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Habitat alterations and fish assemblage structure in the Missouri River system, USA: Is ecomorphology an explanation?

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Sampling was conducted over a two-year period to determine if fish body morphology (as indicated by the Fineness Ratio (FR), an index of fish streamlining) and habitat alterations can interact to influence fish assemblage structure in three human-altered segments of the Missouri River. It was hypothesized that segments with more variability in depths, velocities, and substrates would have a fish assemblage characterized by more diversity in streamlining. Conversely, it was hypothesized that fish assemblages in more altered river segments would exhibit less diversity in streamlining, i.e., less variability from optimal values because of more uniform habitat conditions. In faster more uniform habitats, fewer variations from optimal streamlining would be adaptive. The three flowing segments studied encompassed the mouth of the Yellowstone River (YSS; moderately altered), the area below Garrison Dam, North Dakota (GOS; below dam-highly altered) and the segment from St. Joseph to Kansas City, Missouri (SKS; channelized-highly altered). The three segments exhibited greatly different fish assemblages. Small native minnows (Cyprinidae), particularly flathead chub (*Platygobio gracilis*), and deep-bodied suckers, such as bigmouth buffalo (*Ictiobus cyprinellus*), were common in the YSS. The GOS was dominated by the dorsally compressed fathead minnow (*Pimephales promelas*). Emerald shiner (*Notropis atherinoides*) and gizzard shad (*Dorosoma cepedianum*) dominated the fish assemblage in the SKS. When FR and physical conditions were analyzed across all habitat types, the least altered, more natural YSS was characterized by higher diversity of FR and higher variability in velocity and depth than the most altered SKS. Results for the GOS were more difficult to interpret. The fish assemblage in the highly channelized SKS exhibited the weighted mean FR that was closest to the optimal 4.5 value (FR = 4.42) with the smallest deviation from optimal (0.08). The highest mean and highest maximum current velocity use in the three segments was found for species such as sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), and blue sucker (*Cycleptus elongatus*), that were nearly optimally streamlined. Deep-bodied species with FRs typically below 3.5, such as *Ictiobus* spp., river carpsucker (*Carpiodes carpio*), and centrarchids, tended to exhibit the lowest mean and lowest maximum current velocity use in the three segments. Results of this study can be useful in helping to understand fish assemblage composition in relation to river alterations in various geographical areas. Because the fineness ratio is only a simple index of streamlining and does not account for other anatomical (e.g., fins) and behavioral aspects of fishes, more studies on different species are needed to develop a stronger understanding of how fish cope with the current. Because of the complexity of interacting natural and human-caused factors affecting these highly altered large river systems, fish streamlining is only one of several factors that may influence the observed fish community structure of a large river system. Streamlining deserves consideration, however, for inclusion in more complex models explaining and predicting fish community structure in large rivers.

Key Words: fish morphology, streamlining, Missouri River, fineness ratio, river alteration

Introduction

Numerous natural and human-induced factors interacting in complex ways can lead to the species composition of a fish assemblage observed throughout a river system (Karr et al. 1985; Jackson et al. 2001; Agostinho et al. 2004). These factors can include the historical biogeography, species access from other river systems, habitat fragmentation, reservoir influences, temperature and other water quality influences.
Regulation and impoundment of large rivers, including damming and channelization, have resulted in major habitat changes in these important aquatic systems. Dams have interrupted ecological processes by reducing nutrient flow, altering temperature regimes, trapping sediment, and changing the frequency and timing of discharge (Hesse 1987; Gup 1994; Ligon *et al.* 1995; Poff *et al.* 1997). Channelization, the artificial straightening and dredging of rivers, has modified or eliminated natural river features such as channel meandering and pool-riffle sequence and changed river hydrology and morphology (Swales 1988). The loss of these features from channelization results in more uniformity in river characteristics, including depths, velocities, and substrates (Congdon 1971; Simpson et al. 1982; Swales 1982; Scarnecchia 1988; Hesse and Sheets 1993).

Large river modifications such as dams and channelization have also impacted fish assemblage structure. The effects of dams and channelization on fish diversity, richness, density, and productivity have been well documented (Portt et al. 1986; Swales 1988; Neves and Angermeier 1990; Brittain et al. 1993; Agostinho and Zalewski 1995; Jurajda 1995; Kubecka and Vostradovsky 1995).

One potential indicator of habitat changes leading to changes in fish assemblage structure in altered rivers is a change in the ecomorphological composition of the fish community. In the evolution of riverine fish, many environmental conditions influence fish physiology, behavior, and morphology (Moyle and Cech 1988; Danzmann et al. 1993; Fujii 1993). These variable conditions ultimately result in a wide variety of body shapes. A few studies have analyzed the links between fish assemblage structure, river and stream characteristics (e.g., natural versus altered), and fish ecomorphology. Scarnecchia (1988) found that channelized reaches of an Iowa stream had lower species diversity than unchannelized reaches, and the species present in the channelized reaches showed less divergence from optimal streamlining. Consistent with this result, Willis et al. (2005) studied the fish species assemblage in the Cinaruco River, Venezuela and reported that there were greater between-species differences in morphology in habitats with less flow and greater complexity. Altered flow regimes and loss of floodplain habitats have been linked to reduced taxonomic and functional diversity species diversity in the fish assemblage (e.g., unregulated Gambia River: White *et al.* 2012).

One environmental factor that fish respond to is current velocity. Different species of fish possess different body types that allow them to move differentially through the water or hold their position in high current velocity (Gibbs-Smith 1962). A streamlined body shape is one such evolutionary response. In water, the flow pattern around any solid body becomes distorted, producing streamwise (i.e., in the direction of flow), favorable, and adverse pressure gradients. For fishes that are more streamlined, i.e., elongate and taper to a point, fluid gradually decelerates in the rear, little or no separation of the boundary layer occurs, and the object is pushed forward by the wedge-like closure of the fluid behind it (Vogel 1981). Although a streamlined body is designed to have zero pressure drag in a fluid, in practice this is not possible, and a streamlined body is defined as a body with least resistance (Webb 1975).

Streamlining in fish has been described by the Fineness Ratio (FR) = l/d, where l is the total length of the body (excluding fins), also known as the standard length (measured from the tip of the fish's snout to the base of the caudal fin), and d is the maximum depth of the body (excluding fins) (Webb 1975;1989). In a river or stream environment, a streamlined fish is one with a body shape that allows the fish to hold its position in relatively high velocity currents. The "optimal" fitness ratio for fishes is 4.5; this value gives minimum drag for maximum body volume (Webb 1975). Fineness ratios can vary between about 3 and 7, however, and result in only about a 10% change in drag from the optimum value.

Nearly one-third of the Missouri River has been channelized and another one-third has been impounded by six mainstem dams. The free-flowing Missouri River was turbid (Evermann and Cox 1896) and exhibited frequent flooding and a diversity of habitats exhibiting a wide range of velocities (Hesse and Sheets, 1993). Since the early twentieth century, it has been characterized by reduced sediment transport and a more stable hydrograph – a result of dam construction and land use practices throughout the basin (Hesse 1987; Hesse et al. 1989). Its once shallow and meandering channel has been channelized for navigation, primarily between Sioux City, Iowa and St. Louis, Missouri. As of 2018, only the upper one-third of the Missouri remains comparatively free-flowing, although it is much altered from its condition two centuries ago.

Present-day Missouri River segments exhibit greatly different hydrological and morphological characteristics. Some riverine segments resemble the historic Missouri River whereas other segments are greatly altered by channelization and impoundment (Hesse et al. 1989; Hesse and Sheets 1993; Young et al. 1997). The environmental differences between these segments, especially as manifested by current velocity, can be expected to influence fish assemblage structure. The hydrologic and morphologic diversity of Missouri River segments presents an opportunity to examine the influence of dams and channelization on fish assemblage structure.

