (3% to 7%) in the Niobrara River compared to the Platte River (1%), while the Platte River had a high proportion of gizzard shad (8%) and freshwater drum *Aplodinotus grunniens* (8%) (Peters and Parham 2008). The Niobrara River enters an inter-reservoir reach of the Missouri River that has a high abundance of centrarchids (Berry et al. 2004; Shuman et al. 2010), which may have contributed to their high abundance found in this study. However, larval gizzard shad and freshwater drum have been collected in the Missouri River just downstream of the Niobrara River confluence (Graeb 2006; Hesse 2008; Wuellner 2008). Additionally, 22% of the larval fish collected in the Platte River were *Macrhybopsis* spp. The Platte River has a high density of shoal chubs *Macrhybopsis hyostoma* with fewer silver chubs *Macrhybopsis storeriana* and sturgeon chubs *Macrhybopsis gelida* (Peters and Parham 2008), while the dominant chub species in the Niobrara River was the flathead chub with only a few silver chubs (Wanner et al. 2009). Most *Macrhybopsis* spp. have been extirpated from the Niobrara River (Schainost 2008) and none have been captured in the adjoining Missouri River from 2003 to 2009 (Shuman et al. 2010). Fourteen *Scaphirhynchus* spp. larvae were collected in the Platte River from 1998 to 2004 while none were collected in the Niobrara River. Although juvenile pallid sturgeon and adult shovelnose sturgeon have been collected in the Niobrara River (Wanner et al. 2010), these species are either not spawning in the Niobrara River or larval densities are at undetectable levels.

The successful spawning of native fish in the Niobrara River likely contributes to the recruitment of fish in the Missouri River. Absolute numbers of larval fish drifting into the Missouri River could not be calculated during this study due to the variable discharge across the highly braided mouth of the Niobrara River. The Niobrara River at the mouth site had substantial variation in widths (180 to 200 m) and depths (0.1 to 2.0 m) during larval fish sampling; however, we sampled a relatively small proportion (drift net opening was 1.0 wide and 0.5 m high) of the volume that entered the Missouri River. The contribution of native fish such as red shiners, sand shiners, river carpsucker, *Lepomis* spp., common carp, and channel catfish is likely substantial given the small cross section sampled in this study. All these species have been found in high abundances in the Missouri River (Shuman et al. 2010). Muth and Schmulbach (1984) conservatively estimated that 10 million larval fish entered the Missouri River at the mouth of the James River (first major tributary downstream of Gavins Point Dam) during from late June to early July 1978. Larval fish contributions from the Niobrara River are likely similar. However, recruitment of flathead chubs, that were spawned in the Niobrara River, to the Missouri River must be limited since no adult flathead chubs have been collected in that river from 2003 to 2009 using multiple sampling gears (Shuman et al. 2010). However, a few adult flathead chubs have been collected in the delta area found downstream of the Niobrara River confluence at the headwaters of Lewis and Clark Lake (Kaemingk et al. 2007). Flathead chubs may be more vulnerable to predation due to the dense populations of sauger, walleye, and smallmouth bass *Micropterus dolomieu* in the less turbid Missouri River.

The results of our study showed that abiotic factors such as water temperature, discharge, dissolved oxygen, turbidity, and conductivity were important in the initiation and duration of spawning for various fish species in the Niobrara River. The timing, occurrence, and abundance

of the larval fish collected in the Niobrara River corresponded with documented life history traits of these fish (Pflieger 1997). The fish species present in the Niobrara River are adapted to the naturally harsh conditions of high variability in discharge, high turbidity and sediment load, and water temperatures ranging from 0 to 35 °C. Currently, the Niobrara River retains a natural hydrograph and temperature regime and provides important seasonal habitats for the successful spawning of native fishes. 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. Adequate amounts of high quality water at natural discharges are needed for all life stages of native fish. Reduced flows would likely jeopardize native fish populations and eliminate some productivity of fish in the Niobrara River.

Acknowledgments

We thank Nebraska Public Power District (NPPD), National Park Service (NPS), U.S. Fish and Wildlife Service (USFWS) Region 6 - Water Resources Division, USFWS Region 6 - Aquatic Nuisance Species Coordinator, Nebraska Game and Parks Commission for funding this study. Missouri Department of Conservation and U.S. Army Corps of Engineers provided data entry and compilation. We also thank field technicians from the USFWS - Great Plains Fish and Wildlife Conservation Office and NPPD. We thank Mark Pegg for reviewing an earlier version of this manuscript.

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Table 1. Larval fish sampling effort including total number of subsamples, time (seconds), and volume of water filtered (m³) during each diel period and sample period at the mouth and downstream of Spencer Dam in the Niobrara River during 2008 and 2009.

Sampling dates	Mouth						Spencer Dam					
	Morning			Afternoon			Morning			Afternoon		
	Samples	Time	Volume	Samples	Time	Volume	Samples	Time	Volume	Samples	Time	Volume
2008												
23-24 April	10	720	196	10	600	151	3	900	260	17	5,100	985
5-8 May	21	2,520	534	28	3,480	550	16	3,780	1,284	32	8,700	2,765
12-13 May	10	600	185	10	600	187	10	3,000	866	10	3,000	784
19-22 May	18	1,140	229	0	0	0	19	5,700	1,232	10	3,660	833
3-5 June	8	480	181	10	600	223	8	1,860	281	8	1,440	228
9-10 June	10	600	381	10	600	331	8	600	366	8	600	378
23-27 June	16	960	609	8	480	158	18	5,400	1,024	10	3,000	553
30 June - 1 July	8	480	162	8	480	56	8	2,400	322	8	2,400	344
7-8 July	8	480	141	8	540	166	8	2,400	349	8	2,400	361
14-16 July	8	480	123	8	480	134	8	2,400	271	8	2,400	251
21-22 July	8	480	67	8	480	142	8	2,400	480	8	2,400	377
28-29 July	8	480	129	8	480	230	8	2,460	95	7	2,160	170
5-6 August	8	1,320	419	8	1,440	337	8	2,400	103	8	2,400	103
12-13 August	8	480	200	8	480	101	8	2,400	227	7	2,100	316
18-20 August	8	480	153	8	480	134	8	2,400	164	8	2,400	133
Total	157	11,700	3,707	140	11,220	2,900	146	40,500	7,322	157	44,160	8,580
2009												
5-6 May	5	180	98	6	360	163	8	2,340	720	7	2,100	662
12-13 May	8	480	178	8	480	143	8	2,400	592	8	2,400	436
20-21 May	8	480	169	8	480	135	7	2,100	214	8	2,400	201
27-28 May	8	480	151	8	480	157	8	2,400	415	8	2,400	533
2-3 June	8	480	172	8	480	160	7	2,100	346	8	2,400	212
8-9 June	8	480	154	8	480	164	8	4,800	751	8	4,800	728
16-17 June	8	480	129	8	480	135	8	4,800	1,244	7	4,200	746
22-23 June	6	360	111	7	420	126	6	3,600	892	8	4,800	536
29-30 June	8	480	90	8	480	109	8	4,800	619	6	3,600	600
7-8 July	8	480	52	8	480	56	8	4,800	978	8	4,800	850
14-15 July	7	420	65	8	480	84	8	2,400	678	6	3,600	692
20-21 July	8	480	112	8	480	127	6	3,600	504	6	3,600	740
27-28 July	8	480	48	8	480	54	6	3,600	1,180	6	3,600	890
3-4 August	8	480	171	8	480	62	5	3,000	865	6	3,600	956
10-11 August	8	480	86	8	480	26	6	3,600	808	6	3,600	948
17-18 August	8	420	124	8	480	127	5	3,000	616	4	2,400	258
Total	121	7,140	1,907	125	7,500	1,829	112	53,340	11,424	110	54,300	9,986

Table 2. Mean values and standard error in parentheses of environmental variables measured at the mouth and downstream of Spencer Dam in the Niobrara River during 2008 and 2009.

