PRIMARY RESEARCH PAPER

Morphological diversity among fishes in a Great Plains river drainage

Christopher W. Hoagstrom · Charles R. Berry

Abstract Longitudinal succession of stream fish faunas is commonly related to increasing stream size and stability. However, effects of succession on assemblage morphology are seldom quantified. We used an ecomorphological approach to determine differences in faunal structure among distinct stream types of the Cheyenne River drainage in South Dakota, USA. During May–October 2004 we collected fishes monthly from five streams. We examined 28 morphological traits of the dominant fish species and compared morphological structure among faunas using univariate analysis of variance (ANOVA) tests and multivariate ordination and distance calculation techniques. Species richness and composition varied between smaller creeks and larger rivers. Morphological diversity increased with richness, but richer assemblages were also more tightly packed in morphospace, partly because of increased cyprinid richness. Some morphological differences were predicted by variation in mean discharge and discharge flashiness (flow stability). Fishes of more stable or larger river stations characteristically had smaller heads and mouths and longer intestines. Larger mean standard length was also associated with less flashy flow regimes and higher mean discharge. All assemblages were hyperdispersed in morphological space, consistent with the harsh zoogeographical history of the region and suggesting the presence of open niches. Increasing species and morphological diversity despite increasing discharge flashiness suggests higher niche diversity in Great Plains rivers compared to adjacent creeks.

Keywords Ecomorphology · Niche diversity · Cheyenne River · Hydrology · Hyperdispersed assemblages · Stream continua

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Introduction

Ecological processes change in transition from headwater streams to river mouths (Vannote et al., 1980; Minshall et al., 1985). However, longitudinal transitions in food web structure and trophic complexity are poorly understood (Power & Dietrich 2002). Longitudinal fish faunal succession is well documented (e.g. Sheldon 1968; Schlosser 1990), but its relation to

niche dimensions is less understood. Landmark studies demonstrated that fish species diversity increased downstream if habitat diversity increased (Gorman & Karr, 1978) or habitat stability increased (Horwitz 1978), both of which favor trophic and habitat specialists (Poff & Allan, 1995), perhaps because of increased niche space (Schlosser, 1987).

The multidimensional niche of a fish species is difficult to define, but morphological traits are useful indicators of niche dimensions (Gatz, 1979; Watson & Balon, 1984), because fish morphology partly reflects the evolutionary influence of environmental conditions (Hubbs, 1940; Lamouroux et al., 2002). Findley (1973, 1976; Gatz 1980) pioneered an approach to array species within multidimensional niche space using ordination and distance analyses on a large suite of measurements of trophic and habitat related morphological characters. This approach has been used to estimate niche space among and within fish assemblages (Winemiller, 1991; Adite & Winemiller, 1997), reveal patterns of ecomorphological convergence and divergence (Winemiller, 1991; Winemiller et al., 1995), document habitat associations (Motta et al., 1995), identify functional groups (Piet, 1998), and establish a link between habitat complexity and morphological diversity (Willis et al., 2005). Winemiller (1991) proposed that morphological diversity within fish faunas increases with habitat volume, habitat diversity, environmental stability, and levels of interspecific competition and predation, all of which commonly increase with stream size (Minshall et al., 1985; Schlosser, 1990). Variability in fish size contributes to morphological diversity (Winemiller, 1991). Greater pool depth downstream is critical for supporting larger fishes (Schlosser, 1987; 1990), perhaps because fish size is correlated with habitat volume (Larimore & Smith, 1963). Thus, there appears to be a relation between the stream continuum and fish morphological diversity, as evidenced by higher trophic diversity in larger streams (Bayley & Li, 1992; Poff & Allan, 1995).

Here we assess relations of fish length and morphological diversity to stream type in the Cheyenne River drainage of the North American Great Plains. Stream types are distributed along two confluent stream continua and represent the range of perennial-warmwater streams that is present. We expect fish length and species diversity to increase downstream (Schlosser, 1987; Rahel & Hubert, 1991;

Bayley & Li, 1992) and that higher species diversity will correspond to higher morphological diversity (Winemiller, 1991; Willis et al., 2005). Also, species replacements due to faunal zonation (Rahel & Hubert, 1991; Quist et al., 2004a), if present, could cause morphological differentiation among assemblages (Winemiller, 1991).

Study area

The Cheyenne River watershed lies entirely within the Great Plains physiographic province (Holliday et al., 2002) and has an area of 65,398 km^2, primarily in Wyoming and South Dakota, USA. There are two main forks of the Cheyenne River, the Belle Fourche River and Upper Cheyenne River (Fig. 1). Both begin in highlands of the Powder River Basin in northeastern Wyoming, but their courses diverge to encircle the Black Hills with the Belle Fourche River on the north and Upper Cheyenne River on the south. The forks eventually join to form the Lower Cheyenne River. Dams and reservoirs are present on both forks and on streams of the Black Hills, but the combination of perennial tributary streams, the two forks of the Cheyenne River, and the Lower Cheyenne River forms two confluent stream continua within an extensive undammed portion of the drainage, downstream from the Black Hills. Both continua are approximately 360 km in length (stream km estimates from National Hydrography Database 1:100,000 scale data).

The five streams we studied included Beaver Creek, Whitewood Creek, the Belle Fourche River below Belle Fourche Dam, the Upper Cheyenne River below Angostura Dam, and the Lower Cheyenne River, which represent the variety of perennial-warmwater streams that is present. Our study was conducted during a drought period that began in 2001, so we used US Geological Survey gage data from water years 2002 through 2004 to characterize the flow regime of each stream. In both stream continua, mean discharge and discharge flashiness increased from upstream to downstream (Table 1). The Whitewood Creek—Belle Fourche River— Lower Cheyenne River continuum had a more variable annual flow regime than the Beaver Creek—Upper Cheyenne River—Lower Cheyenne River continuum.

Fig. 1 Map of the Cheyenne River drainage in South Dakota, with locations of five sampling stations (*circles*) and five US Geological Survey gaging stations (*triangles*) on five different streams. Major dams and reservoirs, shown in black, are: A = Belle Fourche Dam, B = Orman Reservoir, C = Deerfield Reservoir, D = Pactola Reservoir, E = Sheridan Reservoir, F = Stockade Reservoir, G = Angostura Reservoir. The dashed line indicates the boundary of the Black Hills
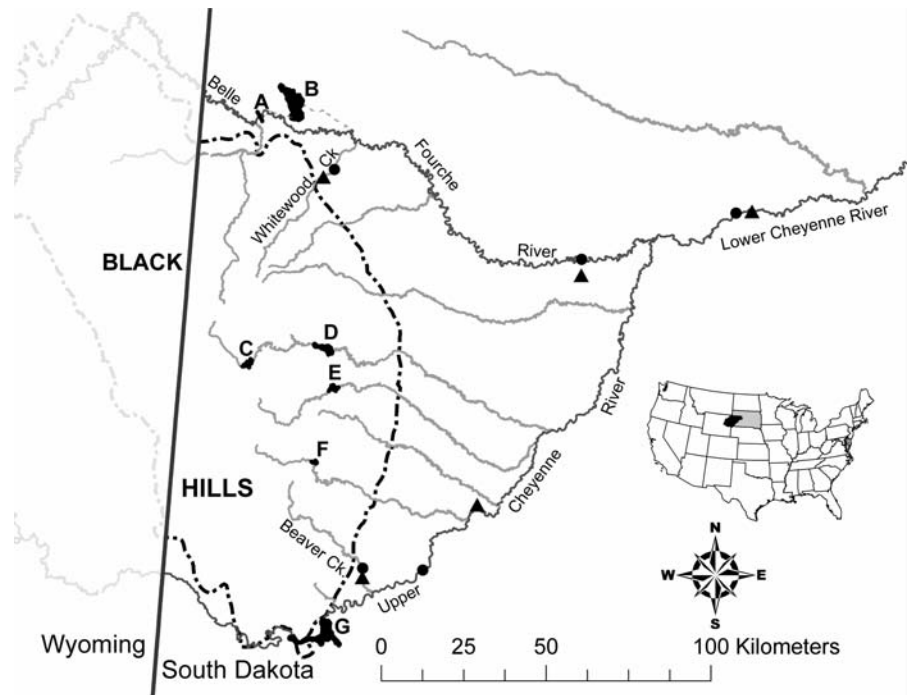

Table 1 Drainage area, mean discharge (Mean Q), and discharge flashiness (R-B Index, Baker et al., 2004) for each sampling station based on mean daily discharge records from nearby US Geological Survey gages for the water years 2002 through 2004

Gage	Area (km^2)	Mean Q ± SD (m^3/s)[a]	R-B Index
Beaver Creek near Buffalo Gap[b]	337	0.18 ± 0.08	0.05
Whitewood Creek near Whitewood[c]	201	0.37 ± 0.45	0.16
Cheyenne River near Red Shirt[d]	26,418	2.03 ± 0.66	0.09
Belle Fourche River near Elm Springs[e]	18,674	2.93 ± 4.64	0.20
Cheyenne River near Plainview[f]	56,048	7.17 ± 8.35	0.22

Gage and sampling station locations are shown on Fig. 1

[a] Analysis of Variance of log$_e$–transformed Q indicated significant variation among stations (F = 5013, df = 4, 5475, P < 0.01). Tukey Honestly Significant Difference post-hoc tests indicated all stream pairs varied (pairwise mean differences [PMDs] > |0.46|, P < 0.01), except the Upper Cheyenne River and Belle Fourche River (PMD = 0.06, P = 0.31).