As part of a multi-state Missouri River benthic fish study characterizing fish communities in un-impounded reaches of the Missouri River, efforts were made to not only describe the fish communities, but to identify factors leading to between-segment differences in fish species composition, life history, and ecomorphology. This study addressed the ecomorphological differences. The objective of this study was to investigate the relationships among river alterations, streamlining and fish assemblage structure in segments of the Missouri River. It was hypothesized that segments that have more variability in depths, velocities, and substrates would have a fish assemblage characterized by more diversity in streamlining. In faster, more uniform habitats, fewer variations from optimal streamlining would be adaptive. Conversely, it was hypothesized that fish assemblages in more altered river segments would exhibit less diversity in streamlining, i.e., less variability from optimal values because of the presence of more uniform habitat conditions. If these hypotheses are supported, ecomorphology of the fish community would be one of several key metrics potentially useful in understanding and modeling fish assemblage structure in large rivers.

Methods

Study Area: The relationship between fish morphology and habitat alteration was examined with a data set from three Missouri River (USA) segments. Two of the study segments are in the state of North Dakota. One North Dakota segment extends 76 km from the Yellowstone-Missouri River confluence (Missouri River km (rkm) 2546.0) near the North Dakota-Montana border to its lower boundary of Lake Sakakawea (rkm 2470.3) and is hereafter referred to as the Yellowstone-Sakakawea Segment (YSS; Fig. 1). The second North Dakota segment extends 184 km from

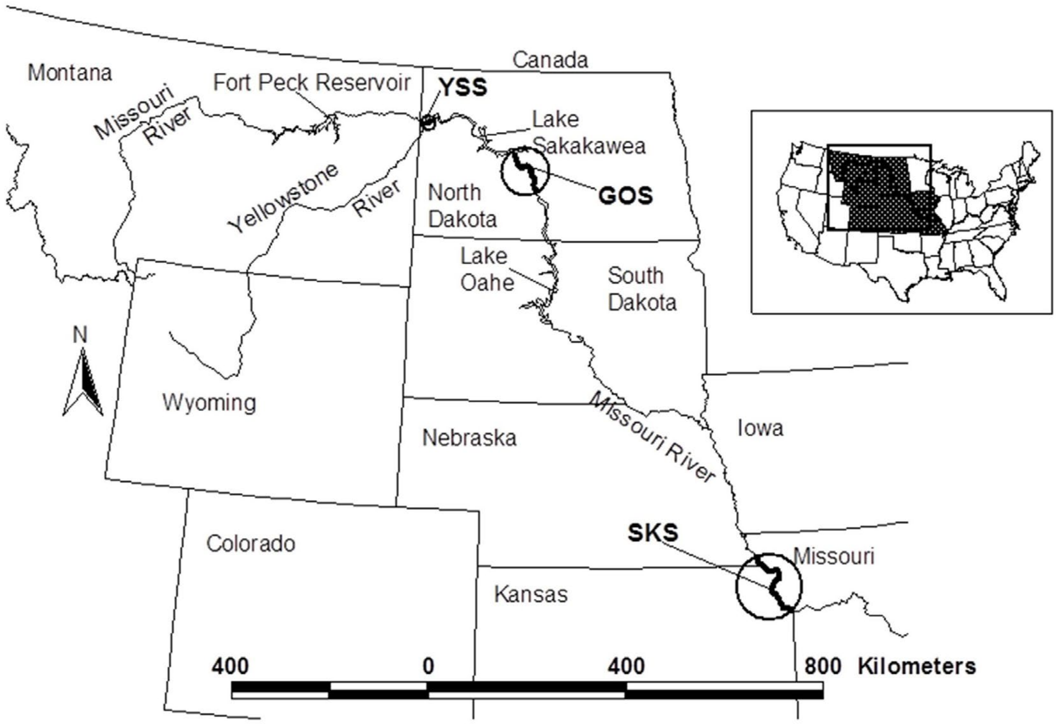

Figure 1. Map showing location of study segments (YSS=Yellowstone-Sakakawea Segment, GOS=Garrison-Oahe Segment, SKS=St. Joseph-Kansas City Segment).

Garrison Dam (rkm 2235.4) in south-central North Dakota to its lower boundary of Lake Oahe (rkm 2051.9) near the North Dakota-South Dakota border and is hereafter referred to as the Garrison-Oahe Segment (GOS; Fig. 1). The third study segment flows along the Kansas-Missouri border and extends 117 km from its upper boundary at St. Joseph, Missouri (rkm 708.1) to its lower boundary near Kansas City, Missouri (rkm 591.4) and is hereafter referred to as the St. Joseph-Kansas City Segment (SKS; Fig. 1).

The three segments exhibit differing levels of modification. The YSS is the least altered study segment. This segment has a semi-natural hydrograph, a result of the merging of the free-flowing Yellowstone River and the Missouri River, which is regulated upriver by Fort Peck Dam. This segment has no major shoreline development and few revetted banks (rip-rap). Lack of shoreline development and revetted banks allows the main river channel to meander naturally, which creates a diversity of off-channel habitats. The GOS, in contrast, has fewer pre-impoundment physical and biological characteristics. Garrison Dam and Lake Sakakawea have created an alluvium sink, thereby reducing the sediment load in the river below the dam (Berkas 1995). The river below the dam is uncharacteristically clear and natural aggradative and degradative processes have been disrupted. The dam strongly regulates the hydrograph. Furthermore, hypolimnetic withdrawals from Lake Sakakawea have created uncharacteristically cool water temperatures during the summer with maximum summer temperatures approximately 9 °C cooler than before impoundment (Everett 1999). This segment also has numerous revetments and considerable (25-40%) shoreline development and bank stabilization.

The SKS is the most heavily modified study segment. Wing-dams, dikes, and rip-rap have been used to form and maintain a navigation channel. These modifications have greatly narrowed and deepened the river channel (Sayre and Kennedy 1978), changing the depth-velocity profile (Latka et al. 1993) and reducing the diversity of depths, velocities, and substrates in the river (Hesse and Sheets 1993). These structures also prevent natural meandering of the main river channel.

Data Collection: Fish assemblage and habitat data used in this analysis were collected using standardized sampling procedures as part of the multi-state Missouri River benthic fish study (Sappington et al. 1998) over a two-year period (1997: Year 1 and 1998: Year 2). Stratified random sampling was used to collect fish in the three study segments where the strata were macrohabitat types. The macrohabitats were main channel cross-over, outside bend, inside bend, secondary channel: non-connected, secondary channel: connected, and tributary mouth. In the segments, macrohabitats served as sampling units. Throughout the un-impounded portions of the Missouri River basin, the standardized sampling procedures developed defined macrohabitat characteristics and outlined the protocol for sampling fish in each macrohabitat type. In each segment, fish were collected from five randomly selected sample units of each stratum from July through September in both sample years. Several fishing gears were used to enable sampling of a wide variety of species and sizes within sample units, thereby ensuring accurate description of the fish assemblage in each segment. These gears were bag seines, a benthic beam trawl, trammel nets, a boat-mounted electrofisher, gill nets and hoop nets, with specifications of each gear type detailed in Sappington et al. (1998).

To characterize habitat, water depth (m), velocity (m/sec), and substrate (% silt, % sand, % gravel) were measured at each subsample following the successful deployment and retrieval of fish collection gears and later used to characterize segments and segment macrohabitats. An in-depth description of habitats, measurement of habitat variables, and fish collection techniques, is presented in Sappington et al. 1998). Water depth was measured with a sonar device to the nearest 0.1 m. In macrohabitat sample units deeper than 1.5 m, the boat was first anchored in the sample unit and then current velocity was measured with the aid of an A55M sounding reel and hangar bar (19.1 mm x 304.8 mm). A Marsh-McBirney Flowmate Model 2000 probe was attached to the hangar bar and lowered near bottom with the sounding reel. A 22.7-kg sounding weight was used to keep the current velocity meter probe pointed into the current and positioned directly below the boat. Current velocity was measured to the nearest 0.1 m/sec.