Sampling dates	Mouth					Spencer Dam				
	Temperature (°C)	Turbidity (NTU)	Conductivity (µS/cm)	DO (mg/L)	Velocity (m/s)	Temperature (°C)	Turbidity (NTU)	Conductivity (µS/cm)	DO (mg/L)	Velocity (m/s)
2008										
23-24 April	14.1 (0.0)	120.6 (1.7)			0.53 (0.02)	12.8 (0.3)	58.1 (1.3)			0.41 (0.03)
5-8 May	15.7 (0.2)	138.8 (3.3)	257.7 (1.3)	9.3 (0.0)	0.45 (0.03)	15.3 (0.3)	68.0 (2.4)	242.0 (3.8)	10.0 (0.1)	0.65 (0.01)
12-13 May	15.1 (0.1)	108.0 (0.0)	256.5 (2.0)	8.8 (0.0)	0.62 (0.02)	14.2 (0.7)	51.3 (1.0)	228.5 (3.9)	9.9 (0.1)	0.55 (0.01)
19-22 May	15.0 (0.1)	77.3 (1.2)	232.1 (6.9)	8.9 (0.1)	0.41 (0.03)	17.1 (0.1)	27.7 (1.0)	233.2 (0.5)	9.3 (0.1)	0.44 (0.01)
3-5 June	22.1 (0.4)	181.7 (10.4)	290.7 (5.1)	7.9 (0.0)	0.75 (0.03)	22.6 (0.6)	88.5 (3.1)	258.9 (3.7)	8.1 (0.2)	0.31 (0.01)
9-10 June	22.2 (0.5)	598.0 (29.9)	326.6 (6.4)	7.7 (0.1)	1.19 (0.04)	20.4 (0.7)	469.1 (17.0)	289.1 (2.8)	8.4 (0.1)	1.27 (0.03)
23-27 June		112.2 (5.7)			1.07 (0.07)	20.3 (0.1)	60.0 (1.9)	247.6 (0.4)	8.4 (0.1)	0.38 (0.01)
30 June - 1 July	24.8 (0.7)	93.9 (5.1)	311.5 (5.7)	8.9 (0.1)	0.45 (0.06)	25.1 (0.6)	48.6 (1.8)	282.5 (5.0)	7.6 (0.1)	0.28 (0.01)
7-8 July	27.0 (0.7)	85.9 (1.6)	315.9 (3.7)	8.1 (0.6)	0.62 (0.04)	26.7 (0.7)	45.6 (1.7)	273.9 (3.9)	7.2 (0.1)	0.30 (0.01)
14-16 July		80.6 (2.7)			0.54 (0.02)	26.0 (0.4)	36.6 (0.7)	265.9 (1.3)	7.1 (0.1)	0.22 (0.01)
21-22 July		102.1 (4.6)			0.44 (0.04)		71.6 (5.1)			0.36 (0.02)
28-29 July		78.8 (3.1)			0.75 (0.06)		39.0 (1.9)			0.11 (0.01)
5-6 August		62.9 (2.9)			0.60 (0.08)		38.4 (2.9)			0.09 (0.01)
12-13 August		138.1 (7.7)			0.63 (0.12)		64.5 (7.2)			0.24 (0.02)
18-20 August	24.1 (0.7)	83.1 (1.9)	243.0 (4.0)	8.5 (0.2)	0.60 (0.02)	25.7 (0.6)	49.5 (2.0)	250.8 (1.9)	8.8 (0.1)	0.12 (0.01)
2009										
5-6 May	18.5 (0.9)	98.2 (3.3)	260.6 (11.9)	9.1 (0.1)	1.01 (0.08)	18.2 (0.6)	47.3 (1.2)	250.4 (3.3)	9.0 (0.1)	0.62 (0.01)
12-13 May	17.6 (0.1)	86.0 (6.5)	257.0 (4.0)	9.4 (0.0)	0.67 (0.02)	17.1 (0.2)	38.1 (1.1)	243.2 (1.7)	9.5 (0.0)	0.43 (0.02)
20-21 May		73.3 (7.0)			0.63 (0.02)		25.8 (1.2)			0.18 (0.01)
27-28 May	15.8 (0.2)	118.7 (4.3)	247.3 (3.3)	9.5 (0.0)	0.64 (0.03)	16.6 (0.6)	91.7 (4.0)	248.5 (4.3)	9.6 (0.1)	0.39 (0.01)
2-3 June	18.3 (1.2)	62.3 (2.1)	250.0 (6.3)	9.7 (0.2)	0.69 (0.03)	17.8 (1.1)	28.5 (1.2)	231.5 (5.1)	10.1 (0.1)	0.25 (0.02)
8-9 June	15.9 (0.7)	77.2 (3.1)	209.9 (23.7)	9.0 (0.0)	0.66 (0.01)	15.9 (0.4)	36.5 (1.1)	214.8 (1.2)	9.7 (0.0)	0.31 (0.02)
16-17 June		113.0 (4.8)	284.0 (7.2)	7.6 (0.1)	0.55 (0.02)		97.0 (13.0)	264.8 (6.1)	8.3 (0.1)	0.44 (0.03)
22-23 June					0.61 (0.02)					0.34 (0.06)
29-30 June	26.7 (1.3)	125.0 (3.8)	297.8 (6.9)	7.7 (0.1)	0.41 (0.01)	25.1 (1.2)	59.0 (4.0)	272.2 (6.7)	8.6 (0.1)	0.29 (0.03)
7-8 July	26.8 (1.3)	103.2 (2.4)	274.0 (6.4)	7.5 (0.1)	0.22 (0.01)	26.6 (1.4)	83.7 (1.9)	263.3 (6.9)	8.4 (0.0)	0.38 (0.02)
14-15 July	25.7 (0.7)	148.3 (14.4)	276.2 (4.3)	8.0 (0.3)	0.33 (0.04)	24.9 (1.2)	350.8 (31.9)	249.0 (4.9)	8.5 (0.1)	0.49 (0.05)
20-21 July	22.1 (0.5)	122.7 (1.7)	276.7 (1.5)	8.2 (0.1)	0.50 (0.01)	24.0 (0.9)	105.0 (11.8)	269.3 (6.4)	8.9 (0.1)	0.35 (0.03)
27-28 July	25.9 (1.3)	67.0 (1.7)	292.8 (6.2)	8.3 (0.1)	0.21 (0.03)	25.0 (1.1)	44.2 (2.1)	266.0 (5.7)	8.7 (0.1)	0.58 (0.05)
3-4 August	26.6 (1.4)	70.7 (2.5)	258.2 (6.2)	9.5 (0.1)	0.49 (0.06)	25.6 (1.2)	37.0 (0.0)	260.8 (6.0)	8.8 (0.2)	0.55 (0.05)
10-11 August	25.6 (1.2)	88.0 (1.8)	276.5 (7.4)	8.2 (0.2)	0.23 (0.03)	25.6 (1.1)	53.7 (5.5)	266.0 (4.8)	8.7 (0.1)	0.49 (0.02)
17-18 August	24.9 (1.2)	121.0 (4.8)	255.0 (6.1)	9.3 (0.2)	0.56 (0.06)	23.3 (1.8)	88.0 (2.0)	238.0 (6.9)	8.9 (0.1)	0.32 (0.05)

Table 3. Results of the Principal Component Analysis (PCA) for the axes retained for interpretation. Eigen vectors (correlations) for each abiotic factor (values > 0.4 are in bold) were considered biologically significant (Hair et al. 1984).

Variables	PC1	PC2
Turbidity	0.17	0.62
Conductivity	0.41	0.34
Dissolved oxygen	-0.49	0.04
Mean daily temperature	0.54	-0.17
Cumulative degree days	0.51	-0.22
Water velocity	-0.04	0.64
Eigenvalues (λ)	2.88	1.72
% of explanation	47.96	28.70

Table 4. Total catch and monthly mean catch per unit effort (CPUE; number of larval fish/100 m³ of water filtered) and standard error in parentheses of larval fish collected at the mouth of the Niobrara River from April to August 2008 and May to August 2009.

Taxon	2008						2009				
	Total catch	April	May	June	July	August	Total catch	May	June	July	August
Total larval fish	720	0	1.707 (0.612)	16.450 (2.305)	26.831 (2.688)	6.138 (1.933)	397	4.243 (0.813)	16.849 (1.547)	24.753 (3.340)	0.582 (0.292)
Shortnose gar <i>Lepisosteus platostomus</i>	0	0	0	0	0	0	3	0.187 (0.131)	0.071 (0.071)	0	0
Red shiner /sand shiner <i>Cyprinella lutrensis</i> / <i>Notropis stramineus</i>	276	0	0	1.973 (0.635)	16.530 (1.908)	4.515 (1.668)	196	0.702 (0.316)	7.718 (1.019)	16.064 (2.711)	0.388 (0.226)
Flathead chub <i>Platygobio gracilis</i>	2	0	0	0	0.089 (0.089)	0.117 (0.117)	9	0.101 (0.101)	0.558 (0.211)	0	0
Common carp <i>Cyprinus carpio</i>	5	0	0.241 (0.241)	0.292 (0.213)	0	0	61	1.826 (0.404)	2.596 (0.533)	0.103 (0.103)	0
Unknown cyprinid	0	0	0	0	0	0	1	0	0.062 (0.062)	0	0
River carpsucker <i>Carpiodes carpio</i>	352	0	1.296 (0.561)	12.948 (1.963)	6.143 (1.395)	0.803 (0.614)	39	0.293 (0.166)	1.681 (0.390)	2.288 (0.705)	0
Shorthead redhorse <i>Moxostoma macrolepidotum</i>	1	0	0	0.065 (0.065)	0	0	2	0	0.156 (0.110)	0	0
Channel catfish <i>Ictalurus punctatus</i>	5	0	0	0.080 (0.056)	0.118 (0.086)	0.091 (0.091)	8	0	0.436 (0.216)	0.273 (0.205)	0
Grass pickerel <i>Esox americanus vermiculatus</i>	0	0	0	0	0	0	1	0.074 (0.074)	0	0	0
<i>Lepomis</i> spp.	37	0	0	0.486 (0.412)	1.950 (0.457)	0.521 (0.259)	50	0.483 (0.330)	2.197 (0.657)	4.688 (1.632)	0.194 (0.194)
Largemouth bass <i>Micropterus salmoides</i>	2	0	0	0.078 (0.078)	0.074 (0.074)	0	4	0	0.314 (0.188)	0	0
<i>Pomoxis</i> spp.	3	0	0.105 (0.105)	0	0.241 (0.177)	0	9	0.254 (0.184)	0.502 (0.255)	0	0
Unknown centrarchid	9	0	0	0.119 (0.068)	0.398 (0.226)	0.091 (0.064)	9	0.173 (0.122)	0.323 (0.164)	1.337 (0.991)	0
Sauger <i>Sander canadense</i>	0	0	0	0	0	0	1	0.077 (0.077)	0	0	0
Unidentified larval fish	28	0	0.065 (0.065)	0.409 (0.263)	1.287 (0.425)	0	4	0.074 (0.074)	0.234 (0.142)	0	0
Fish eggs	210	0	0.474 (0.292)	6.976 (0.899)	6.059 (1.448)	0.091 (0.091)	218	5.749 (1.755)	11.475 (2.646)	3.478 (1.209)	0

Table 5. Total catch and monthly mean catch per unit effort (CPUE; number of larval fish/100 m³ of water filtered) and standard error in parentheses of larval fish collected downstream of Spencer Dam on the Niobrara River from April to August 2008 and May to August 2009.