Nearby sampling stations

[b] Beaver Creek

[c] Whitewood Creek

[d] Upper Cheyenne River

[e] Belle Fourche River

[f] Lower Cheyenne River

Methods

Fish collection

We sampled one station per stream, each being selected to be representative of a stream type and used one station on the Lower Cheyenne River for both continua (Fig. 1). We conducted fish collections monthly from May through October 2004 and used a mesohabitat approach to representatively sample fishes (Vadas & Orth, 1998). We conducted monthly sampling over a 36-h period at each station, during

which we made the maximum number of mesohabitat collections possible, using multiple capture methods depending upon habitat conditions (Table 2; Bramblett & Fausch 1991). We conducted night sampling from May through July and determined that capture composition did not vary between day and night (unpublished data).

Following criteria described by Winemiller (1991), we measured 28 morphological traits using clear plastic rulers and ocular micrometry (Adite & Winemiller, 1997; Table 3). With the exception of mouth position code, gill raker code, and maximum standard length, all traits were converted to ratios of standard length, body depth, body width, or head length (Winemiller, 1991). We conducted measurements on three adult-sized individuals of each species that was dominant at one or more stations (Watson & Balon, 1984; Winemiller, 1991; Willis et al., 2005), with the exception that specimens of large-bodied species were selected to reflect the average size of individuals normally encountered (Appendix 1). Dominant species, summed by order of rank, comprised 99% of each fish fauna (Winemiller, 1991). For each species, the three specimens selected for study were similar in size to reduce allometric variation among individuals (Winemiller, 1991).

Data analyses

All analyses included only the dominant species so that comparisons reflected characteristic station faunas, uninfluenced by incidental species. Relative abundance was based on cumulative standard length rather than the number of individuals collected, to better represent the total biomass of each station fauna. We constructed a presence–absence matrix (stations in columns, species in rows) and used the approach recommended by Gotelli (2000; Gotelli & Entsminger, 2001b, 2003) to determine whether species distributions were random. This analysis uses the C-score (Stone & Roberts, 1990) to quantify species co-occurrence patterns, comparing the empirical C-score with the average of many Monte Carlo simulations. We used EcoSim 7.0 software (Gotelli & Entsminger, 2001a) and selected the Gotelli Swap algorithm, which analyzed a random set of presence–absence matrices (1,000 iterations) with row and column totals held constant.

We also performed descriptive analyses on the presence-absence matrix to examine patterns of faunal similarity among stations in relation to stream size and stability. We determined dominant species richness by station as well as both percent-unshared species (faunal turnover; Russell, 1998) and faunal similarity (Sørensen's Index; Legendre & Legendre, 1998) between station pairs. Sørensen's Index varies from 0 to 1, with higher values indicating higher similarity. We also calculated dominant species diversity for each station with Fisher's α, using cumulative standard lengths as relative abundances, and calculated error bars for use in a statistical comparison (Kempton & Taylor, 1974; Magurran, 2004). Fisher's α is a rigorous diversity measure that approximates the number of species represented by a single individual and comparisons are unaffected by sample size if the total number of individuals collected per station is above 1,000.

We used multiple linear regression to determine the influence of mean discharge (stream size) and

Table 2 Total sampling effort for each station by gear type

Study station	Seine (m^2)	Bag (m^2)	Backpack (h)	Hoops (h)	Traps (h)	Poles (h)	Lines (h)
Beaver Creek	6,073.9	0.0	3.2	49.7	86.1	0.0	0.0
Whitewood Creek	4,274.2	0.0	3.9	112.0	114.6	0.0	0.0
Upper Cheyenne River	9,376.3	7,466.8	0.0	299.0	364.7	52.4	57.0
Belle Fourche River	3,732.8	2,428.5	0.0	415.3	498.9	43.5	165.0
Lower Cheyenne River	10,420.2	4,822.1	0.0	379.9	282.4	4.5	153.0

Sampling gears included a 3.7-m long flat seine with 3.0 mm mesh and lead weights every 15.2 cm (seine), a 10.6-m long bag seine with 6.0 mm mesh, (bag) a battery powered backpack electrofisher (backpack), 25.4-mm mesh bar measure mini hoop nets that were 3.6 m long with 0.8 m hoops (hoops), Gee minnow traps with 3.0 mm mesh (traps), light fishing tackle with artificial lures and earthworms (poles), and 20 hook trot lines, size 10/0–12/0 Circle Sea hooks, baited with chicken gizzards (lines). Stations are ordered by mean discharge

Table 3 Morphological traits used for ecomorphological analyses

Trait	Trait code	Trait definition and ratio denominators
Body depth	BD	Maximum vertical distance from dorsum to ventrum, divided by standard length;
Body depth below midline	BDBM	Maximum vertical distance from midline to ventrum, midline = imaginary line from pupil through the ultimate vertebra, divided by body depth;
Body width	BW	Maximum horizontal distance from side to side, divided by standard length;
Caudal peduncle length	PL	Distance from posterior proximal margin of anal fin to caudal margin of the ultimate vertebra, divided by standard length;
Caudal peduncle depth	PD	Minimum vertical distance from dorsum to ventrum of the caudal peduncle, divided by body depth;
Head length	HL	Distance from tip of the upper jaw to the most-caudal extension of the operculum, divided by standard length;
Head depth	HD	Vertical distance from dorsum to ventrum passing through the pupil, divided by body depth;
Head width	HW	Maximum distance between the opercles when they are in their normally closed position, divided by standard length;
Eye position	EP	Vertical distance from the center of the pupil to ventrum, divided by head depth;
Eye diameter	ED	Horizontal distance from eye margin to eye margin, divided by head length;
Mouth position code	MP	Coded as 1 for superior, 2 for terminal, 3 for inferior, and 4 for bottom;
Mouth width	MW	Horizontal distance measured inside of fully open mouth at widest point, divided by body width;
Mouth height	MH	Vertical distance measured inside of fully open mouth at tallest point, divided by body depth;
Snout length	SnL	Distance form the pupil of the eye to tip of the upper jaw with mouth shut, divided by head length;
Dorsal fin base length	DFL	Distance from the anterior proximal margin to posterior proximal margin of the dorsal fin, divided by standard length;
Dorsal fin height	DFH	Maximum distance from proximal to distal margin of the dorsal fin (excluding filaments), divided by standard length;
Pectoral fin height	PcFH	Maximum distance from proximal to distal margin of the pectoral fin, divided by standard length;
Caudal fin length	CFL	Maximum distance from proximal to distal margin of the caudal fin (excluding filaments), divided by standard length;
Caudal fin height	CFH	Maximum vertical distance across fully spread caudal fin, divided by standard length;
Pelvic fin height	PlFH	Maximum distance from proximal to distal margin of the anal fin, divided by standard length;
Anal fin base length	AFL	Distance from anterior proximal margin to posterior proximal margin of the anal fin, divided by standard length;
Anal fin height	AFH	Maximum distance from proximal to distal margin of the anal fin, divided by standard length;
Jaw tooth length	JTL	Maximum length of teeth on jaws, divided by standard length;
Gill raker code	GRC	Coded as 0 for absent, 1 for short, blunt, or toothlike, 2 for intermediate or long and sparse, 3 for long and comb-like;
Gill raker length	GRL	Maximum gill raker length, divided by standard length;
Gut length	GutL	Measured from the beginning of the esophagus to anus (fully extended without stretching), divided by standard length;
Swim bladder length	SBL	Maximum straight line distance from anterior to posterior margins, divided by standard length;
Maximum standard length	MaxSL	Maximum standard length by station or for the entire study, depending upon the analysis.