A bottom substrate sample was collected with an iron pipe (61.0 cm in length x 10.2 cm in diameter) that had one end closed. One end of a nylon rope was attached to the open end of the pipe and the other connected to the boat. The pipe was then dragged through the area of the gear sample. The pipe contents were emptied onto the boat and the percentage of silt (particle size <= 0.06 mm), sand (particle size 0.06 <= 2.0 mm), and gravel (particle size 2.0 mm <= 16 mm) were visually estimated. Later, the geometric mean of substrate size was calculated for each subsample (McMahon et al. 1997). Depth, velocity, and substrate were also measured with the same devices in shallow macrohabitat replicates (less than 1.5 m deep) at each fish collection subsample. Water column depth and water velocity were measured with the aid of a standard wading rod at three points along the gear sampling area. Substrate was measured in these shallow habitats with the same methods as for macrohabitats greater than 1.5 m deep.

Fish Assemblages: *Fineness Ratio* -- In Year 2, the standard body length and maximum body depth of 10-20 fish for each species were measured for calculating FRs in the YSS and the GOS. For the SKS, standard body length and maximum body depth were measured for most species (10-20 fish/species) from museum specimens collected from this segment in

1992 (Dr. Thomas Wenke, Fort Hays State University, Hays, Kansas) and later housed at Sternberg Museum of Natural History (Fort Hays State University, Hays, Kansas). For five species (flathead chub; goldeye; emerald shiner, *Notropis atherinoides*; spottail shiner, *Notropis hudsonius*; and smallmouth buffalo, *Ictiobus bubalus*), comparisons were made between measurements taken from live and preserved specimens to determine if they differed. A collection of 20 fish for each species was made and measurements were taken from these live specimens in the field. These fish were then preserved in 10% formalin for four weeks and measured again in the laboratory. For each species, the live and preserved FRs differed by no more than 0.03. For species in the SKS segment for which there were no museum specimens, FRs were obtained from the other Missouri River segments in this study (Sappington et al. 1998). The species included the flathead chub, *Platygobio gracilis*; sicklefin chub, *Macrhybopsis meeki*; shovelnose sturgeon, *Scaphirhynchus platorynchus*, longnose gar, *Lepisosteus osseus*; flathead catfish, *Pylodictis olivaris*; and quillback, *Carpiodes cyprinus*). Although aspects of body shape within a species has been shown to vary with environmental conditions (Hopper et al. 2017), in our case, it was necessary to assume that differences in body morphology within a species among segments were small compared to differences among species.

Bow calipers (300-mm gape) were used to measure maximum body depth for large fish, whereas dial calipers (150-mm gape) were used to measure maximum body depth for small fish. Standard body length and maximum body depth were recorded to the nearest 0.01 mm. For some species of fish, changes in morphology associated with ontogeny can occur (Reis et al. 1998; Hood and Heins 2000). Therefore, plots of FR versus standard length were constructed for most individual species to determine if FR remained constant over a variety of fish lengths. In cases where FR changed as fish length increased, fish were separated into length groups and FR computed for each of these groups.

Mean assemblage FR for each segment was calculated by weighting according to relative abundances of the different species, i.e., by dividing the number of individuals of a species by the total number of individuals for all species (Scarnecchia 1988). Relative abundances were calculated for all species for which FRs were obtained. We excluded any species with a relative abundance less than 0.1% in a segment from all analyses. Weighted FR means were then calculated for each river segment by multiplying the relative abundance of each species by its mean FR, and summing for all species in the segment. Deviation of segment weighted mean FRs from optimal (4.50) was determined by subtracting each weighted FR value from 4.50.

Fineness ratios were also computed for each macrohabitat in a segment to examine the relationship between FR and macrohabitat physical conditions. First, the FRs for each macrohabitat subsample were weighted by fish relative abundance and summed, obtaining a weighted FR for the subsample. Then, the subsample FRs were averaged to obtain the replicate FR. Next, replicate FRs were averaged to obtain the macrohabitat mean FR for a year. Finally, yearly FR means were averaged for each macrohabitat type.

Variability in FR was examined using coefficient of variation (CV), the standard deviation divided by the mean (Zar 1984). For each segment, CV was calculated for each macrohabitat replicate in a year. Then, macrohabitat replicate values were averaged, giving the yearly mean for each macrohabitat type. Finally, yearly macrohabitat CV values were averaged.

Variation in FR across macrohabitat types was also computed for each segment. CV values obtained for each macrohabitat type were averaged within years. Finally, yearly values were averaged, yielding the CV for the segment.

Additionally, the diversity and evenness of fish among various FR categories were examined for each segment. FR heterogeneity in each segment was determined with the reciprocal of Simpson's index (1/D; Williams 1964). Species evenness for each segment was computed with Smith and Wilson's index (E; Smith and Wilson 1996). FR categories were classified into eight classes: <3.00, 3.00-3.49, 3.50-3.99, 4.00-4.49, 4.50-4.99, 5.00-5.49, 5.50-5.99, and >5.99.

Physical Characteristics and Fish - Physical conditions in each segment were characterized at the macrohabitat level. Mean velocity was computed by first averaging subsample measurements taken at a macrohabitat replicate. Next, replicates were averaged, giving the yearly mean for each macrohabitat type. Finally, yearly values were averaged to obtain the overall mean depth, velocity, and substrate size for each macrohabitat type.

Variation in depth, velocity, and substrate within and across macrohabitat types in each segment was determined with CV. Calculation of CV for the three physical variables followed the procedures used for computing CV for FR.

Mean current velocity use and maximum current velocity use by fish were examined for each species and for the eight FR categories. Mean use for individual species was computed using subsample observations. A subsample taken within a macrohabitat replicate that contained at least one fish was considered an observation for a species. These observations were averaged to obtain the mean current velocity used by the species. Mean use for each FR category was obtained by first computing the mean current velocity used by each species. Then, species were placed into categories based on their FR. Finally, mean velocity values for species in a category were averaged. The maximum current velocity used by a species or a FR category is the highest current velocity measured in a subsample observation containing a species or a species from a FR category. Use by FR categories was examined for each segment using bar plots.

Statistical Analyses: Each of the six macrohabitat types was found in each segment; however, not all types were common enough among segments to permit comparison of their physical variables and FRs. Therefore, mean weighted FR, current velocity, depth, and substrate were compared among segments for only main channel cross-over, outside bend, and inside bend macrohabitats in each segment. Comparisons were made by performing Friedman's analysis of variance on ranks (test statistic=x_r^2; Friedman 1937) with segments serving as treatments and years as blocks. A Tukey-type multiple comparison procedure for ranked data was performed following a significant ANOVA (Zar 1984).

Relations between habitat variables and fish assemblage FRs were evaluated with regression methods. Linear least-squares regression was used to examine the relationship between FR variability and variability in physical variables among macrohabitat types. FR variability (expressed as CV) served as the dependent variable and variability (expressed as CV) in current velocity, depth, and substrate size served as predictor variables. For each physical variable, this analysis was used to test the null hypothesis that there is no linear relationship between FR variability and variability in the physical variable (current velocity, depth, or substrate size). Probabilities were significant at the 0.05 level ($P<0.05$).