Taxon	2008						2009				
	Total catch	April	May	June	July	August	Total catch	May	June	July	August
Total larval fish	1,797	0	0.112 (0.043)	27.100 (2.647)	23.005 (1.564)	39.241 (7.983)	3,668	3.221 (0.736)	29.186 (2.655)	31.484 (5.084)	4.924 (0.806)
Shortnose gar <i>Lepisosteus platostomus</i>	0	0	0	0	0	0	0	0	0	0	0
Red shiner /sand shiner <i>Cyprinella lutrensis</i> / <i>Notropis stramineus</i>	1,152	0	0	9.786 (1.510)	18.871 (1.444)	38.877 (7.985)	3,005	1.846 (0.527)	21.012 (2.382)	27.874 (4.828)	4.490 (0.767)
Flathead chub <i>Platygobio gracilis</i>	24	0	0.019 (0.019)	0.525 (0.122)	0.081 (0.057)	0	42	0.326 (0.117)	0.824 (0.299)	0.165 (0.068)	0
Common carp <i>Cyprinus carpio</i>	7	0	0.030 (0.021)	0.127 (0.076)	0.062 (0.044)	0	57	0.481 (0.144)	0.680 (0.174)	0.081 (0.049)	0.027 (0.027)
Unknown cyprinid	0	0	0	0	0	0	5	0	0.051 (0.027)	0.019 (0.019)	0
River carpsucker <i>Carpionodes carpio</i>	550	0	0.013 (0.013)	15.631 (1.840)	3.347 (0.525)	0	280	0.182 (0.088)	4.513 (0.754)	1.697 (0.274)	0.039 (0.027)
Shorthead redhorse <i>Moxostoma macrolepidotum</i>	1	0	0.012 (0.012)	0	0	0	2	0	0.018 (0.013)	0	0
Channel catfish <i>Ictalurus punctatus</i>	0	0	0	0	0	0	2	0	0	0.043 (0.033)	0
Grass pickerel <i>Esox americanus vermiculatus</i>	1	0	0	0	0.043 (0.043)	0	0	0	0	0	0
<i>Lepomis</i> spp.	18	0	0.015 (0.015)	0.259 (0.099)	0.189 (0.076)	0.097 (0.097)	118	0.031 (0.031)	1.048 (0.258)	0.714 (0.155)	0.233 (0.122)
Largemouth bass <i>Micropterus salmoides</i>	0	0	0	0	0	0	7	0	0.074 (0.031)	0.025 (0.025)	0
<i>Pomoxis</i> spp.	1	0	0.013 (0.013)	0	0	0	27	0.256 (0.090)	0.190 (0.072)	0.024 (0.024)	0.018 (0.018)
Unknown centrarchid	4	0	0	0.053 (0.053)	0.066 (0.047)	0.102 (0.102)	80	0.099 (0.059)	0.479 (0.130)	0.492 (0.150)	0.018 (0.018)
Sauger <i>Sander canadense</i>	1	0	0.010 (0.010)	0	0	0	0	0	0	0	0
Unidentified larval fish	38	0	0	0.719 (0.301)	0.348 (0.127)	0.165 (0.165)	43	0	0.298 (0.085)	0.350 (0.113)	0.109 (0.058)
Fish eggs	709	0	1.234 (0.244)	12.256 (1.349)	9.722 (1.000)	0.092 (0.065)	1,713	2.570 (0.599)	13.232 (1.848)	8.193 (1.439)	0.909 (0.277)

Table 6. Results of Kolmogorov-Smirnoff tests comparing length frequency distributions of the five most abundant larval fish taxa collected between sampling sites and years in the Niobrara River. *Significant results ($P \leq 0.008$) after Bonferroni corrections.

Source	<i>D</i>	<i>P</i>
Red/sand shiner		
Mouth 2008 vs. Mouth 2009	0.14	0.021
Mouth 2008 vs. Spencer Dam 2008	0.20	<0.001*
Mouth 2008 vs. Spencer Dam 2009	0.16	<0.001*
Mouth 2009 vs. Spencer Dam 2008	0.34	<0.001*
Mouth 2009 vs. Spencer Dam 2009	0.10	0.079
Spencer Dam 2008 vs. Spencer Dam 2009	0.18	<0.001*
Common carp		
Mouth 2008 vs. Mouth 2009	0.40	0.346
Mouth 2008 vs. Spencer Dam 2008	0.37	0.737
Mouth 2008 vs. Spencer Dam 2009	0.40	0.366
Mouth 2009 vs. Spencer Dam 2008	0.28	0.604
Mouth 2009 vs. Spencer Dam 2009	0.23	0.103
Spencer Dam 2008 vs. Spencer Dam 2009	0.38	0.245
Flathead chub		
Mouth 2008 vs. Mouth 2009	1.00	0.200
Mouth 2008 vs. Spencer Dam 2008	0.55	0.957
Mouth 2008 vs. Spencer Dam 2009	0.68	0.667
Mouth 2009 vs. Spencer Dam 2008	0.45	0.105
Mouth 2009 vs. Spencer Dam 2009	0.32	0.360
Spencer Dam 2008 vs. Spencer Dam 2009	0.18	0.686
River carpsucker		
Mouth 2008 vs. Mouth 2009	0.28	0.007*
Mouth 2008 vs. Spencer Dam 2008	0.09	0.154
Mouth 2008 vs. Spencer Dam 2009	0.15	0.002*
Mouth 2009 vs. Spencer Dam 2008	0.33	0.001*
Mouth 2009 vs. Spencer Dam 2009	0.33	0.001*
Spencer Dam 2008 vs. Spencer Dam 2009	0.19	<0.001*
<i>Lepomis</i> spp.		
Mouth 2008 vs. Mouth 2009	0.21	0.348
Mouth 2008 vs. Spencer Dam 2008	0.31	0.179
Mouth 2008 vs. Spencer Dam 2009	0.29	0.026
Mouth 2009 vs. Spencer Dam 2008	0.18	0.763
Mouth 2009 vs. Spencer Dam 2009	0.21	0.098
Spencer Dam 2008 vs. Spencer Dam 2009	0.24	0.270

Table 7. Results of *t*-tests comparing catch per unit effort [$\log_{10}(\text{CPUE}+1)$] between diel periods (morning and afternoon) at each sampling site and year for Total CPUE and the most common larval taxa collected in the Niobrara River. *Significant results ($P \leq 0.008$) after Bonferroni corrections; $df = 1$ for all comparisons.

Taxa	Morning		Afternoon		<i>t</i>	<i>P</i>
	Mean CPUE	Transformed mean CPUE	Mean CPUE	Transformed mean CPUE		
2008 Mouth						
Total CPUE	13.066 (1.672)	0.633 (0.055)	10.536 (1.357)	0.606 (0.055)	-0.34	0.733
Red /sand shiner	5.248 (0.995)	0.319 (0.044)	5.150 (0.892)	0.365 (0.046)	0.72	0.469
Common carp	0.172 (0.136)	0.016 (0.010)	0.102 (0.102)	0.008 (0.008)	-0.59	0.558
Flathead chub	0.041 (0.041)	0.006 (0.006)	0.040 (0.040)	0.006 (0.006)	0.04	0.967
River carpsucker	6.031 (1.051)	0.337 (0.046)	3.951 (0.766)	0.293 (0.043)	-0.70	0.482
<i>Lepomis</i> spp.	0.676 (0.193)	0.083 (0.021)	0.667 (0.258)	0.067 (0.021)	-0.54	0.588
2008 Spencer Dam						
Total CPUE	19.945 (2.884)	0.866 (0.059)	15.410 (1.695)	0.727 (0.057)	-1.70	0.090
Red /sand shiner	15.231 (2.844)	0.683 (0.058)	10.247 (1.275)	0.575 (0.053)	-1.37	0.171
Common carp	0.072 (0.032)	0.017 (0.007)	0.035 (0.028)	0.007 (0.005)	-1.11	0.268
Flathead chub	0.229 (0.061)	0.050 (0.013)	0.063 (0.028)	0.015 (0.007)	-2.45	0.015
River carpsucker	3.799 (0.614)	0.338 (0.041)	4.759 (0.917)	0.300 (0.042)	-0.63	0.527
<i>Lepomis</i> spp.	0.115 (0.044)	0.025 (0.009)	0.129 (0.049)	0.027 (0.010)	0.14	0.888
2009 Mouth						
Total CPUE	11.574 (1.409)	0.724 (0.058)	13.873 (1.840)	0.753 (0.059)	0.35	0.730
Red /sand shiner	5.904 (1.061)	0.414 (0.052)	7.613 (1.352)	0.468 (0.055)	0.71	0.479
Common carp	1.375 (0.293)	0.169 (0.032)	1.182 (0.293)	0.134 (0.030)	-0.79	0.433
Flathead chub	0.249 (0.115)	0.034 (0.015)	0.151 (0.087)	0.021 (0.012)	-0.72	0.473
River carpsucker	0.916 (0.226)	0.117 (0.028)	1.440 (0.391)	0.133 (0.032)	0.38	0.703
<i>Lepomis</i> spp.	2.084 (0.516)	0.181 (0.037)	2.000 (0.814)	0.128 (0.034)	-1.05	0.292
2009 Spencer Dam						
Total CPUE	17.330 (2.613)	0.906 (0.056)	20.693 (2.366)	1.014 (0.058)	1.34	0.182
Red /sand shiner	13.192 (2.449)	0.745 (0.055)	16.734 (2.035)	0.927 (0.056)	2.31	0.022
Common carp	0.324 (0.076)	0.076 (0.017)	0.445 (0.127)	0.086 (0.020)	0.38	0.707
Flathead chub	0.254 (0.076)	0.055 (0.015)	0.560 (0.202)	0.087 (0.022)	1.17	0.242
River carpsucker	1.897 (0.455)	0.243 (0.033)	2.051 (0.359)	0.291 (0.035)	0.99	0.323
<i>Lepomis</i> spp.	0.734 (0.144)	0.146 (0.024)	0.391 (0.136)	0.071 (0.019)	-2.50	0.013

Table 8. Two-way analysis of variance (ANOVA) comparing relative abundance [$\log_{10}(\text{CPUE}+1)$] between sampling sites and years for the most common larval taxa collected in the Niobrara River in 2008 and 2009. Significant results ($P \leq 0.05$) denoted by asterisks.