Trait definitions follow Trautman (1981), Winemiller (1991), and Adite and Winemiller (1997)

discharge flashiness (R-B index, stream stability) on dominant species richness and species diversity. We considered discharge a superior estimate of stream size to watershed area because upstream dams and diversity confounded the relation of watershed to stream size in our study area. The R-B index is a superior measure of discharge flashiness because it incorporates a temporal component of flow variability into the flashiness estimate (Baker et al., 2004). It is a discharge oscillation to total discharge ratio that typically varies from 0 to 1, with higher values indicating flashier flow regimes.

We compared cumulative mean standard length (SL; all species combined) among stations. We used Analysis of Variance (ANOVA) with Tukey Honestly Significant Difference (HSD) post-hoc tests and multiple linear regression to determine whether SL varied among stations and whether variation was related to mean discharge or discharge flashiness. Standard lengths were $\log_e$-transformed. We also used ANOVA to compare standard lengths among sampling stations for each species that was dominant at multiple stations to determine how individual species contributed to the overall trend.

As an exploratory technique, we used ANOVA to individually compare the 28 morphological traits among stations (Winemiller et al., 1995). We conducted a Principal Components Analysis (PCA) on the 22-species correlation matrix of $\log_{10}$-transformed morphological-trait data to reduce the morphological data to fewer dimensions and assess morphological differences among stations by comparing average PC scores (Mahon, 1984; Winemiller, 1991; Piet, 1998). We considered Principal Component axes to be nontrivial if eigenvalues exceeded null eigenvalues calculated using the broken-stick model (Jackson, 1993). The PCA and broken-stick model calculations were performed using PC-ORD for windows, version 4.25 software (MjM Software, Gleneden Beach, Oregon, USA). We calculated means and standard deviations of PCA scores for fishes on each nontrivial axis. Mean score indicated morphological position on each PC axis and standard deviation indicated morphological diversity (Willis et al., 2005). We used multiple linear regression to determine the influence of mean discharge and discharge flashiness on morphological position and morphological diversity.

We calculated Euclidean distances among all species pairs using all 28 morphological traits by

station and for all stations (Gatz, 1979; Winemiller, 1991; Adite & Winemiller, 1997). Prior to calculations, the means of all morphological measures were standardized to fit a Gaussian distribution (mean = 0, standard deviation = 1), which adjusts for differing scales among measures (Gatz, 1979; Watson & Balon, 1984; Winemiller, 1991). From the Euclidian distance calculations we determined: (1) distance to nearest neighbor for each species per fauna and mean nearest neighbor distance per fauna, (2) average between-species distance for each species per fauna and mean distance per fauna, (3) distance to the morphological centroid (hypothetical average fish based on the mean values of all species) for each species per fauna and mean distance to centroid per fauna. Distance to nearest neighbor provides an estimate of species dispersion, average between-species distance provides an estimate of ecological similarity among species, and distance to centroid provides an estimate of total niche space occupied (Findley, 1976; Gatz, 1979; Winemiller, 1991; Adite & Winemiller, 1997). We used ANOVA to compare mean distance to nearest neighbor, paired distances among all species, and distance to centroid among stations and simple linear regression to test the relation between species richness and mean nearest-neighbor distance, standard deviation of nearest-neighbor distance, and mean distance to centroid (Winemiller, 1991). Standard deviation of nearest-neighbor distance is an estimate of the evenness of species packing within morphological space (Findley, 1976; Winemiller, 1991). Finally, we investigated the relation between morphological similarity and co-occurrence by determining the nearest neighbor of each species and calculating the percentage of species that co-occurred with their nearest neighbor (Winston, 1995).

Results

We collected a total of 18,721 fish of 28 species. Twenty-two species were dominant at one or more stations (Table 4; Appendix 1). Station fish assemblages had significantly less co-occurrence than expected by chance (Fig. 2). Number of dominant species (richness) was lower in creek stations than river stations (Fig. 3), but was poorly predicted by mean discharge (Q) or discharge flashiness (R-B; $b'_Q =$ 0.68, $b'_{R-B} = 0.00$, $r^2 = 0.5$, $F = 0.9$, $P = 0.53$).

Table 4 Numerical abundance and *cumulative standard length* (dm, in italics) of dominant fish species by sampling station

Species	Beaver C.		Whitewood C.		Upper Cheyenne R.	
Hiodon alosoides (Rafinesque)	–	–	–	–	47[a]	*146*
Dorosoma cepedianum (Lesueur)[c]	–	–	–	–	*	*
Cyprinella lutrensis lutrensis (Baird & Girard)	–	–	–	–	374[a]	*165*
Cyprinus carpio Linnaeus[c]	–	–	–	–	20[b]	*31*
Hybognathus argyritis Girard	–	–	–	–	–	–
Hybognathus placitus Girard	–	–	–	–	–	–
Macrhybopsis gelida (Girard)	–	–	–	–	–	–
Notropis stramineus missuriensis (Cope)	–	–	–	–	433[a]	*182*
Pimephales promelas Rafinesque	–	–	263[b]	*104*	*	*
Platygobio gracilis (Richardson)	–	–	–	–	–	–
Rhinichthys cataractae cataractae (Valenciennes)	634[a]	*358*	1957[a]	*922*	–	–
Semotilus atromaculatus (Mitchill)	1822[a]	*1326*	2325[a]	*1104*	*	*
Carpiodes carpio carpio (Rafinesque)	–	–	–	–	13	*39*
Catostomus commersonii (Lacepède)	393[a]	*585*	176[a]	*251*	15	*11*
Catostomus platyrhynchus (Cope)	25[b]	*20*	*	*	–	–
Moxostoma macrolepidotum (Lesueur)	–	–	–	–	345[a]	*226*
Ameiurus melas (Rafinesque)	–	–	–	–	–	–
Ictalurus punctatus (Rafinesque)	–	–	–	–	15[a]	*66*
Noturus flavus Rafinesque	22[a]	*20*	31[a]	*18*	47[a]	*43*
Salmo trutta Linnaeus[c]	–	–	*	*	–	–
Fundulus kansae Garman	–	–	–	–	–	–
Fundulus sciadicus Cope	90[a]	*28*	–	–	88[a]	*29*
Ambloplites rupestris (Rafinesque) [c]	–	–	–	–	*	*
Lepomis cyanellus Rafinesque	72[a]	*57*	*	*	12	*9*
Lepomis humilis (Girard)	–	–	–	–	–	–
Lepomis macrochirus macrochirus Rafinesque[c]	–	–	–	–	*	*
Micropterus dolomieu Lacepède[c]	–	–	–	–	303[a]	*248*
Sander canadensis Griffith & Smith	–	–	–	–	–	–
Species	Belle Fourche R.		Lower Cheyenne R.			
Hiodon alosoides (Rafinesque)	12[b]	*37*	*	*		
Dorosoma cepedianum (Lesueur) [c]	*	*	*	*		
Cyprinella lutrensis lutrensis (Baird & Girard)	2127[a]	*743*	104[a]	*31*		
Cyprinus carpio Linnaeus[c]	15[b]	*15*	30[b]	*29*		
Hybognathus argyritis Girard	32	*34*	18	*13*		
Hybognathus placitus Girard	–	–	167[a]	*97*		
Macrhybopsis gelida (Girard)	–	–	43[a]	*25*		
Notropis stramineus missuriensis (Cope)	1854[a]	*659*	427[a]	*155*		
Pimephales promelas Rafinesque	41[b]	*14*	*	*		
Platygobio gracilis (Richardson)	286[a]	*161*	1723[a]	*865*		
Rhinichthys cataractae cataractae (Valenciennes)	251[a]	*120*	363[a]	*180*		
Semotilus atromaculatus (Mitchill)	*	*	–	–		
Carpiodes carpio carpio (Rafinesque)	24[a]	*33*	53[a]	*25*		
Catostomus commersonii (Lacepède)	35[a]	*47*	*	*		
Catostomus platyrhynchus (Cope)	–	–	–	–		

Table 4 continued

Species	Beaver C.		Whitewood C.		Upper Cheyenne R.
Moxostoma macrolepidotum (Lesueur)	208[a]	*209*	60[a]	*103*	
Ameiurus melas (Rafinesque)	*	*	*	*	
Ictalurus punctatus (Rafinesque)	504[a]	*507*	499[a]	*586*	
Noturus flavus Rafinesque	125[a]	*105*	34[a]	*27*	
Salmo trutta Linnaeus[c]	–	–	–	–	
Fundulus kansae Garman	73[b]	*26*	*	*	
Fundulus sciadicus Cope	–	–	–	–	
Ambloplites rupestris (Rafinesque) [c]	–	–	–	–	
Lepomis cyanellus Rafinesque	*	*	*	*	
Lepomis humilis (Girard)	*	*	*	*	
Lepomis macrochirus macrochirus Rafinesque[c]	–	–	–	–	
Micropterus dolomieu Lacepède[c]	–	–	–	–	
Sander canadensis Griffith & Smith	3	*11*	4	*13*	