Results

Species Composition of Fish Assemblages: Species and family composition differed greatly among the three segments. Small native minnows (Cyprinidae), such as flathead chub and western silvery minnow (*Hybognathus argyritis*) were common in the YSS, constituting 59% of the fish there (Table 1), whereas in the GOS and the SKS, minnows constituted only 32% and 40% of the fish, respectively (Table 1). Goldeye (16%) and native deep-bodied suckers such as bigmouth buffalo (*Ictiobus cyprinellus*) and smallmouth buffalo (Catostomidae; 10%) were also common in the YSS.

The GOS was dominated by the dorsally compressed fathead minnow (*Pimephales promelas*, 32%) and shovelnose sturgeon (24%; Table 1). Two other dorsally compressed species, white sucker (*Catostomus commersoni*, 14%) and longnose sucker (*Catostomus*, 10%) were also common in the GOS. Many native species of Cyprinidae and deep-bodied Catostomidae found in the YSS were absent in the GOS (Table 1).

Emerald shiner and gizzard shad (*Dorosoma cepedianum*) were common in the channelized SKS, constituting 51% of the fish there (Table 1). The gizzard shad was absent from both the YSS and the GOS. In addition, catfishes (Ictaluridae) were common in the SKS, constituting 18% of the fish (Table 1).

Streamlined species such as sicklefin chub and sturgeon chub (*Macrhybopsis gelida*) that use sand-gravel habitat with steady velocities were common in the YSS, but were absent in the GOS and rare in the SKS (Table 1). These and other streamlined species were most commonly found in macrohabitats that exhibited the highest current velocities. However, few fish of any species were captured in main channel cross-over habitat in the GOS and the SKS (Table 1). Deep-bodied, poorly streamlined fishes were virtually absent from main channel cross-over habitat, which exhibited the highest current velocities.

Physical Characteristics of River Segments: Overall, the YSS exhibited highest numerical variability in habitat features of the three segments. Variation in velocity (CV = 0.38) and in depth (CV = 0.37) when computed *across* macrohabitat types was highest in the YSS. The GOS showed the highest substrate variation (1.11). Variation in depth, current velocity, and substrate across macrohabitats was lowest in the SKS (depth = 0.11, velocity = 0.07, substrate = 0.07). However, despite these differences in CV of habitat features across macrohabitat types, CVs of depth, current velocity, and substrate were not significantly different *within* habitat types for any of the three river segments (P>0.05).

Among the three segments, main channel cross-over tended to have greater depths and velocities than the other two macrohabitats (Table 2). The coarsest substrate was found in outside bend macrohabitat in the three segments, with the SKS and the GOS having much coarser substrate in this habitat than the YSS. The YSS tended to have less coarse substrate than the GOS and SKS across macrohabitat types (Table 2).

For most macrohabitats, mean depth, mean current velocity, and mean substrate size differed significantly among segments (Friedman's ANOVA, $P<0.05$; Table 3). Macrohabitat depth, current velocity, and substrate size tended to differ significantly between the SKS and the YSS (P<0.05) and the GOS ($P<0.05$), whereas the YSS and the GOS did not tend to differ significantly from one another ($P>0.05$; Table 3). However, inside bend current velocity ($P=0.21$) and main channel cross-over substrate ($P=0.72$) did not differ significantly (P>0.05) among segments

Streamlining and Fineness Ratio: The fish assemblage in the highly channelized SKS exhibited the weighted mean FR that was closest to the optimal 4.5 value. This segment had the smallest deviation from optimal (0.08; FR=4.42), whereas the GOS exhibited the mean FR with the largest deviation from optimal (0.81; FR=5.56). For the YSS, the mean FR (4.73) computed from the three macrohabitats deviated 0.23 from optimal. Variation in weighted mean FRs when computed across macrohabitat types was highest in the YSS (0.33), second highest in the SKS (0.26), and lowest in the GOS (0.25). Weighted mean FRs in macrohabitats tended to be highest in the GOS and lowest in the SKS when the same macrohabitat types were compared across segments (Table 2). Variation

Table 1. Species relative abundance (rel. abun.) as a fraction of 1.00 in macrohabitats (CHXO=main channel cross-over, ISB=inside bend, and OSB=outside bend).

SPECIES	Yellowstone-Sakakawea Segment CHXO	ISB	OSB	Combined Rel. Abun. CHXO, ISB, OSB
STURGEONS; ACIPENSERIDAE				0.04
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	0.28	0.20	0.52	0.04
MOONEYES; HIODONTIDAE				0.16
Goldeye, *Hiodon alosoides*	0.04	0.32	0.64	0.16
PIKES; ESOCIDAE				<0.01
Northern pike, *Esox lucius*		0.33	0.67	<0.01
CODS; GADIDAE				0.04
Burbot, *Lota lota*			1.00	0.04
MINNOWS; CYPRINIDAE				0.59
Common carp, *Cyprinus carpio*	0.08	0.08	0.83	0.01
Common carp < 150 mm, *Cyprinus carpio*		1.00		0.01
Emerald shiner, *Notropis atherinoides*		0.25	0.75	0.06
Flathead chub, *Platygobio gracilis*	0.01	0.83	0.16	0.37
Sicklefin chub, *Macrhybopsis meeki*	0.20	0.20	0.60	0.03
Spottail shiner, *Notropis hudsonius*		0.09	0.91	0.01
Sturgeon chub, *Macrhybopsis gelida*	0.05	0.63	0.32	0.03
Western silvery minnow, *Hybognathus argyritis*		0.81	0.19	0.07
SUCKERS; CATOSTOMIDAE				0.1
Bigmouth buffalo, *Ictiobus cyprinellus*		1.00		0.01
River carpsucker, *Carpiodes carpio*			1.00	0.03
River carpsucker < 150 mm, *Carpiodes carpio*		1.00		0.01
Shorthead redhorse, *Moxostoma macrolepidotum*			1.00	<0.01
Smallmouth buffalo, *Ictiobus bubalus*			1.00	0.02
Smallmouth buffalo < 150 mm, *Ictiobus bubalus*		1.00		0.03
BULLHEAD CATFISHES; ICTALURIDAE				0.06
Channel catfish, *Ictalurus punctatus*	0.10	0.28	0.62	0.04
Stonecat, *Noturus flavus*	0.05	0.05	0.90	0.02
PERCHES; PERCIDAE				0.05
Sauger, *Sander canadensis*			1.00	0.04
Walleye, *Sander vitreus*			1.00	<0.01
Yellow perch, *Perca flavescens*		0.67	0.33	<0.01
SUNFISHES; CENTRARCHIDAE				<0.01
White crappie, *Pomoxis annularis*		1.00		<0.01
DRUMS; SCIAENIDAE				<0.01
Freshwater drum, *Aplodinotus grunniens*			1.00	<0.01

in macrohabitat mean FRs were also highest in the GOS and SKS and lowest in the YSS (Table 2). Variation in mean FRs in the three macrohabitats did not differ significantly ($P>0.05$). Among the segments, mean FRs differed significantly only between the YSS and the GOS (Table 3).

Table 1 (cont.). Species relative abundance (rel. abun.) as a fraction of 1.00 in macrohabitats (CHXO=main channel cross-over, ISB=inside bend, and OSB=outside bend).

(Table I. Continued.)