Source	F	df	P
All larval fish			
Year	11.97	1	<0.001*
Sample site	23.00	1	<0.001*
Year x site	0.33	1	0.566
Red/sand shiner			
Year	16.88	1	<0.001*
Sample site	81.92	1	<0.001*
Year x site	2.08	1	0.149
Common carp			
Year	69.95	1	<0.001*
Sample site	8.28	1	0.004*
Year x site	7.83	1	0.005*
Flathead chub			
Year	12.58	1	<0.001*
Sample site	16.55	1	<0.001*
Year x site	1.03	1	0.311
River carpsucker			
Year	18.45	1	<0.001*
Sample site	6.52	1	0.011*
Year x site	6.13	1	0.013*
<i>Lepomis</i> spp.			
Year	25.08	1	<0.001*
Sample site	8.69	1	0.003*
Year x site	0.02	1	0.888

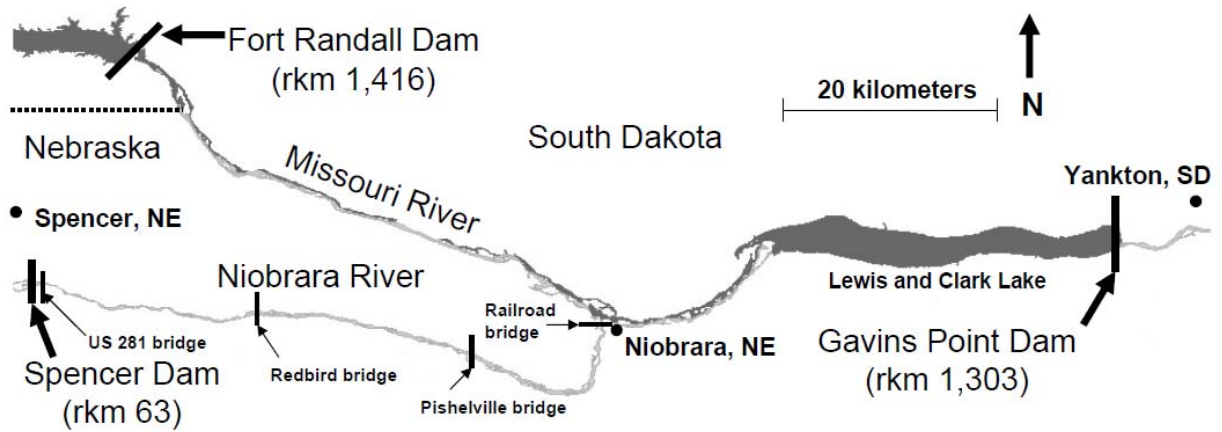


Figure 1. Niobrara River downstream of Spencer Dam, Nebraska and the Missouri River downstream of Fort Randall Dam to Gavins Point Dam, South Dakota and Nebraska. In 2008 and 2009, larval fishes were collected at the U.S. Highway 281 bridge downstream of Spencer Dam and at the railroad bridge near the mouth.

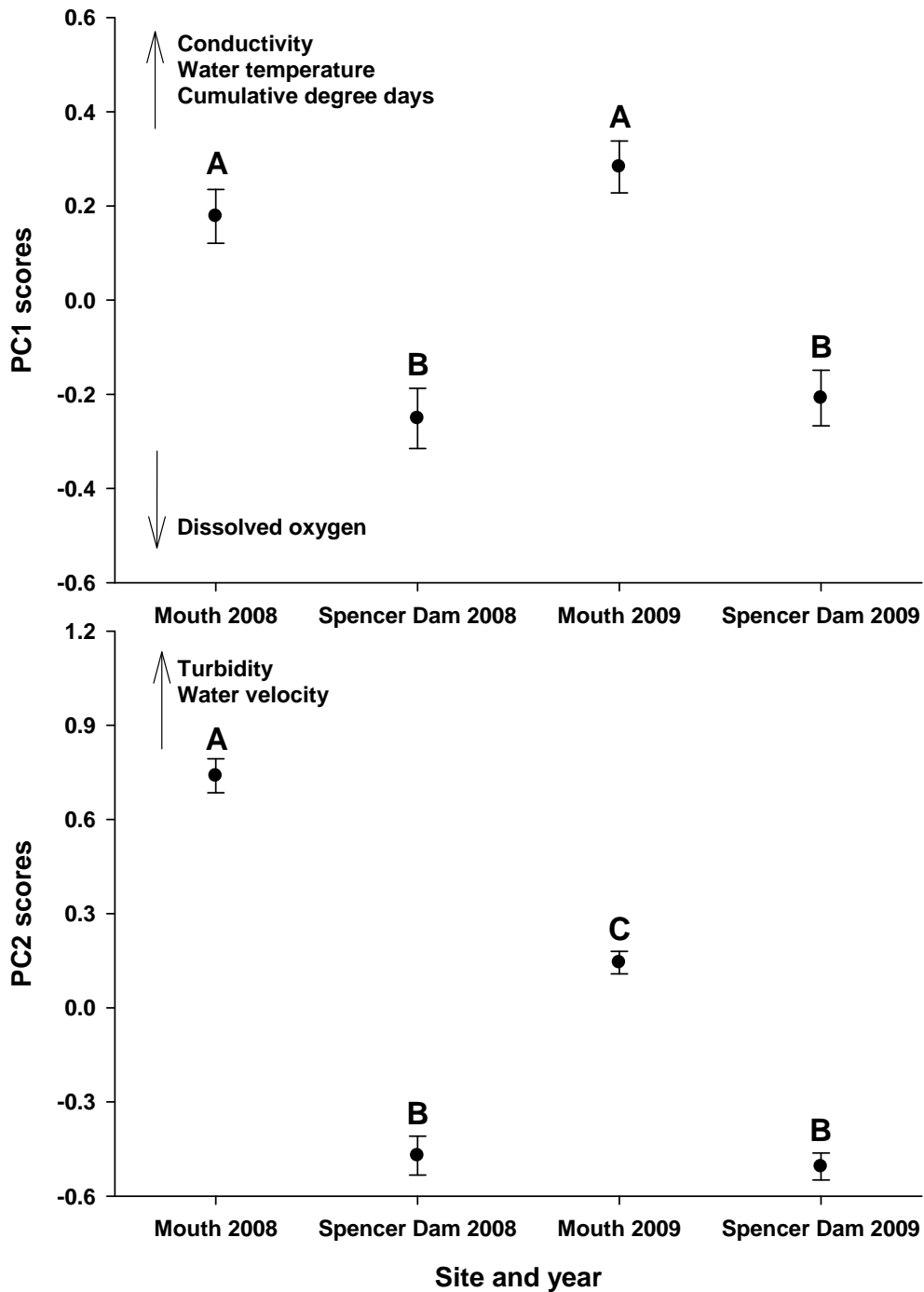


Figure 2. Mean principle component analysis (PCA) scores and standard error bars for Axis 1 (top) and Axis 2 (bottom) for each sampling site and year derived from the abiotic factors matrix. Two-sample *t*-tests were applied to the factor scores of the retained principal components to compare differences between sample sites each year. Sample sites that share a common letter were not significantly different at $\alpha = 0.008$ after Bonferroni corrections.