* Species present, but omitted from analyses due to rarity (see text)

[a] Species present in every monthly sample

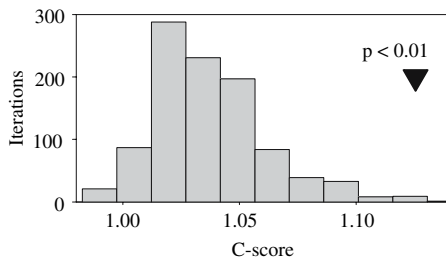[b] Species present in five of six monthly samples

[c] Non-native species

Fig. 2 Co-occurrence patterns among sampling stations. The histogram gives the frequencies of simulated C-scores for fish assemblages (1,000 iterations) and the down triangle indicates the observed C-score. The tail probability of the observed C-score being from a randomly assembled matrix is also given
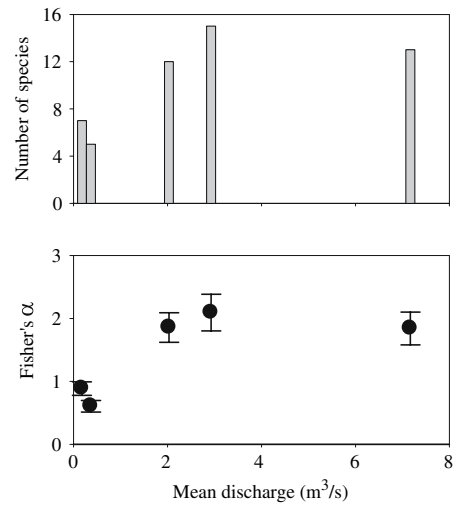

Fig. 3 Dominant species richness (top) and species diversity (Fisher's α; bottom) by sampling station, ordered by mean discharge (Table 1)

Table 5 Upper triangle shows percent unshared dominant fish species (unshared species / total species) among stations

Stream	Beaver	Whitewood	Upper Cheyenne	Belle Fourche	Lower Cheyenne
Beaver		50	73	84	89
Whitewood	0.5		87	75	88
Upper Cheyenne	0.4	0.2		50	61
Belle Fourche	0.3	0.4	0.7		35
Lower Cheyenne	0.2	0.2	0.6	0.8	

Lower triangle shows Sørensen's index of faunal similarity

Number of unshared dominant species varied from
35% to 89% and was highest between river stations
and creek stations (Table 5). Similarly, Sørensen's
index of faunal similarity varied from 0.2 to 0.8 with
river stations being most similar (Table 5). Species
diversity (Fisher's α) was lower in creek stations than
river stations (Fig. 3), but unrelated to mean discharge
or discharge flashiness ($b'_Q = 0.73$, $b'_{R-B} = -0.09$,
$r^2 = 0.4$, $F = 0.8$, $P = 0.55$).

Average SL was variable among stations
($F = 579.2$, $P < 0.01$) and statistically different
among all station pairs (Tukey HSD pairwise mean
differences (PMDs) $>|0.10|$, $P < 0.01$), except
between the Upper Cheyenne River and Lower
Cheyenne River (PMD = 0.03, $P = 0.14$). The mean
SL of Beaver Creek fish was highest, followed by the
Upper and Lower Cheyenne Rivers, Whitewood
Creek, and the Belle Fourche River (Fig. 4). Multiple
linear regression indicated that mean discharge and
mean discharge flashiness predicted mean SL ($b'_Q =$
0.81, $b'_{R-B} = -1.39$, $r^2 = 1.0$, $F = 28.0$, $P = 0.03$).
Few species increased in mean SL from smaller to
larger streams (Fig. 5). *Moxostoma macrolepidotum*
was the primary exception.

All morphological traits were similar among
station faunas (Table 6; $F < 2.0$, df = 4, 47,
$P > 0.12$ for all comparisons) except caudal fin
length ($F = 3.3$, $P = 0.02$). Caudal fin length was
lower in Beaver Creek than in the Lower Cheyenne
River (PMD = -0.04, $P = 0.03$), but similar among
other stations (PMDs $< |0.04|$, $P > 0.08$). The first
three PC axes modeled 51% of the total variation in
morphological space among all 22 species (Table 7).
Additional PC axes modeled little variation (<8.9%)
and were trivial based on broken-stick eigenvalues
that exceeded PCA eigenvalues. Multiple regressions
of mean PCA scores for fish species indicated that
PC1 scores varied with discharge and discharge
flashiness among stations, but not PC2 or PC3 scores
(Table 8). Multiple regressions of PCA score stan-
dard deviation indicated that variation among station
scores was unrelated to mean discharge or discharge
flashiness (Table 8).

Species with high PC1 scores (*Noturus flavus*,
Fundulus spp., Perciformes) had large, terminal, or
superior mouths and short intestines, indicative of
their carnivorous habits, whereas species with small,
subterminal mouths, and long intestines (*Hybogna-
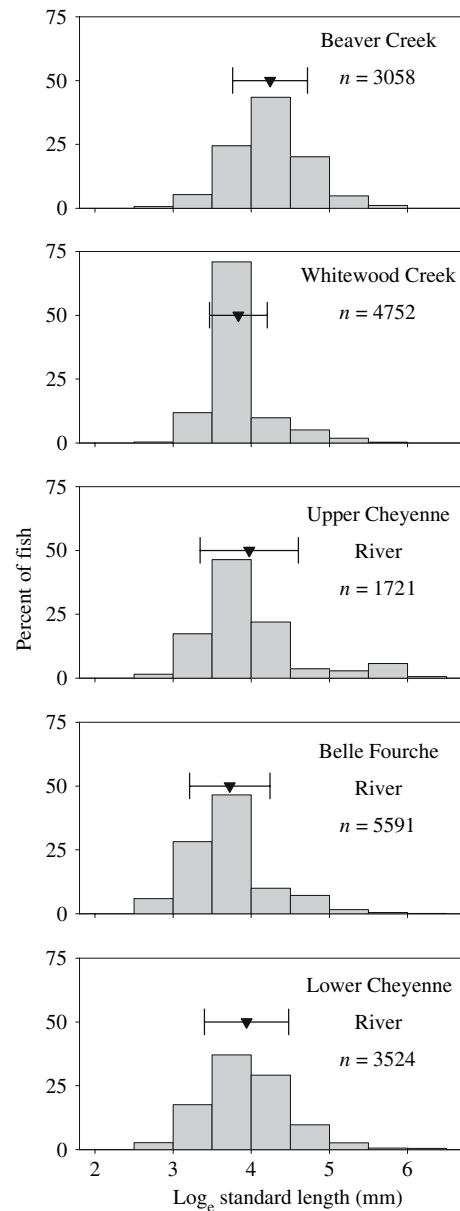thus argyritis*, *Carpiodes carpio carpio*, *Moxostoma*

Fig. 4 Frequency histograms of log$_e$-transformed fish standard
lengths (SL) by sampling station. Mean log$_e$-transformed SL
(*black triangle*) is also shown with the standard deviation
(*error bars*)

macrolepidotum) scored lowest. Species with high
PC2 scores were deep-bodied (*Hiodon alosoides*,
Cyprinus carpio, *Carpiodes carpio carpio*, Centrar-
chidae) and those scoring lowest were dorso-ventrally
compressed (*Macrhybopsis gelida*, *N. flavus*). High
scoring species on PC3 (*Carpiodes carpio carpio*,
N. flavus, *Lepomis cyanellus*) had no obvious