SPECIES	Garrison-Oahe Segment CHXO	ISB	OSB	Combined Rel. Abun. CHXO, ISB, OSB
STURGEONS; ACIPENSERIDAE				0.24
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	0.61	0.18	0.20	0.24
SALMON, TROUT, WHITEFISH; SALMONIDAE				0.01
Cisco, *Coregonus artedi*			1.00	0.01
SMELT; OSMERIDAE				0.05
Rainbow smelt, *Osmerus mordax*	0.08	0.25	0.67	0.05
PIKES; ESOCIDAE				<0.01
Northern pike, *Esox lucius*			1.00	<0.01
CODS; GADIDAE				0.02
Burbot, *Lota lota*		0.25	0.75	0.02
MINNOWS; CYPRINIDAE				0.37
Common carp, *Cyprinus carpio*			1.00	0.05
Fathead minnow, *Pimephales promelas*		0.10	0.90	0.32
SUCKERS; CATOSTOMIDAE				0.29
Longnose sucker, *Catostomus catostomus*	0.36	0.14	0.50	0.04
Longnose sucker < 150 mm, *Catostomus catostomus*		1.00		0.06
River carpsucker, *Carpiodes carpio*	0.33		0.67	0.04
Shorthead redhorse, *Moxostoma macrolepidotum*			1.00	0.01
White sucker, *Catostomus commersonii*	0.18	0.23	0.59	0.02
White sucker < 150 mm, *Catostomus commersonii*		1.00		0.12
PERCHES; PERCIDAE				0.02
Walleye, *Sander vitreus*		0.25	0.75	0.02

Variation in FRs tended to be lowest in macrohabitats with uniform velocities and substrates. Among macrohabitat types, variation in FRs was positively related to variation in velocities in the three segments (YSS, r=0.62, P=0.03; GOS, r=0.61, P=0.04; SKS, r=0.82, P=0.004; Table 4). This relation existed for substrate size in the three segments as well (YSS, r=0.67, P=0.03; GOS, r=0.69, P=0.02; SKS, r=0.75, P=0.003). Variation in FRs was not related to depth variation in any of the segments (P>0.05).

In terms of FRs, in the GOS, relative abundance was low in all macrohabitats for fish exhibiting FRs less than 4.5. The evenness of fish among FR categories was more uniform in the YSS (E=0.65) than in the GOS (E=0.07) and the SKS (E=0.18) (Fig. 2). FR category heterogeneity was highest for the YSS (l/D=4.37) and lowest for the SKS (l/D=2.90; GOS, l/D=2.95).

In terms of species, the highest mean and highest maximum current velocity use in the three segments was found for species such as sicklefin chub, sturgeon chub, and blue sucker (*Cycleptus elongatus*) that were optimally or nearly optimally streamlined (FRs≅4.5; Table 5). However, the shovelnose sturgeon was also frequently found in habitats with high current velocities even though it possessed a non-optimal FR (≅8.5). Deep-bodied species with FRs typically below 3.5, such as buffalo fish, river carpsucker (*Carpiodes carpio*), and centrarchids, tended to inhabit the lowest mean and lowest maximum current velocity areas in the three segments (Table 5). Examples of different body forms exhibited by fish captured in this study are depicted in Figure 3.

In terms of FRs, mean current velocity use among FR categories tended to be highest for

Table 1 (cont.). Species relative abundance (rel. abun.) as a fraction of 1.00 in macrohabitats (CHXO=main channel cross-over, ISB=inside bend, and OSB=outside bend).

(Table I. Continued.)

SPECIES	St. Joseph-Kansas City Segment CHXO	ISB	OSB	Combined Rel. Abun. CHXO, ISB, OSB
River shiner, *Notropis blennius*		0.71	0.29	0.02
Sand shiner, *Notropis stramineus*		0.39	0.61	<0.01
Sicklefin chub, *Macrhybopsis meeki*		1.00		<0.01
Silver chub, *Macrhybopsis storeriana*		0.80	0.20	0.01
Sturgeon chub, *Macrhybopsis gelida*	0.08	0.50	0.42	<0.01
SUCKERS; CATOSTOMIDAE				0.02
Blue sucker, *Cycleptus elongatus*		0.72	0.28	0.01
Quillback, *Carpiodes cyprinus*		0.88	0.13	<0.01
River carpsucker, *Carpiodes carpio*		1.00		<0.01
River carpsucker <150 mm, *Carpiodes carpio*		0.91	0.09	0.01
Smallmouth buffalo, *Ictiobus bubalus*			1.00	<0.01
BULLHEAD CATFISHES; ICTALURIDAE				0.19
Blue catfish, *Ictalurus furcatus*	0.02	0.98		0.01
Channel catfish, *Ictalurus punctatus*	0.22	0.52	0.26	0.14
Flathead catfish, *Pylodictis olivaris*		0.09	0.91	0.04
Slender madtom, *Noturus exilis*			1.00	<0.01
Stonecat, *Noturus flavus*		0.57	0.43	<0.01
PERCHES; PERCIDAE				<0.01
Sauger, *Sander canadensis*		0.12	0.88	<0.01
TEMPERATE BASSES; PERCICHTHYIDAE				<0.01
White bass, *Morone chrysops*		0.81	0.19	<0.01
SUNFISHES; CENTRARCHIDAE				0.02
Bluegill, *Lepomis macrochirus*		0.40	0.60	<0.01
Green sunfish, *Lepomis cyanellus*		0.03	0.97	0.01
Largemouth bass, *Micropterus salmoides*		0.12	0.88	<0.01
Orangespotted sunfish, *Lepomis humilis*		0.88	0.12	<0.01
White crappie, *Pomoxis annularis*		1.00		<0.01
DRUMS; SCIAENIDAE				0.04
Freshwater drum, *Aplodinotus grunniens*		0.42	0.58	0.04

fish with FRs greater than 4.5, whereas the lowest mean current velocity use was exhibited by fish with FRs less than 4.0 (Fig. 4). The maximum current velocity used by any species in a segment was highest for fish with near optimum FRs (Fig. 4), and tended to be lowest for fish with FRs below 4.0. However, the lowest maximum current velocities used in the SKS were found for fish with FRs between 3.5-4.0 and 5.0-5.5.

Discussion

Assemblage Fineness Ratio: When FR and physical conditions were analyzed *across* habitat types, the more natural YSS was characterized by

Table 2. Mean weighted Fineness ratio and physical characterization (mean, coefficient of variation (CV)) for Yellowstone-Sakakawea Segment (YSS), Garrison-Oahe Segment (GOS), and St.Joseph-Kansas City Segment (SKS) macrohabitats.

		Macrohabitat								
		Main Channel Cross-over			Inside Bend			Outside Bend		
Variable		YSS	GOS	SKS	YSS	GOS	SKS	YSS	GOS	SKS
Mean Weighted Fineness Ratio		5.54	5.85	4.51	4.60	5.39	4.99	4.93	4.49	4.12
	CV	0.14	0.13	0.21	0.14	0.26	0.33	0.14	0.29	0.22
Mean Depth (m)		4.55	3.08	6.08	2.76	1.74	2.19	3.51	3.19	1.32
	CV	0.25	0.21	0.21	0.59	0.75	0.82	0.29	0.16	1.12
Mean Current Velocity (m/sec)		1.12	1.05	1.67	0.84	0.68	0.38	0.73	0.84	0.46
	CV	0.15	0.21	0.14	0.55	0.69	0.84	0.15	0.18	0.72
Geometric Mean of Substrate (mm)		1.56	5.59	1.12	0.96	1.42	9.93	1.94	11.21	28.83
	CV	0.94	1.75	0.06	1.31	0.41	0.30	1.69	1.18	0.43

higher diversity of FR than the more altered GOS and SKS. Conditions in the YSS were associated with the highest diversity of ecomorphological types, some optimally streamlined, and some not. Modified river conditions in the GOS and the SKS, associated with channelization and revetment (Kellerhals and Church 1989; Hesse and Sheets 1993), were associated with lower diversity of FRs. In this study, a strong relationship was found between variability in FR and variability in habitat characteristics; as variability in habitat characteristics decreased, so did variability in FR. This result suggests that the habitat differences and changes in the SKS (Table 3) that have led to reduced habitat variability are associated with fish assemblages characterized by a reduced diversity of body forms (i.e., fish with less deviation from optimal streamlining). Results for the GOS were more difficult to interpret. The results for YSS and SKS support our hypothesis that segments that have less variability in water depth, velocity, and substrate size exhibit fish assemblages characterized by less diversity in streamlining.