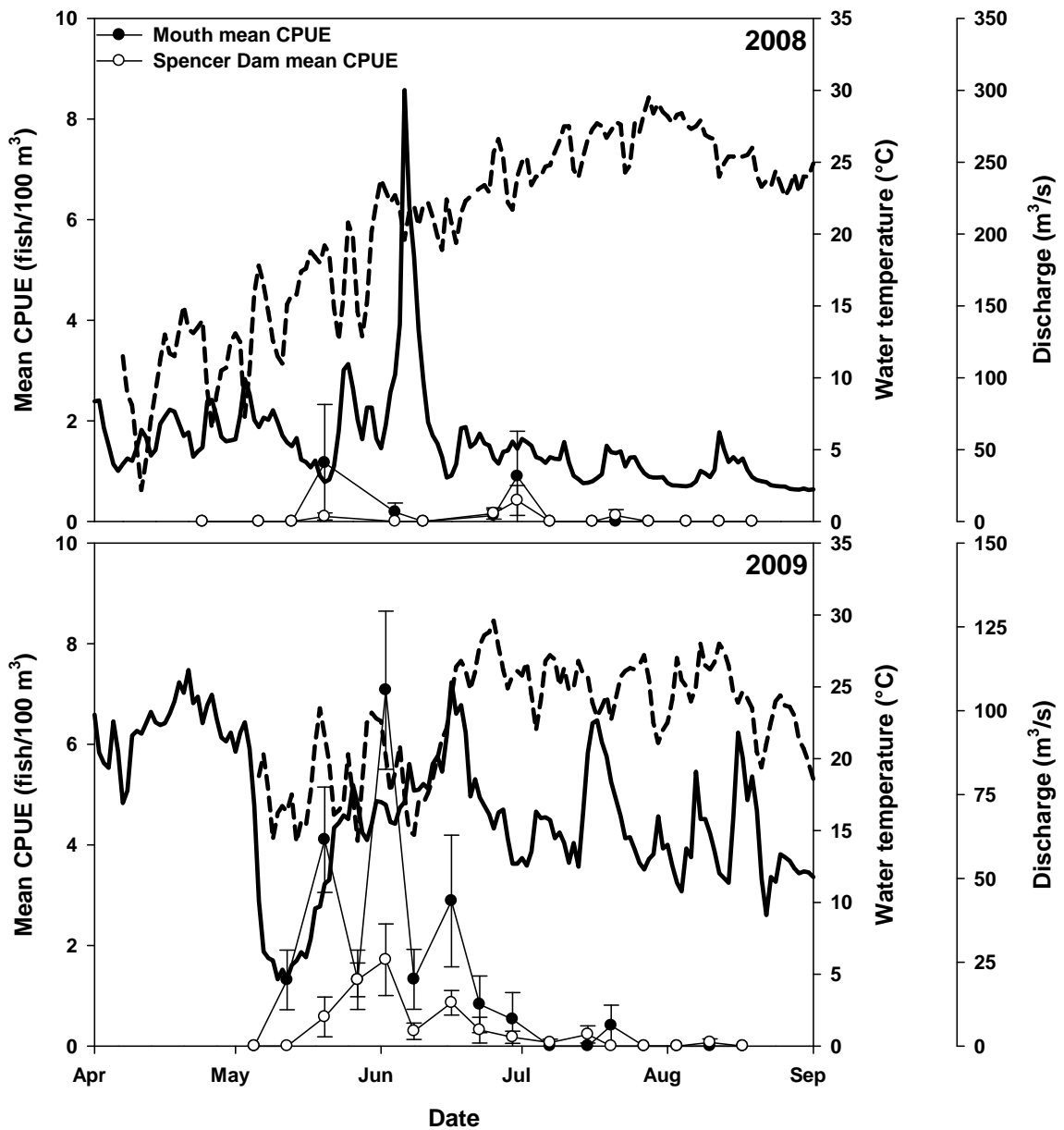


Figure 3. Relative abundance of common carp collected at two sites in the Niobrara River in 2008 and 2009 in relation to mean daily temperature (dashed line) and mean daily discharge (solid line) recorded at the Pischelville Bridge (http://waterdata.usgs.gov/usa/nwis/uv?site_no=06465500). Note that axes differ for discharge between 2008 and 2009.

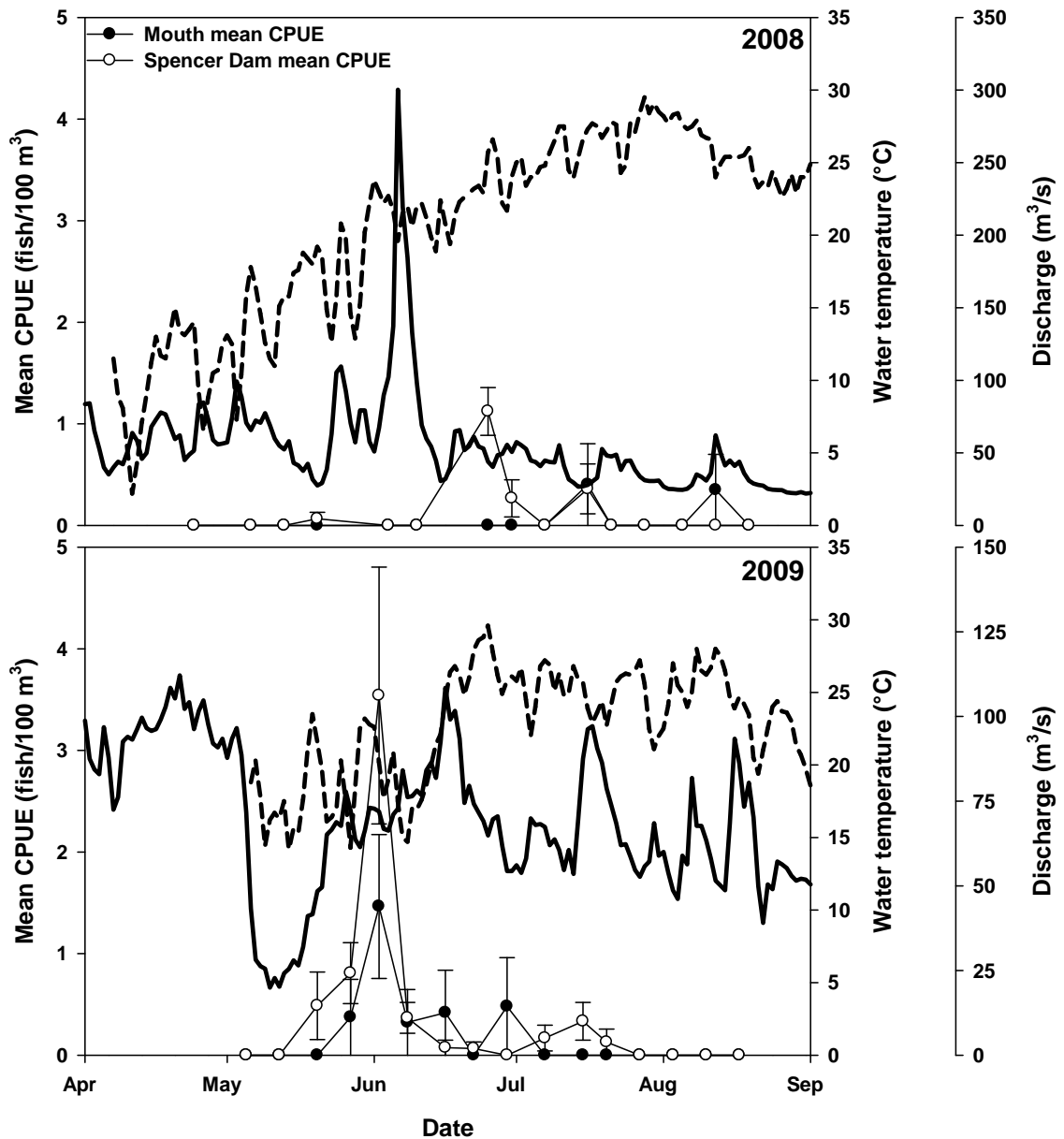


Figure 4. Relative abundance of flathead chubs collected at two sites in the Niobrara River in 2008 and 2009 in relation to mean daily temperature (dashed line) and mean daily discharge (solid line) recorded at the Pischelville Bridge (http://waterdata.usgs.gov/usa/nwis/uv?site_no=06465500). Note that axes differ for discharge between 2008 and 2009.

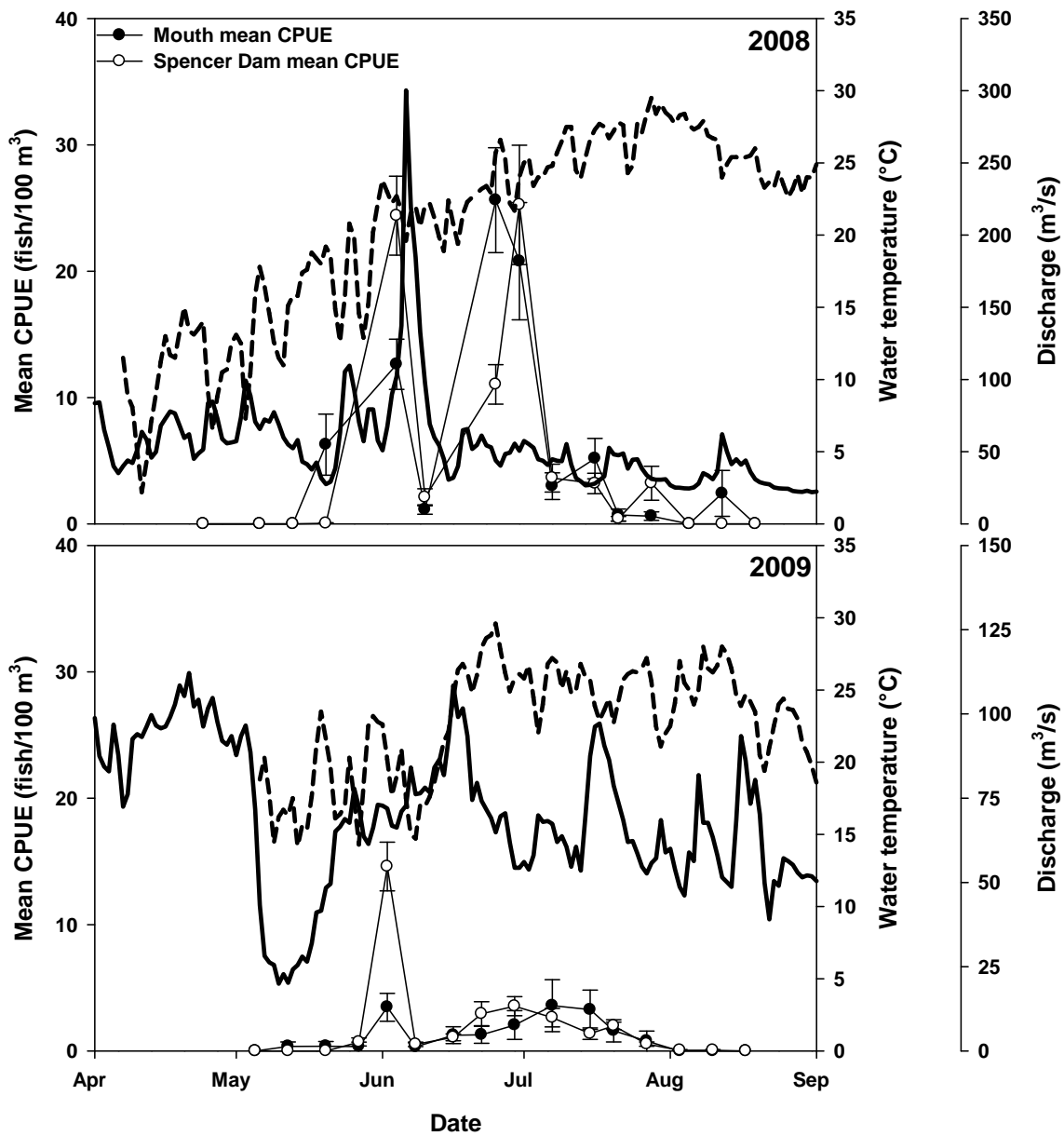


Figure 5. Relative abundance of river carpsucker collected at two sites in the Niobrara River in 2008 and 2009 in relation to mean daily temperature (dashed line) and mean daily discharge (solid line) recorded at the Pischelville Bridge (http://waterdata.usgs.gov/usa/nwis/uv?site_no=06465500). Note that axes differ for discharge between 2008 and 2009.