Fig. 5 Graphs of mean standard length with standard deviation (*error bars*) for dominant fish species by sampling stations, ordered by mean discharge (Table 1). Results of analysis of variance tests are shown for species that were dominant at more than one station (* = *P* < 0.05)
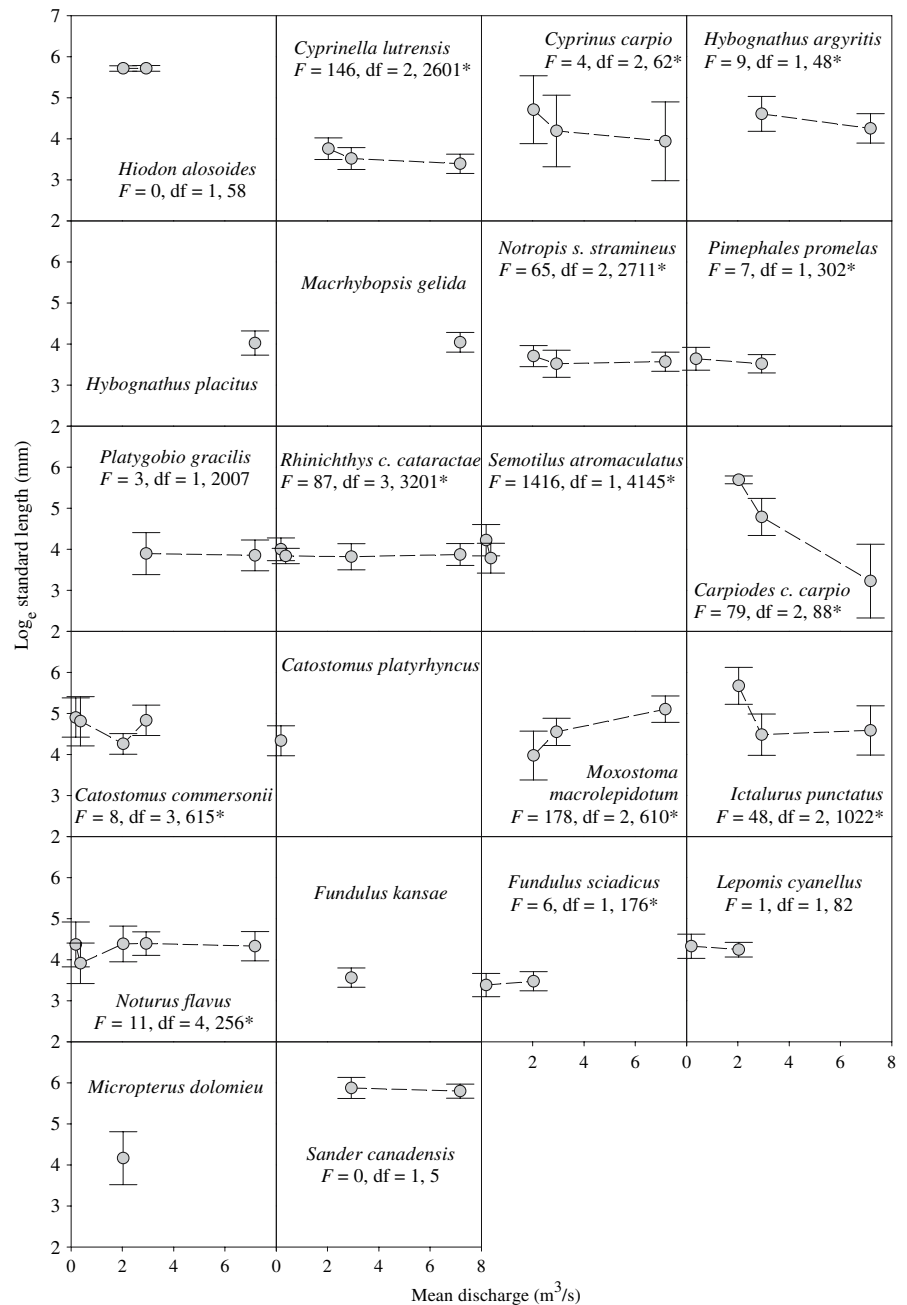
morphological similarity but, according to eigenvector loadings, shared a combination of wide bodies and heads, high eye position, small eyes, long snouts and dorsal fins, tall pelvic and anal fins, long gill rakers, short swim bladders, and large maximum SL. Species scoring low on PC3 were opposite and also difficult to interpret as a group (*H. alosoides*, *Cyprinella lutrensis lutrensis*, *Fundulus sciadicus*).

The 22 fish species were broadly distributed within morphospace (Fig. 6). Fish assemblages of river stations occupied the majority of the morphospace used by the entire species pool. Assemblages of creek stations, particularly the 5-species assemblage of Whitewood Creek, occupied smaller portions of the total morphospace. River assemblages exhibited more species clustering than creek assemblages.

Table 6 Mean values and coefficients of variation (CV) of 28 morphological traits for five fish faunas

Trait code	Whitewood Creek		Beaver Creek		Upper Cheyenne River		Belle Fourche River		Lower Cheyenne River	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
BD	0.2	8.8	0.3	3.8	0.3	4.5	0.3	4.5	0.2	4.0
BDBM	0.6	12.6	0.6	10.7	0.5	5.8	0.5	5.3	0.5	5.3
BW	0.2	9.3	0.2	12.0	0.1	6.3	0.1	5.6	0.1	5.3
PL	0.2	4.3	0.2	6.0	0.2	4.3	0.2	4.2	0.2	5.2
PD	0.5	6.2	0.5	6.0	0.4	6.0	0.5	6.1	0.4	7.2
HL	0.3	15.6	0.3	5.5	0.3	5.2	0.3	8.9	0.3	10.3
HD	0.6	7.3	0.6	7.3	0.5	7.3	0.5	5.7	0.5	5.8
HW	0.2	6.3	0.2	7.7	0.2	5.1	0.2	5.4	0.2	6.1
EP	0.7	6.5	0.8	7.7	0.7	6.5	0.7	6.6	0.7	7.5
ED	0.4	6.4	0.4	3.2	0.4	4.3	0.4	3.2	0.4	2.8
MP	3.0	4.2	2.6	2.0	2.6	2.2	2.9	3.4	3.1	4.8
MW	0.5	2.1	0.5	2.8	0.5	2.4	0.5	2.5	0.5	2.8
MH	0.3	3.3	0.3	3.1	0.3	2.5	0.3	1.5	0.4	1.5
SnL	0.8	3.9	0.7	4.1	0.6	3.4	0.6	2.5	0.6	2.3
DFL	0.1	8.6	0.2	1.5	0.2	1.6	0.2	1.4	0.2	1.4
DFH	0.2	7.8	0.2	7.4	0.2	4.1	0.2	5.1	0.2	6.2
PcFH	0.2	8.7	0.2	7.2	0.2	10.3	0.2	8.0	0.2	7.9
CFL	0.2	10.6	0.2	8.8	0.3	8.5	0.2	8.7	0.3	11.8
CFH	0.3	5.0	0.3	5.2	0.3	5.2	0.3	4.8	0.3	4.2
PlFH	0.1	5.3	0.2	4.2	0.2	4.9	0.2	5.4	0.2	7.0
AFL	0.1	2.4	0.1	2.9	0.2	2.2	0.1	1.9	0.1	2.4
AFH	0.2	3.6	0.2	5.1	0.2	5.7	0.2	4.4	0.2	6.1
JTL	0.0	-	0.0	0.6	0.0	0.7	0.0	0.4	0.0	0.3
GRC	1.4	2.6	1.6	2.9	1.8	3.2	1.7	2.7	1.5	2.3
GRL	0.0	2.4	0.0	1.3	0.0	1.5	0.0	1.8	0.0	1.4
GutL	1.3	1.7	1.5	1.0	1.5	1.2	1.8	1.1	2.1	1.0
SBL	0.3	1.9	0.3	2.2	0.3	3.0	0.3	2.9	0.3	2.5
MaxSL	168.4	1.9	162.6	2.0	230.2	1.5	214.5	1.4	221.0	1.2

Except for mouth position, gill raker code, and maximum standard length (SL), all measures are ratios (Table 2). Trait codes are in Table 2

The most notable species cluster included species with negative scores on PC1 and PC2, or PC2 and PC3 (Fig. 6). These were mostly small-bodied cyprinids (*C. lutrensis lutrensis*, *H. argyritis*, *Hybognathus placitus*, *Notropis stramineus missuriensis*, *Pimephales promelas*, *Platygobio gracilis*) along with a catostomid (*Catostomus commersonii*), an ictalurid (*Ictalurus punctatus*), and a funduliid (*Fundulus kansae*).

Euclidian distance measures indicated high morphological similarity among station faunas. Mean nearest-neighbor distance, average pairwise difference, and mean distance to centroid were similar among stations (Figs. 7–9). However, number of species per fauna predicted mean nearest-neighbor distance and mean distance to centroid (Fig. 10). Standard deviation of nearest-neighbor distances was not predicted by species richness, but was comparatively low for Whitewood Creek (Fig. 10). Nineteen of 22 species (86%) cooccurred with their nearest neighbor at one or more stations (Table 9).