The data also support our hypothesis that fish assemblages in more altered river segments exhibit more optimal streamlining (≅4.5) and less variability from optimal values because of the presence of more uniform velocities. The most altered segment (SKS) exhibited a near optimal assemblage FR (4.42) and exhibited the lowest variability in current velocity (CV=0.07). High current velocity coupled with low variability in current velocity in this segment led to a near optimal FR. The other two segments exhibited non-optimal assemblage FRs (YSS=4.73, GOS=5.56) and higher variability in current velocity, depth, and substrate than the SKS. The assemblage FRs for both the YSS and GOS indicate that the fish assemblages are dorso-ventrally flattened. Fish with this flattened body shape would be better able deal with the high current velocities found for the macrohabitats in both segments than fish that are sub-optimally streamlined (i.e., FR <4.5). This result is also supported by other studies relating fineness ratio, as an index of streamlining, with increased swimming efficiency (e.g., Ohlberger et al. 2006).

Even though body morphology appears to be one component in shaping fish assemblages in these three segments of the Missouri River, other ecological factors undoubtedly also influence assemblage structure. Most likely, latitudinal differences between segments (e.g., as manifested by water temperature) in

Table 3. Results of Friedman's ANOVA and multiple comparison testing of segment mean weighted Fineness Ratio and physical variables measured in main channel cross-over (CHXO), inside bend (ISB), and outside bend (OSB) macrohabitats (x_r^2 = Friedman's test statistic, YSS=Yellowstone-Sakakawea Segment, GOS=Garrison-Oahe Segment, SKS=St. Joseph-Kansas City Segment). A segment is significantly different from segments whose abbreviation is below it.

Physical Variable	Macrohabitat	Results of omnibus ***ANOVA p-value	x_r^2	Results of multiple comparison testing: Segment YSS	GOS	SKS
Mean Weighted Fineness Ratio	**CHXO	0.0428	7.01	SKS		YSS
	ISB	0.4790	2.70	-	-	-
	OSB	0.5606	2.55	-	-	-
Mean Depth (m)	**CHXO	<0.0001	40.05	GOS, SKS	YSS, SKS	YSS, GOS
	*ISB	0.0403	7.10		SKS	GOS
	**OSB	0.0005	35.47	SKS	SKS	YSS, GOS
Mean Current Velocity (m/sec)	**CHXO	<0.0001	39.86	SKS	SKS	YSS, GOS
	ISB	0.2141	4.60	-	-	-
	**OSB	0.0005	35.46	SKS	SKS	YSS, GOS
Geometric Mean of Substrate (mm)	CHXO	0.7209	1.90	-	-	-
	*ISB	0.0005	39.80	SKS	SKS	YSS, GOS
	**OSB	<0.0001	41.07	SKS	SKS	YSS, GOS

*Tukey-type multiple comparison test was performed on ranks.
**Tukey-type multiple comparison test for unequal sample sizes was performed on ranks.
***Friedman's Analysis of Variance performed on ranks.
-multiple comparison test was not performed.

addition to physical characteristics (e.g., water depth, velocity, and substrate) fragmentation (Perkin and Gido 2011) and predators (Power et al. 1985) are also responsible for shaping present fish assemblages. These factors can reduce (or increase) the abundance of certain fishes (Layher and Maughan 1985; Hubert and Rahel 1989; Wootton and Oemke 1992). For example, gizzard shad, a common species in the SKS, are not highly cold tolerant and are near the northwestern edge of their range in South Dakota (Wuellner et al. 2008) making them highly unlikely to be commonly observed in the GOS and YSS. Species such as longnose sucker and burbot (*Lota lota*) were probably never common in segments of the lower Missouri River (e.g., SKS), with the southern extent of their ranges reaching 40° north latitude (Scott and Crossman, 1973). The northern extent of the lower Missouri River is approximately 42° north latitude. The abundance of species such as longnose sucker, which were common in the GOS but nearly absent from the YSS, can also be limited by water temperature. Longnose suckers are most often found in streams and lakes that are characterized by very cool water (Scott and Crossman 1973). The preferred temperature range for longnose sucker is 10-15 °C (Brown and Graham 1953) with the upper lethal temperature (50% mortality in 24 hours) for this species near 27 °C (Black 1953). Water temperatures rarely exceeded 16 °C in the GOS because of hypolimnetic releases from Garrison Dam, but frequently exceeded 23 °C in the YSS (Young et al. 1997). Warm water temperatures most likely limited longnose sucker numbers in the YSS. Access to segments physically isolated by dams can also be a problem, especially hindering upriver colonization. Besides fish morphology, many factors are thus responsible for shaping the fish assemblages found in the three Missouri River segments. For that reason, in interpreting results from this study relating ecomorphology to fish assemblage structure, more emphasis

Table 4. Relationship between mean weighted Fineness Ratio coefficient of variation (CV) and physical variable coefficients of variation in Yellowstone-Sakakawea Segment (YSS), Garrison-Oahe Segment (GOS), and St. Joseph-Kansas City Segment (SKS) macrohabitats

	Segment		
Physical Variable	YSS	GOS	SKS
Current Velocity (m/sec)			
r	0.62	0.69	0.82
P-value	0.0314	0.0410	0.0040
Depth (m)			
r	0.18	0.40	0.24
P-value	0.5400	0.1320	0.4715
Substrate Geometric Mean (mm)			
r	0.67	0.69	0.75
P-value	0.0310	0.0211	0.0030

should be placed on the overall morphological character of the fish community, weighted by abundance of ecomorphological types, in response to conditions, not on the abundance of any individual species, which can vary widely in ecological requirements and tolerances.

Streamlining and Body Form: Results of this study support the idea that in the Missouri River, body shape may impose a physical limit on the types of habitats which a fish can successfully inhabit. Poorly streamlined species, such as bigmouth buffalo and white crappie, were almost never found in subsamples from areas with high current velocities; they were found in greatest abundance in subsamples from areas with low current velocities in each study segment. Similar results were reported for a smaller prairie stream by Scarnecchia (1988), where deep-bodied, poorly streamlined fish were uncommon in channelized sections, which contained virtually no habitat unexposed to the current. Unchannelized sections of the stream were more physically diverse, providing areas of low current velocity supporting large numbers of poorly streamlined fish (e.g., green sunfish *Lepomis cyanellus*). In our present study of segments on a much larger river, however, results were consistent with the small stream study on reaches. However, the large river results among segments were less extreme. Species which used the highest average and the highest maximum current velocities, and which would thus be expected to be near-optimally streamlined, nevertheless exhibited greatly different FRs. A few species common to higher velocities, such as longnose sucker, channel catfish (*Ictalurus punctatus*), and blue sucker were optimally streamlined (FR≅4.5). Others, such as sicklefin chub and sturgeon chub were nearly optimally streamlined with FRs slightly greater than 4.5. In contrast, the shovelnose sturgeon, which used moderate to high current velocities in the three segments, was not optimally streamlined (FRs > 8.5).