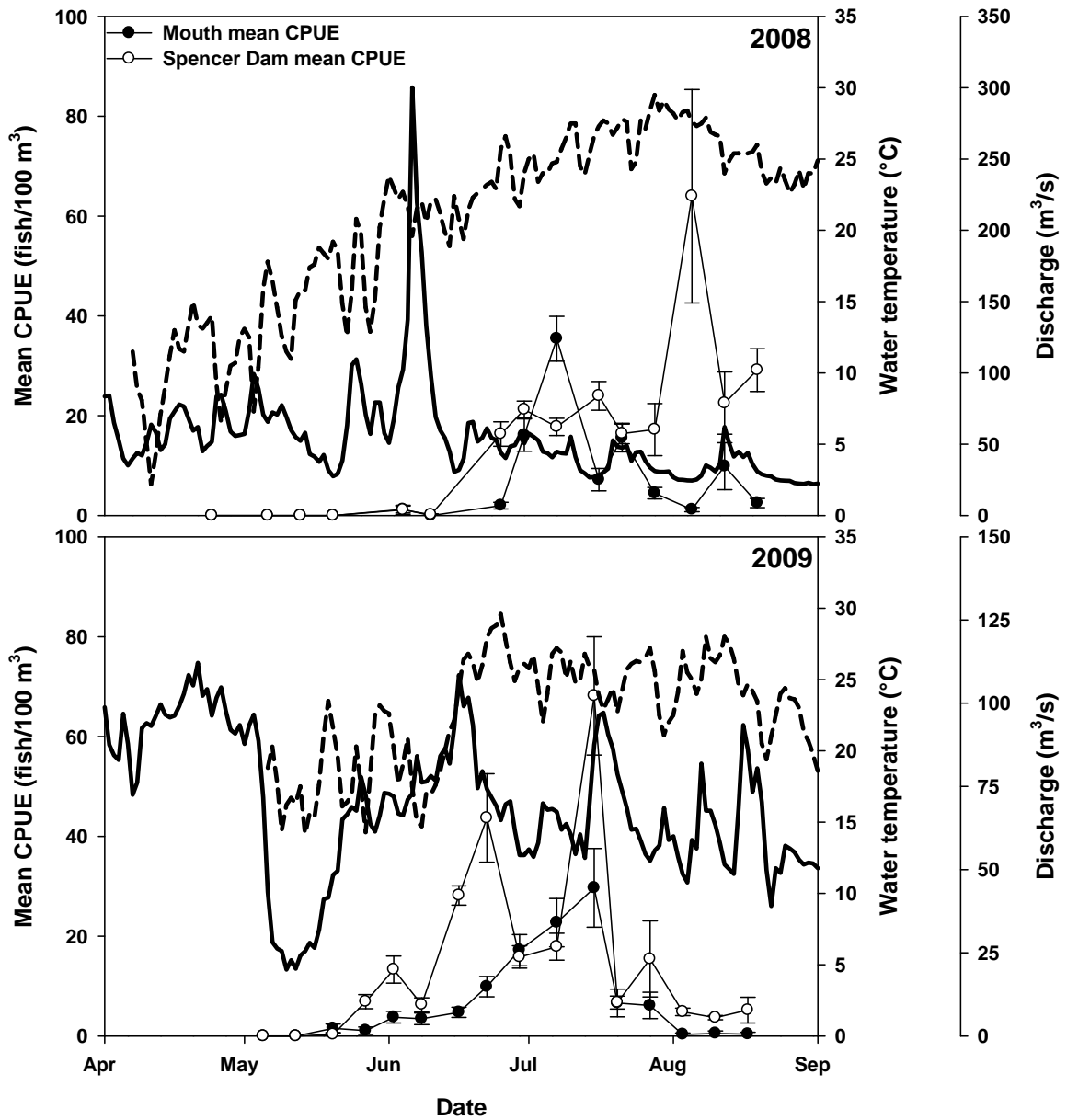


Figure 6. Relative abundance of combined red shiners and sand shiners collected at two sites in the Niobrara River in 2008 and 2009 in relation to mean daily temperature (dashed line) and mean daily discharge (solid line) recorded at the Pischelville Bridge (http://waterdata.usgs.gov/usa/nwis/uv?site_no=06465500). Note that axes differ for discharge between 2008 and 2009.

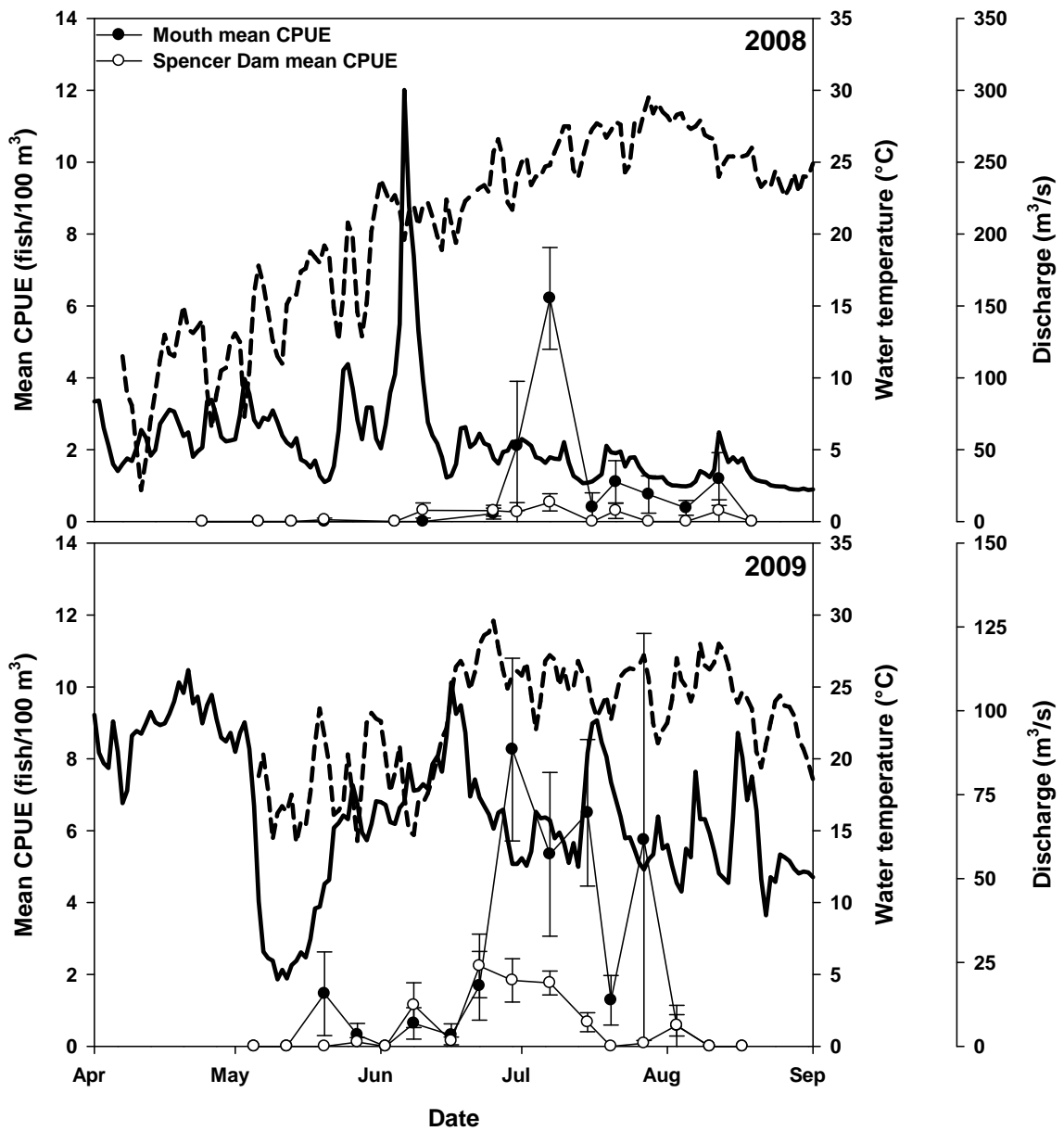


Figure 7. Relative abundance of *Lepomis* spp. collected at two sites in the Niobrara River in 2008 and 2009 in relation to mean daily temperature (dashed line) and mean daily discharge (solid line) recorded at the Pischelville Bridge (http://waterdata.usgs.gov/usa/nwis/uv?site_no=06465500). Note that axes differ for discharge between 2008 and 2009.