Table 7 Axis eigenvalues, explained proportion of variation, cumulative variation explained, and eigenvector loadings for the first three principle components (PCs) based on morphological characters of 22 freshwater fish species

Trait code	PCA axis		
	1	2	3
Eigenvalue	5.64	4.94	3.76
Proportion of variation	0.20	0.18	0.13
Cumulative variation	0.20	0.38	0.51
BD	−	0.36	+
BDBM	+	+	+
BW	−	+	0.28
PL	+	−	−
PD	+	−0.20	−
HL	0.33	+	+
HD	+	−	+
HW	+	−	0.32
EP	+	−	0.29
ED	+	0.26	−0.27
MP	−0.34	−	+
MW	0.35	−	−
MH	0.30	−0.21	−
SnL	−	−0.25	0.25
DFL	+	0.27	0.24
DFH	−	−	+
PcFH	−0.21	−	+
CFL	−	+	+
CFH	−	0.35	−
PlFH	−	+	0.35
AFL	0.22	+	+
AFH	+	−	0.23
JTL	−0.33	−	+
GRC	+	0.31	+
GRL	0.23	0.27	0.22
GutL	−0.27	+	+
SBL	−	0.31	−0.28
MaxSL	−	+	0.23

Eigenvalues between −0.20 and 0.20 are represented only by − or + to emphasize traits with strong relations to each PC

Discussion

Fish assemblages of river stations were more speciose and, as a result, more morphologically diverse than assemblages in creek stations. Although mean distance to centroid did not vary among stations PCA

Table 8 Multiple regression results for analyses of mean principle component (PC) scores for freshwater fishes among five sampling stations and PC score standard deviation (SD) versus mean discharge (Q) and discharge flashiness (R-B index) by station

Axis and metric	B'_Q	$B'_{R\text{-}B}$	F	R^2
PC1 mean	−0.17	−0.86	41.68*	0.98
PC1 SD	0.97	−0.79	0.87	0.47
PC2 mean	0.75	−0.66	0.40	0.29
PC2 SD	1.32	−1.07	5.95	0.86
PC3 mean	−0.13	−0.59	0.89	0.47
PC3 SD	−0.31	−0.57	2.10	0.68

Scores are analyzed for three PC axes. Partial correlation coefficients (B′) are provided

* indicate statistically significant F values ($P < 0.05$)

and regression analyses indicated that richer faunas occupied wider morphospace. Morphologically unique species with high PC scores (*H. alosoides*, *H. argyritis*, *M. gelida*, *Carpiodes carpio carpio*, *M. macrolepidotum*) accounted for higher morphological diversity in river stations. Similar mean distance to centroid among stations may have resulted from a relatively small sample size (few species) and high variance (high species dispersion).

However, declining nearest-neighbor distances with increasing species richness indicated that more speciose assemblages were also more tightly packed in morphospace. This could in part result from chance (Ricklefs & Travis, 1980). Nevertheless, the relation between nearest-neighbor distance and species richness was supported by increased richness of small-bodied cyprinids (and a few other taxa) with relatively similar morphologies.

Faunal replacements caused position in morphospace to vary between creeks and rivers. With the notable exception of *Sander canadensis*, species of larger river stations (Belle Fourche River, Lower Cheyenne River) had smaller heads and mouths, subterminal or inferior mouths, and longer intestines compared to species of creek stations, perhaps reflecting a switch from carnivory to omnivory (Hugueny & Pouilly, 1999; Xie et al., 2001; Pouilly et al., 2003). Thus, distinct differences between creek and river fish faunas of the Great Plains (Cross & Moss, 1987; Bramblett & Fausch, 1991) may indicate trophic differences. Carnivores of small, headwater creeks presumably are adapted to prey upon entrained
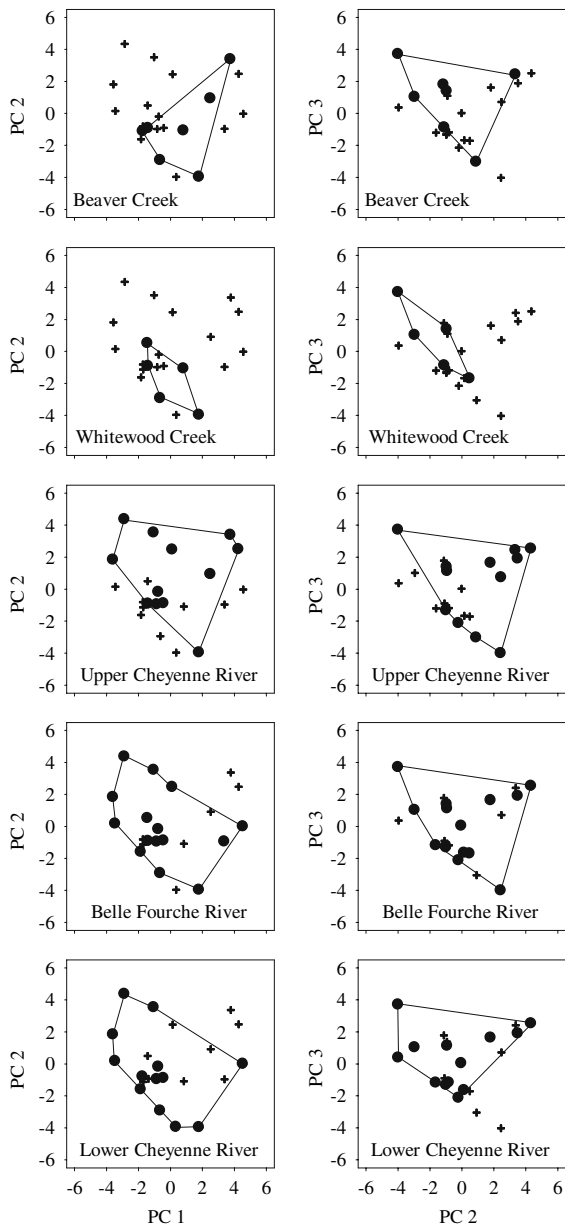
Fig. 6 Scatter plots of the first three principle components axes based on 28 morphological traits and a pooled species data set for five sampling stations. Species present at each named station are highlighted (*bold circles*) and bounded (*lines*)

Fig. 7 Frequency histograms of fish species Euclidian distances to the faunal centroid by sampling station. Mean Euclidian distance to the faunal centroid (*black triangle*) is also shown with the standard deviation (*error bars*). Analysis of variance indicated mean distance to the faunal centroid was similar among stations ($F = 0.1$, $P = 0.98$)

terrestrial invertebrates or large benthic invertebrates associated with coarse substrata, whereas omnivores of larger, mainstem rivers apparently are adapted to use benthic trophic pathways associated with the smaller-sized invertebrate fauna and vegetative
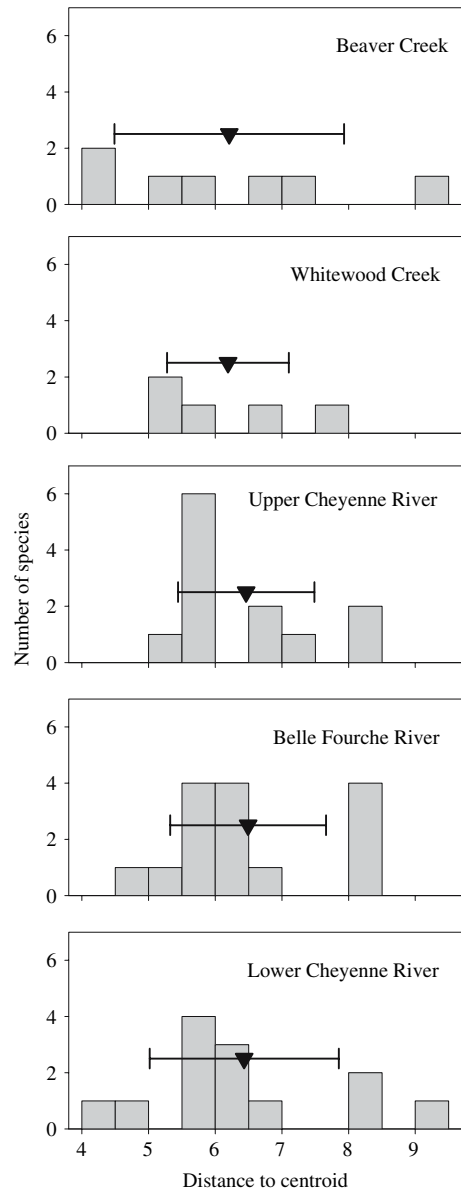
material of finer substrata and detritus (sensu Vannote et al., 1980; Minshall et al., 1985).