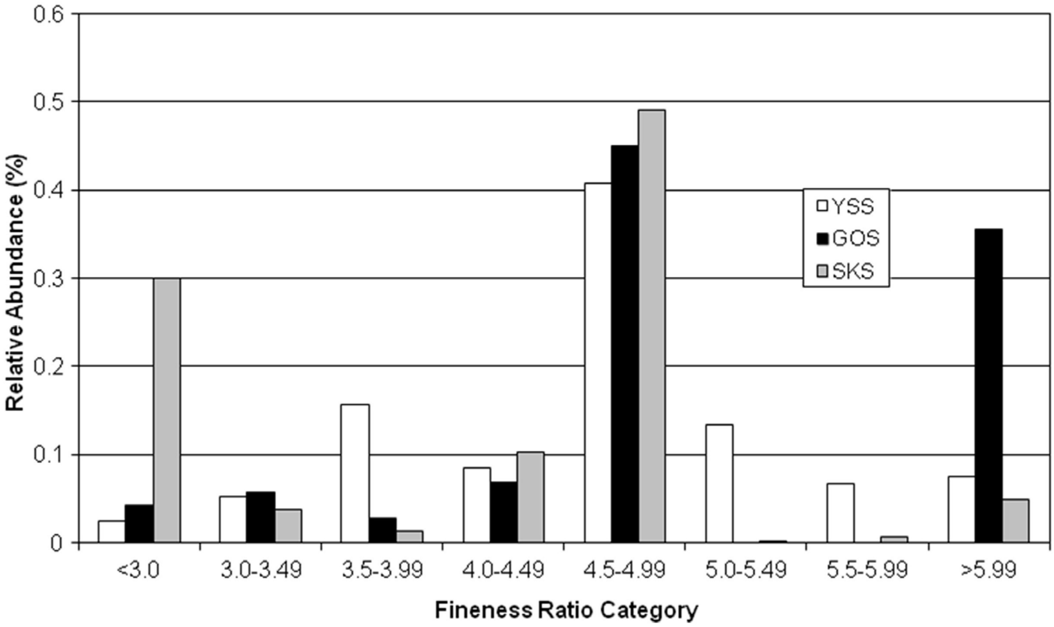

Figure 2. Relative abundance of fineness ratio categories in study segments from main channel cross-over, outside bend, and inside bend macrohabitats (YSS=Yellowstone-Sakakawea Segment, GOS=Garrison-Oahe Segment, SKS=St. Joseph-Kansas City Segment).

Several factors may influence why our results relating the amount of streamlining to velocity and other habitat features may differ in degree, though not in overall pattern, from those of a small stream such as studied by Scarnecchia (1988). One explanation for these greatly different morphological types inhabiting high velocity habitat is that each species copes with the forces of frontal lift and drag differently. This explanation is supported by a laboratory study by Webb (1989). In that study of the ability of three benthic fish species to hold their position in the current, two species, thornback ray (*Raja clavata*) and plaice (*Pleuronectes platessa*), had FRs of approximately 10, while a third species, father lasher (*Myoxocephalus scorpius*), exhibited a near optimal FR of 4.2. Webb (1989) reported that two common patterns of benthic fish body form allow fish to be proficient at station holding in current. Both body forms normalize the coefficients of lift and drag in the frontal area of the fish. The first form is flattened, such as plaice in Webb's (1989) study or shovelnose sturgeon in this study, which has high frontal lift, but counters high lift with low frontal drag. The second form is more fusiform, such as lasher in Webb's (1989) study or sicklefin chub in this study, which has high frontal drag, but counters high drag with low frontal lift. Webb (1989) further hypothesized that the capacity of a fish to hold station with a body form that is dorso-ventrally flattened is best over a flat, smooth substratum where it can minimize frontal lift. Adams et al. (1997) observed that shovelnose sturgeon in an experimental swim tunnel with a smooth substratum held station through substrate appression at current velocities exceeding 0.4 m/sec. Such behavior would explain why shovelnose sturgeon have been found in several studies to occupy habitats with current-swept sandy bottoms (Hurley *et al.* 1987; Curtis *et al.* 1997; Quist *et al.* 1999). Because of this behavior, the shovelnose sturgeon does not conform to the simple hypothesis that non-optimally streamlined fish cannot utilize high current velocity habitats.

Table 5. Mean Fineness ratios, mean current velocity (m/sec), and maximum current velocity for species in the study segments (YSS=Yellowstone-Sakakawea Segment, GOS=Garrison-OaheSegment, SKS=St. Joseph-Kansas City Segment).

SPECIES	Mean Fineness Ratio			Mean Current Velocity			Maximum Current Velocity		
	YSS	GOS	SKS	YSS	GOS	SKS	YSS	GOS	SKS
STURGEONS; ACIPENSERIDAE									
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	8.60	8.58	**8.58**	0.88	0.77	0.42	1.15	1.15	0.90
GARS; LEPISOSTEIDAE									
Longnose gar, *Lepisosteus osseus*			**10.44**			0.08			0.40
Shortnose gar, *Lepisosteus platostomus*			9.69			0.03			0.60
HERRINGS; CLUPEIDAE									
Gizzard shad, *Dorosoma cepedianum*			2.88			0.16			1.55
MOONEYES; HIODONTIDAE									
Goldeye, *Hiodon alosoides*	3.60		3.54	0.16		0.11	1.10		0.70
SALMON, TROUT, WHITEFISH; SALMONIDAE									
Cisco, *Coregonus artedi*		3.68			0.25			0.50	
SMELT; OSMERIDAE									
Rainbow smelt, *Osmerus mordax*		6.50			0.60			1.20	
PIKES; ESOCIDAE									
Northern pike, *Esox Lucius*	6.22	5.81		0.06	0.02		0.30	0.10	
CODS; GADIDAE									
Burbot, *Lota lota*	7.83	7.80		0.25	0.46		0.50	0.75	
MINNOWS; CYPRINIDAE									
Creek chub, *Semotilus atromaculatus*			4.62			0.18			0.35
Common carp, *Cyprinus carpio*	3.19	3.37	**3.37**	0.15	0.03	0.14	1.30	0.35	1.55
Common carp < 150mm, *Cyprinus carpio*	2.91		2.91	0.05		0.03	0.27		0.60
Emerald shiner, *Notropis atherinoides*	5.04	5.12	4.81	0.19	0.00	0.30	0.50	0.00	1.70
Fathead minnow, *Pimephales promelas*		4.51	4.14		0.10	0.11		0.35	0.30
Flathead chub, *Platygobio gracilis*	4.57		**4.57**	0.17		0.46	1.05		1.30
Goldfish, *Carassius auratus*			**2.30**			0.07			0.10
Hybognathus spp.	4.41		4.39			0.23			0.90
Red shiner, *Cyprinella lutrensis*			3.35			0.17			0.55
River shiner, *Notropis blennius*			4.62			0.22			0.85

A second factor is that other aspects of fishes besides their trunk shape influence how fish exist in the current. Fish have not only different trunk shapes (i.e., FRs), but different methods of propulsion and fin usage, and different behaviors. Even though the fish studied by Webb (1989) relied heavily upon body characteristics to hold their position, they also used a variety of behaviors such as fin-beating and substratum grasping. Lasher, which performed poorer than plaice over smooth substratum, performed better than plaice over rough substratum. Lasher used their pectoral fins to grip the substratum surface, aiding in station holding. Perhaps species such as the sicklefin chub, which possesses elongate pectoral fins (Cross and Collins 1995) and are found in high current velocity habitats (Everett, 1999), use this same behavior to aid in holding station.

A third factor may be the scales of the difference in the proximity of treatments between the two studies. In the small stream study (Scarnecchia 1988), the two treatment reaches (channelized and unchannelized) were close together (within 3 km) and all species could gain access to all replicate reaches within and among the two habitat treatments. In this large-river study, treatments (Missouri River segments) were separated by major habitat discontinuities and blockages associated with dams. Species composition among the Missouri River segments was influenced by other factors such as access and larger scale habitat suitability and ecological requirements (e.g., thermal preferences and tolerances of specific species).

A fourth factor may be the differing scales of the two studies. In this study, the larger habitat units in relation to fish size made macrohabitats within the three segments of great importance, whereas sampling of the small stream habitat in Scarnecchia (1988) did not break out macrohabitats within channelized and unchannelized reaches. The channelized reaches

Table 5 (cont.).