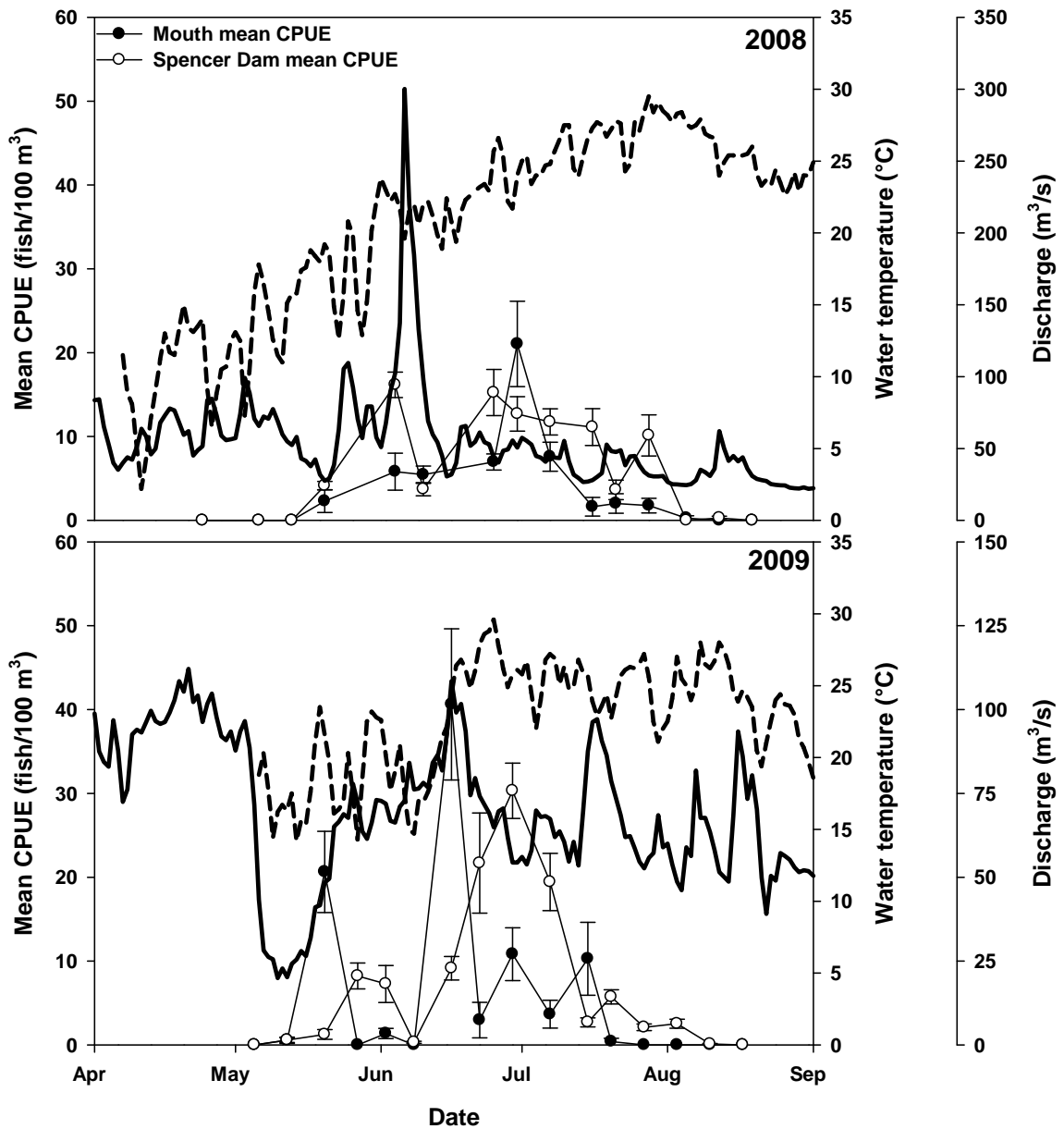


Figure 8. Relative abundance of unidentified fish eggs collected at two sites in the Niobrara River in 2008 and 2009 in relation to mean daily temperature (dashed line) and mean daily discharge (solid line) recorded at the Pischelville Bridge (http://waterdata.usgs.gov/usa/nwis/uv?site_no=06465500). Note that axes differ for discharge between 2008 and 2009.

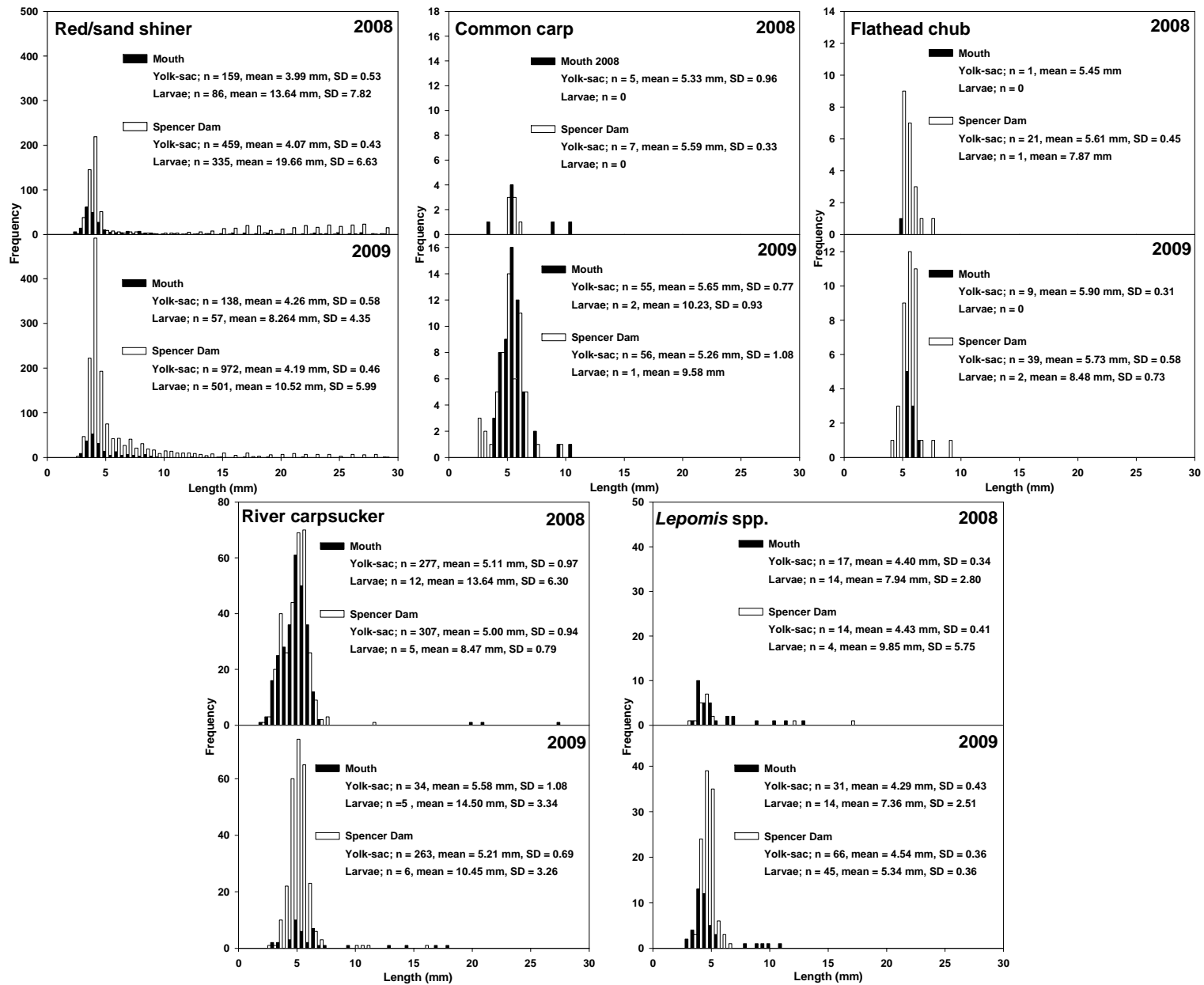


Figure 9. Length frequency distributions of the five most abundant larval taxa (0.5-mm length-groups) collected in the Niobrara River in 2008 and 2009. Note differing y-axes among fish species.