High mean distance to centroid (> 6.0) for all faunas indicates that fishes were hyperdispersed in morphological space. In comparison, Winemiller
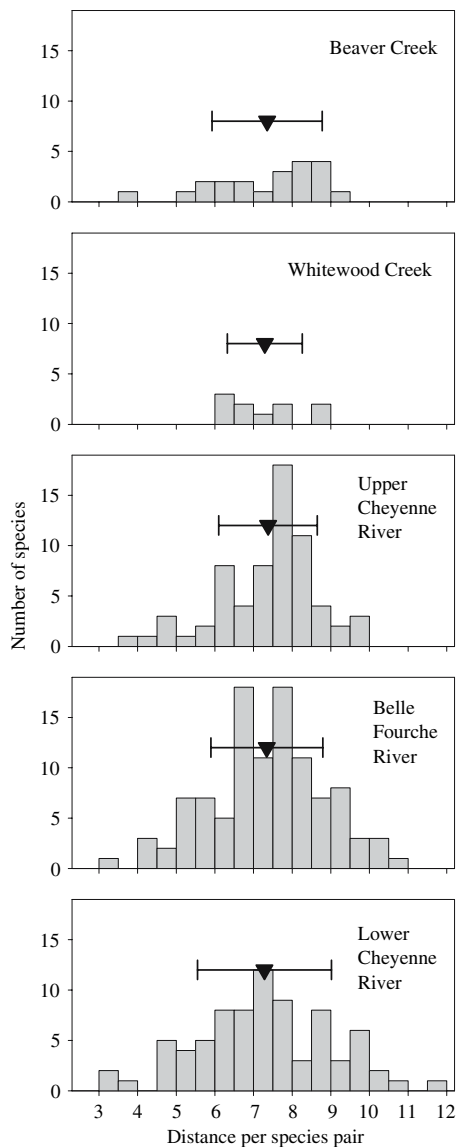
Fig. 8 Frequency histograms of fish species Euclidian distances among all species pairs by sampling station. Mean Euclidian distance among all species pairs (*black triangle*) is also shown with the standard deviation (*error bars*). Analysis of variance indicated mean distance among all species pairs was similar among stations ($F < 0.1$, $P = 1.00$)

Fig. 9 Frequency histograms of fish species similarities to nearest neighbors based on Euclidian distances among species. Mean Euclidian distance to nearest neighbor (*black triangle*) is also shown with the standard deviation (*error bars*). Analysis of variance indicated mean distance to nearest neighbors was similar among stations ($F = 1.2$, $P = 0.33$)

(1991) considered the Alaskan faunas he studied to be hyperdispersed with mean distance to centroid values of 2.0 and 2.5. Hyperdispersion suggests that open niches are available and is presumably a result of recent and repeated colonization of fishes from adjacent, more diverse faunas (Winemiller, 1991). Hyperdispersion is common where prehistoric climate patterns and topography have combined to limit
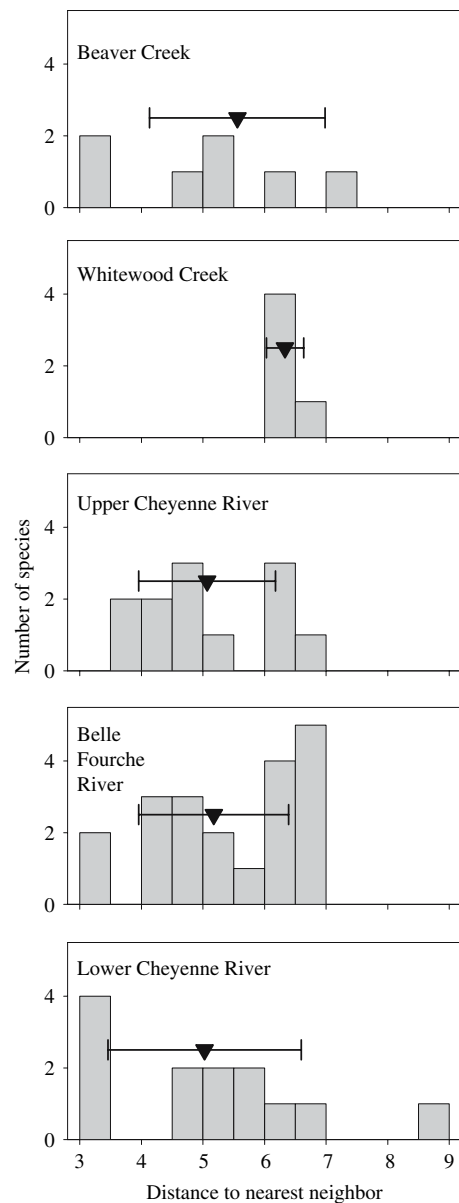
species diversity (Mahon, 1984; Moyle & Herbold, 1987; Hugueny, 1989; Oberdorff et al., 1997). This paradigm fits well with fish assemblages of the Cheyenne River drainage because they have been formed largely within the last 12,000 years as the climate has warmed and are subsets of larger faunas
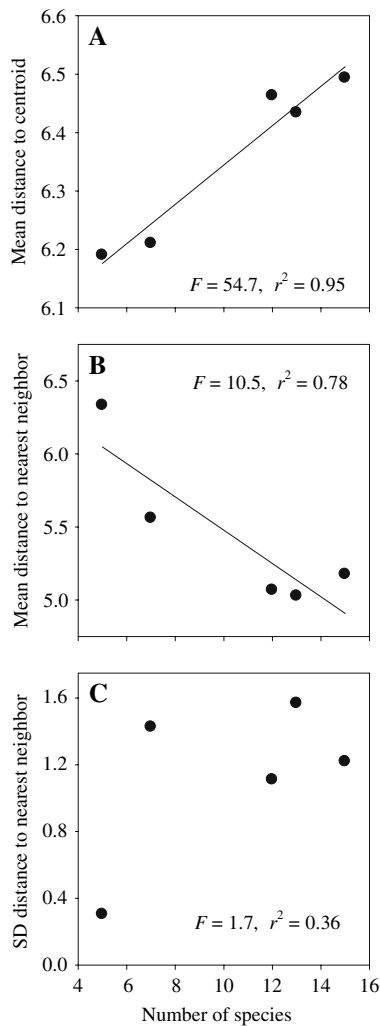
Fig. 10 Three measures of Euclidian distance among fish species plotted against species richness:(**A**) mean distance to the faunal centroid, (**B**) mean distance to the nearest neighbor, and (**C**) standard deviation of mean distance to the nearest neighbor. Results of simple linear regressions are provided for each graph and lines are plotted for statistically significant regressions ($P < 0.05$)

found to the southeast (Cross et al., 1986; Hoagstrom & Berry, 2006). Moreover, hyperdispersed faunas are typically unsaturated and invasible (Hugueny & Paugy, 1995; Belkessam et al., 1997), which has been demonstrated for Great Plains fish faunas (Gido & Brown, 1999; Gido et al., 2004).

The hyperdispersed faunas of the Cheyenne River drainage have high morphological diversity because most genera are represented by a single species. Members of hyperdispersed faunas typically

segregate among habitats and do not exhibit intense interspecific interactions (Moyle et al., 1982; Moyle & Vondracek, 1985; Oberdorff et al., 1998). There are strong relations between habitat availability and fish distribution and abundance in the Great Plains (Hubert & Rahel, 1989; Quist et al., 2004a; b; Brunger Lipsey et al., 2005), which suggest that interspecific interactions are less important in faunal assembly than habitat conditions. A high level of co-occurrence of morphological nearest neighbors in our study supports this contention.

Relations between larger mean SL, less flashy flow regimes, and larger streams support Schlosser (1987) who emphasized the importance of stable environments for larger fishes. However, length distributions varied among species. Some large-bodied fishes (*Cyprinus carpio*, *H. argyritis*, *Carpiodes carpio carpio*, *I. punctatus*) had higher mean SL upstream, perhaps because adults migrated upstream to spawn, but eggs or larvae drifted downstream. Similarly, smaller-bodied species that were most abundant upstream (*C. lutrensis lutrensis*) may have been present downstream as displaced larvae or juveniles (sensu Brown & Armstrong, 1985; Harvey, 1987). Increasing length of *M. macrolepidotum* downstream was clearly related to reproduction and recruitment. Low mean SL in the Upper Cheyenne River resulted from the abundance of young-of-year, whereas high mean SL in the Lower Cheyenne River resulted from the opposite (Hoagstrom et al., 2007b). Perhaps most striking was that the fauna of the smallest stream (Beaver Creek) had the highest mean SL. This was presumably a result of a very stable flow regime and deep pools that supported fish populations with a greater proportion of larger adults (Hoagstrom et al., 2007b). Hence, a general explanation for increasing mean SL with increased flow stability and discharge is lacking, but likely relates to better growth and survival in more benign habitats and reduced susceptibility to predation in deeper habitats (Schlosser, 1987; Harvey & Stewart, 1991).

The native morphological diversity of river stations was presumably higher than at present. Large-river fishes have declined and disappeared from the Cheyenne River drainage since settlement, but have not been replaced by non-natives (Hoagstrom et al., 2006; Hoagstrom et al., 2007a). Missing species such as *Scaphirhynchus platorynchus*, *Lepisosteus platostomus*, *Cycleptus elongatus*, and *Lota lota*

Table 9 Nearest-neighbor distance between dominant species. Species abbreviations, nearest species, Euclidian distance between pairs (ED), and cooccurrence yes (Y) or no (N), are provided

Species	Species code	Nearest neighbor	ED	Y or N
Hiodon alosoides	HIOALO	PIMPRO*	6.6	Y
Cyprinella lutrensis lutrensis	CYPLUT	NOTSTR	3.5	Y
Cyprinus carpio	CYPCAR	CARCAR	4.6	Y
Hybognathus argyritis	HYBARG	PIMPRO*	4.4	Y
Hybognathus placitus	HYBPLA	NOTSTR	4.4	Y
Macrhybopsis gelida	MACGEL	RHICAT	4.7	Y
Notropis stramineus missuriensis	NOTSTR	CYPLUT	3.5	Y
Pimephales promelas	PIMPRO*	NOTSTR	3.5	Y
Platygobio gracilis	PLAGRA	NOTSTR	6.3	Y
Rhinichthys cataractae cataractae	RHICAT	NOTSTR	4.2	Y
Semotilus atromaculatus	SEMATR	PIMPRO	4.8	Y
Carpiodes carpio carpio	CARCAR	CYPCAR	4.6	Y
Catostomus commersonii	CATCOM	CATPLA*	3.4	Y
Catostomus platyrhynchus	CATPLA*	CATCOM	3.4	Y
Moxostoma macrolepidotum	MOXMAC	CARCAR	4.7	Y
Ictalurus punctatus	ICTPUN	SEMATR	6.6	N
Noturus flavus	NOTFLA	MACGEL	6.0	Y
Fundulus kansae	FUNKAN	FUNSCI	6.5	N
Fundulus sciadicus	FUNSCI	SEMATR	5.9	Y
Lepomis cyanellus	LEPCYA*	MICDOL	4.1	Y
Micropterus dolomieu	MICDOL	LEPCYA*	4.1	Y
Sander canadensis	SANCAN	MICDOL	4.8	N

* Species relative dominance < 1.0% where nearest neighbors co-occur

(Hoagstrom & Berry, 2006) had extreme morphologies and presumably increased historical morphological diversity. In contrast, missing native species from creek stations (*Couesius plumbeus*, *Notropis stramineus missuriensis*; Bailey & Allum, 1962) would have increased morphological diversity less because they are relatively similar to extant species (*Rhinichthys cataractae cataractae*, *Semotilus atromaculatus*). Hence, hyperdispersion may have been less in native creek faunas.

This study indicates that increasing species diversity downstream in the Great Plains corresponds to increasing morphological diversity. Elsewhere, such increases are commonly attributed to higher habitat diversity (Gorman & Karr, 1978) or higher habitat stability (Horwitz, 1978). In our study, habitat stability decreased downstream, suggesting that increased niche diversity may account for higher morphological diversity (sensu Scarnecchia, 1988; Willis et al., 2005). Further, niche diversity in our

river stations may have been underestimated because, although the small-bodied cyprinid guild increased morphological similarity in river stations, such species commonly partition habitats (Douglas, 1987). We did not measure habitat diversity directly, but our observations suggest that habitat diversity declined downstream because riffles and pools became less distinct and increasing channel width resulted in a predominance of run habitat (Hampton & Berry, 1997). Rahel and Hubert (1991) found that habitat diversity declined downstream in Horse Creek, Wyoming, a typical Great Plains stream, and concluded that either increased living space or increased habitat stability accounted for increased species diversity. Thus, higher niche diversity our in river stations may reflect increased living space (sensu Rahel & Hubert, 1991), which presumably refers to increased niche space without a measurable increase in structural complexity. Winemiller (1991) referred to this as increasing habitat volume. Hence, studies

that determine how fishes of Great Plains rivers segregate niches in the absence of physical habitat structure will be necessary to further describe trophic relations within these faunas.

Appendix 1

Mean values (rounded to the nearest mm except for coded attributes MP and GRC) for 29 morphological traits of 22 common fish species. Species and trait codes are given in Tables 3 and 6

Character	Species										
	Hio-alo	Cyp-lut	Cyp-car	Hyb-arg	Hyb-pla	Mac-gel	Not-str	Pim-pro	Pla-gra	Rhi-cat	Sem-atr
SL	258	58	113	123	69	58	45	55	91	58	102
BD	67	18	43	33	16	10	11	15	19	14	24
BDBM	37	9	19	16	8	5	5	8	6	7	14
BW	27	6	18	19	7	6	7	8	13	10	16
PL	35	14	22	25	13	13	11	14	19	14	23
PD	25	7	16	17	7	4	5	7	8	6	11
HL	56	14	33	26	17	15	11	13	24	16	29
HD	31	8	20	14	8	7	6	7	14	6	14
HW	27	8	21	18	10	9	8	9	13	11	19
EP	15	5	13	8	5	5	4	5	7	5	9
ED	14	4	7	5	3	3	3	3	4	3	5
MP	2	2	3	3	3	4	3	3	3	3	2
MW	14	3	7	6	4	4	3	3	6	4	9
MH	19	5	9	7	4	5	4	3	11	5	9
SnL	9	4	10	8	5	6	3	4	7	6	9
DFL	24	9	49	14	8	8	6	7	9	7	12
DFH	39	15	22	24	16	12	11	13	19	12	17
PcFH	50	12	23	25	14	11	9	10	24	12	16
CFL	56	14	31	32	18	15	11	12	23	13	22
CFH	79	16	47	44	14	14	10	17	25	11	29
PlFH	32	10	21	18	11	9	7	7	10	9	14
AFL	78	9	11	10	7	8	5	4	5	6	11
AFH	51	10	22	13	11	10	8	7	17	12	15
JTL	1	0	0	0	0	0	0	0	0	0	0
GRC	2	1	2	1	2	1	1	2	1	1	1
GRL	3	0	2	1	0	0	0	1	1	0	1
GutL	220	38	204	746	406	37	42	124	77	41	80
SBL	123	18	42	52	26	7	16	20	34	9	38
MaxSL	350	69	490	145	96	80	63	66	185	122	198

Appendix 1 continued

Character	Species										
	Car-car	Cat-com	Cat-pla	Mox-mac	Ict-pun	Not-fla	Fun-kan	Fun-sci	Lep-cya	Mic-dol	San-can
SL	134	150	109	154	116	90	45	39	87	86	70
BD	46	32	24	40	25	18	9	12	35	25	12
BDBM	22	20	13	21	7	10	5	6	22	13	8
BW	24	25	19	25	18	13	4	6	15	11	9
PL	20	22	20	22	17	15	12	8	19	18	16
PD	19	14	11	17	10	11	6	6	13	11	6
HL	33	38	24	35	31	23	12	11	33	32	23
HD	21	21	14	23	14	9	6	5	20	15	8
HW	25	24	18	24	23	21	8	8	18	17	10
EP	14	16	10	15	9	8	5	4	17	11	5
ED	8	6	4	8	6	3	3	3	7	7	5
MP	4	4	4	4	3	3	1	1	1	1	2
MW	7	7	9	5	10	11	3	3	9	10	7
MH	5	7	3	4	8	8	4	4	11	11	12
SnL	8	17	11	13	12	8	4	3	9	9	7
DFL	55	23	18	30	11	11	8	5	39	36	36
DFH	43	26	19	35	24	18	12	5	16	14	12
PcFH	25	29	23	35	21	18	8	6	20	15	10
CFL	41	29	20	42	31	22	10	9	22	22	15
CFH	44	38	31	47	27	20	11	11	30	28	18
PlFH	24	19	18	26	15	17	5	4	16	14	12
AFL	12	12	11	15	30	17	7	4	17	14	10
AFH	29	27	23	34	16	23	12	6	17	14	12
JTL	0	0	0	0	0	0	0	0	0	0	1
GRC	3	2	2	2	2	1	2	2	2	2	2
GRL	4	2	1	2	2	2	1	0	3	4	2
GutL	641	305	519	370	95	72	66	29	61	77	40
SBL	50	51	24	68	20	7	16	17	28	30	20
MaxSL	346	315	132	321	585	166	56	54	165	340	415

Standard length (SL) was not used in analyses except as the denominator for trait ratios

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