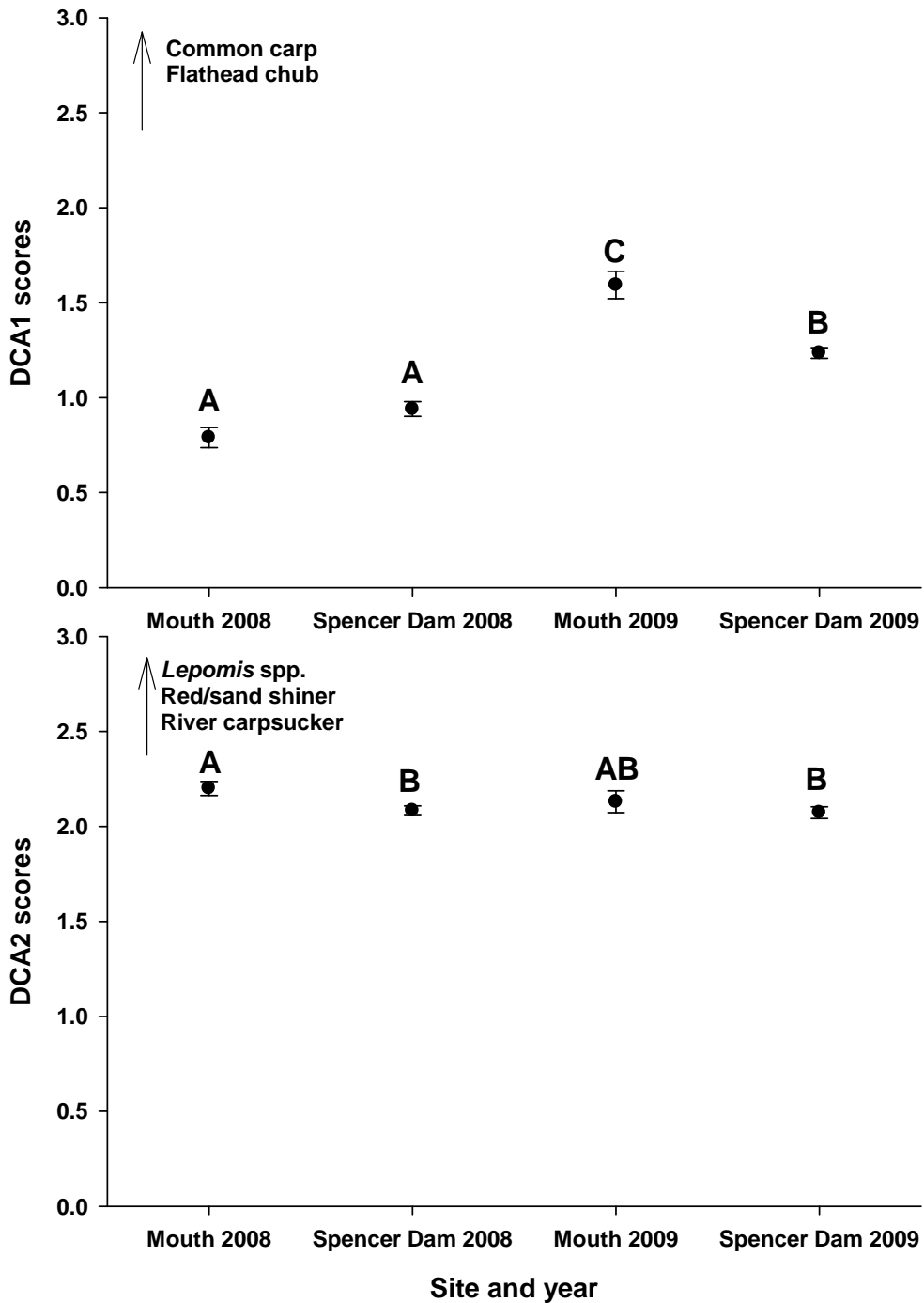


Figure 10. Mean detrended correspondence analysis (DCA) scores and standard error bars for Axis 1 (top) and Axis 2 (bottom) for each sampling site and year derived from larval fish density matrix. Two-sample *t*-tests were applied to the retained DCA axes scores to assess differences in species composition between sample sites each year. Sample sites that share a common letter were not significantly different at $\alpha = 0.008$ after Bonferroni corrections.

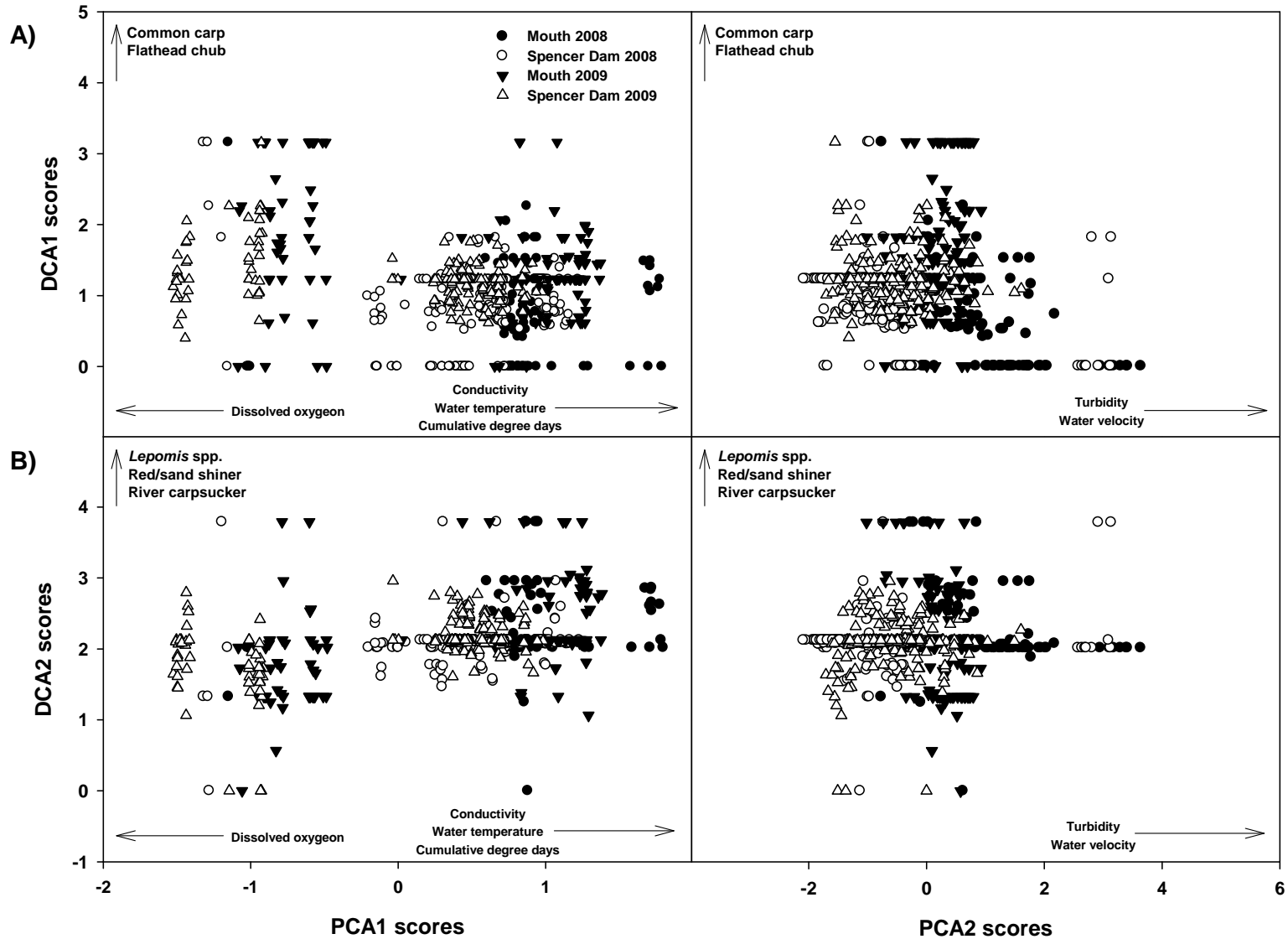


Figure 11. Scatterplot between principle components analysis (PCA) scores and detrended correspondence analysis (DCA) scores for common carp and flathead chubs (A) and for *Lepomis* spp., red/sand shiner, and river carpsuckers (B).

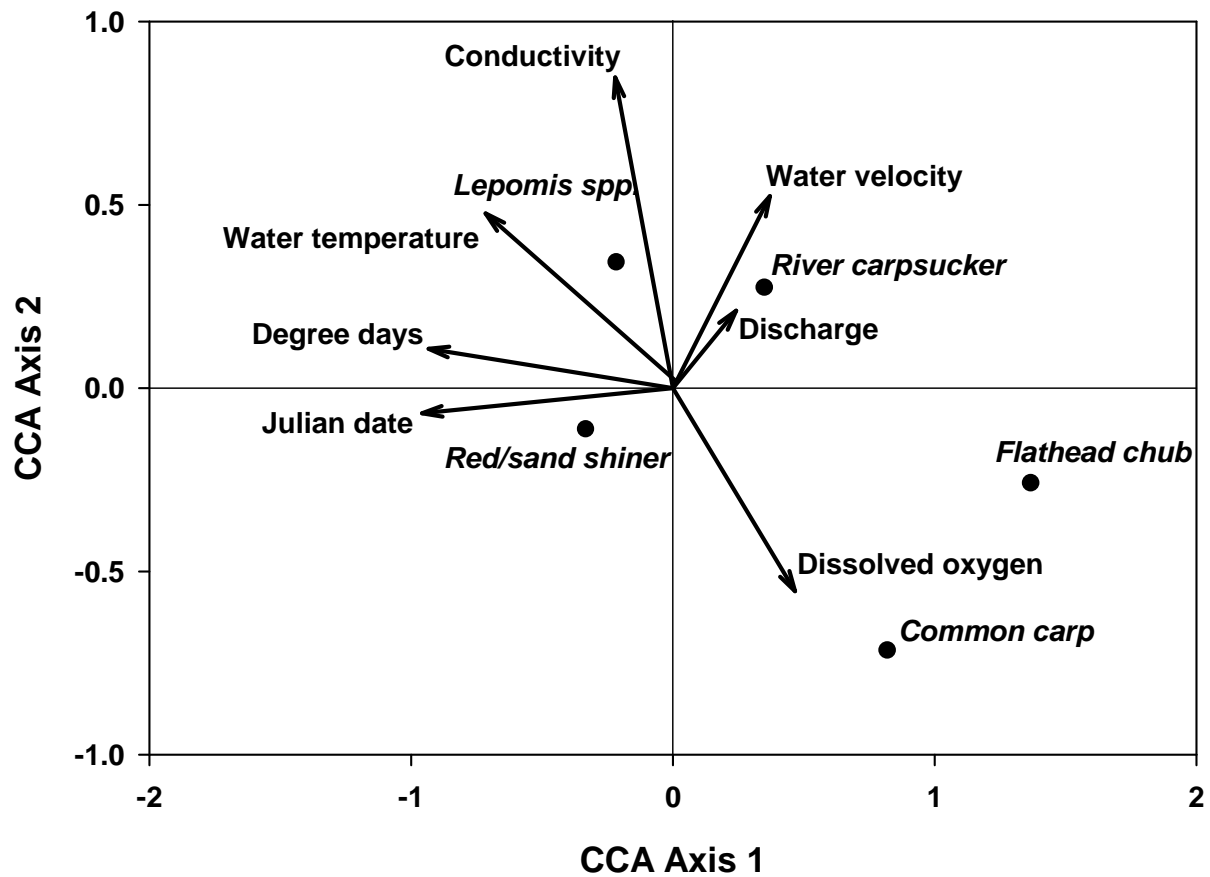


Figure 12. Canonical correspondence ordination biplot showing taxa (species scores) with environmental variables (vectors). Vectors emanate from the grand mean of all explanatory variables, direction of the vectors are relative to the axes and indicate what the axes represent, and the length of the vector indicate the importance of the environmental variable. The position of the species points relative to the arrows indicates how optimum the environmental conditions are to each species.