(Table 5. Continued.)

SPECIES	Mean Fineness Ratio			Mean Current Velocity			Maximum Current Velocity		
	YSS	GOS	SKS	YSS	GOS	SKS	YSS	GOS	SKS
MINNOWS; CYPRINIDAE									
Sand shiner, *Notropis stramineus*			4.49			0.24			0.45
Sicklefin chub, *Macrhybopsis meeki*	5.24		**5.24**	0.97		0.57	1.30		0.75
Silver chub, *Macrhybopsis storeriana*			4.36			0.18			1.40
Spottail shiner, *Notropis hudsonius*	4.46	4.34		0.24	0.01		1.00	0.03	
Sturgeon chub, *Macrhybopsis gelida*	5.45		**5.63**	0.88		1.00	1.25		1.95
Western silvery minnow, *Hybognathus argyritis*	4.23			0.14			0.85		
SUCKERS; CATOSTOMIDAE									
Bigmouth buffalo, *Ictiobus cyprinellus*	3.01			0.02	0.02		0.25	0.10	
Blue sucker, *Cycleptus elongatus*			**4.57**			0.72			1.70
Longnose sucker, *Catostomus catostomus*		4.63			1.00			1.45	
Longnose sucker < 150 mm, *Catostomus catostomus*		4.95			0.07			0.37	
Quillback, *Carpiodes cyprinus*			**2.78**			0.07			0.35
River carpsucker, *Carpiodes carpio*	2.70	2.86	**2.80**	0.06	0.08	0.04	1.00	0.85	0.40
River carpsucker <150 mm, *Carpiodes carpio*	3.27		3.20	0.03		0.13	0.17		0.65
Shorthead redhorse, *Moxostoma macrolepidotum*	4.05	3.70		0.09	0.12		0.35	0.45	
Smallmouth buffalo, *Ictiobus bubalus*	2.80		**2.80**	0.06		0.14	0.90		0.45
Smallmouth buffalo < 150 mm, *Ictiobus bubalus*	3.10			0.05			0.27		
White sucker, *Catostomus commersonii*		4.47			0.27			1.65	
White sucker < 150 mm, *Catostomus commersonii*		4.63			0.04			0.40	
BULLHEAD CATFISHES; ICTALURIDAE									
Blue catfish, *Ictalurus furcatus*			3.91			0.42			1.50
Channel catfish, *Ictalurus punctatus*	4.86		4.84	0.42		0.39	1.35		2.10
Flathead catfish, *Pylodictis olivaris*			**4.67**			0.36			0.85
Slender madtom, *Noturus exilis*			**6.36**			0.45			0.45
Stonecat, *Noturus flavus*	5.78		5.67	0.62		0.59	1.25		1.40
PERCHES; PERCIDAE									
Sauger, *Sander canadensis*	5.98		**6.12**	0.16		0.12	0.50		0.85
Walleye, *Sander vitreus*	4.92	4.96		0.05	0.13		0.35	0.90	
Yellow perch, *Perca flavescens*	3.97			0.10			0.27		
TEMPERATE BASSES; PERCICHTHYIDAE									
White bass, *Morone chrysops*			2.14			0.13			0.85
SUNFISHES; CENTRARCHIDAE									
Bluegill, *Lepomis macrochirus*			2.15			0.05			0.45
Green sunfish, *Lepomis cyanellus*			2.51			0.16			0.45
Largemouth bass, *Micropterus salmoides*			**3.18**			0.05			0.35
Orangespotted sunfish, *Lepomis humilis*			2.40			0.10			0.45
White crappie, *Pomoxis annularis*	2.75		2.63	0.08		0.02	0.17		0.20
DRUMS; SCIAENIDAE									
Freshwater drum, *Aplodinotus grunniens*	3.02		2.97	0.07		0.23	0.30		1.60

Mean Fineness Ratio computed from measured specimens housed in Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas

Mean Fineness Ratio computed from measured specimens collected from other Missouri River segments

of the small stream showed great uniformity at both the macrohabitat and microhabitat scales, whereas in the large channelized segment (SKS), some refuges from the current could still be found at the macrohabitat scale. Fish streamlining, as indicated by fineness ratios, might therefore more strongly dictate who among available species would inhabit local reaches of a small stream (e.g., Scarnecchia 1988) than a large river.

In altered river segments, we have shown that less diversity in assemblage FR is associated with less variability in velocity, depth, and substrate. We conclude that streamlining is one of several factors that may influence the observed fish community structure. Even in these large river systems, streamlining deserves consideration for inclusion in more complex models explaining and predicting fish community structure. However, other ecological, morphological, and behavioral factors also influence fish assemblage structure. Fineness ratio as an ecomorphological index is not fully adequate to indicate how well fish will exist in the current of channelized river segments. At the community level, FRs are probably related to the variability in habitat characteristics and should approach 4.5 (Webb 1975) under conditions of low habitat

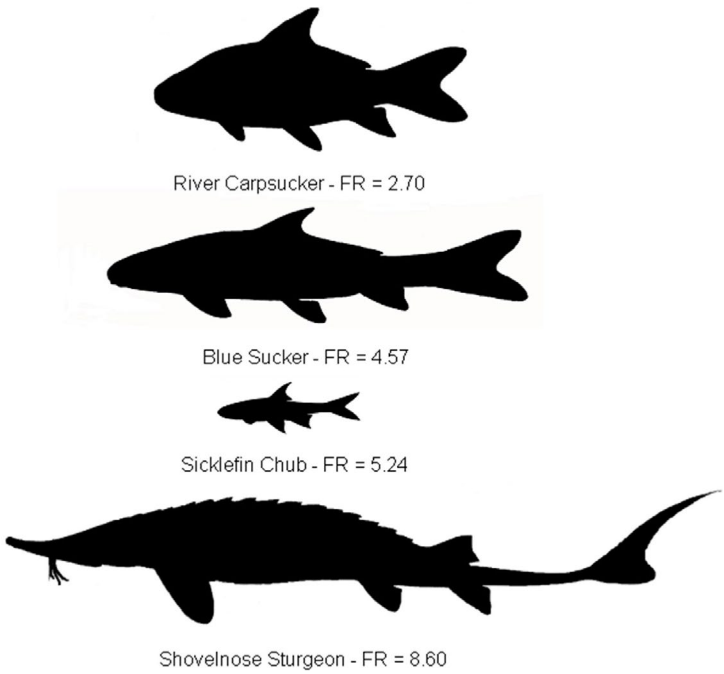

Figure 3. Examples of fish body form and fineness ratios from fishes of the Missouri River.

variability (i.e., current velocity, depth, and substrate). A fish species found occupying high current velocity habitats, however, will not necessarily be optimally streamlined. These fish should exhibit FRs ≥ 4.5 (i.e., be dorso-ventrally flattened; Webb 1989). Different types of fish behavior and the characteristics of the habitat, such as the roughness of the river bottom, probably allow a variety of fish with different types of FRs ≥ 4.5 to use high current velocities. Differences in the usage of fins, as well as whether the fish swim with rigid or non-rigid bodies, and other morphological factors can affect the relation between fineness ratio and swimming performance (Assumpção *et al.* 2012; Walker *et al.* 2013). The conditions that define optimal FRs are probably different for fish communities and even for individual fish. Such differences would be manifested as differences in fish morphology and resulting fish assemblage structure.

To more fully understand the fish community structure in a complex large river, and to more fully evaluate hypotheses forwarded in this paper, more sophisticated indices than, or in addition to, fineness ratio are needed to more clearly depict how fish with different morphologies, different methods of propulsion and fin usage, and different behaviors deal with the current. More controlled laboratory studies are also needed to clarify the biomechanical and behavioral mechanisms by which fish species cope with changing habitats in the altered Missouri River.

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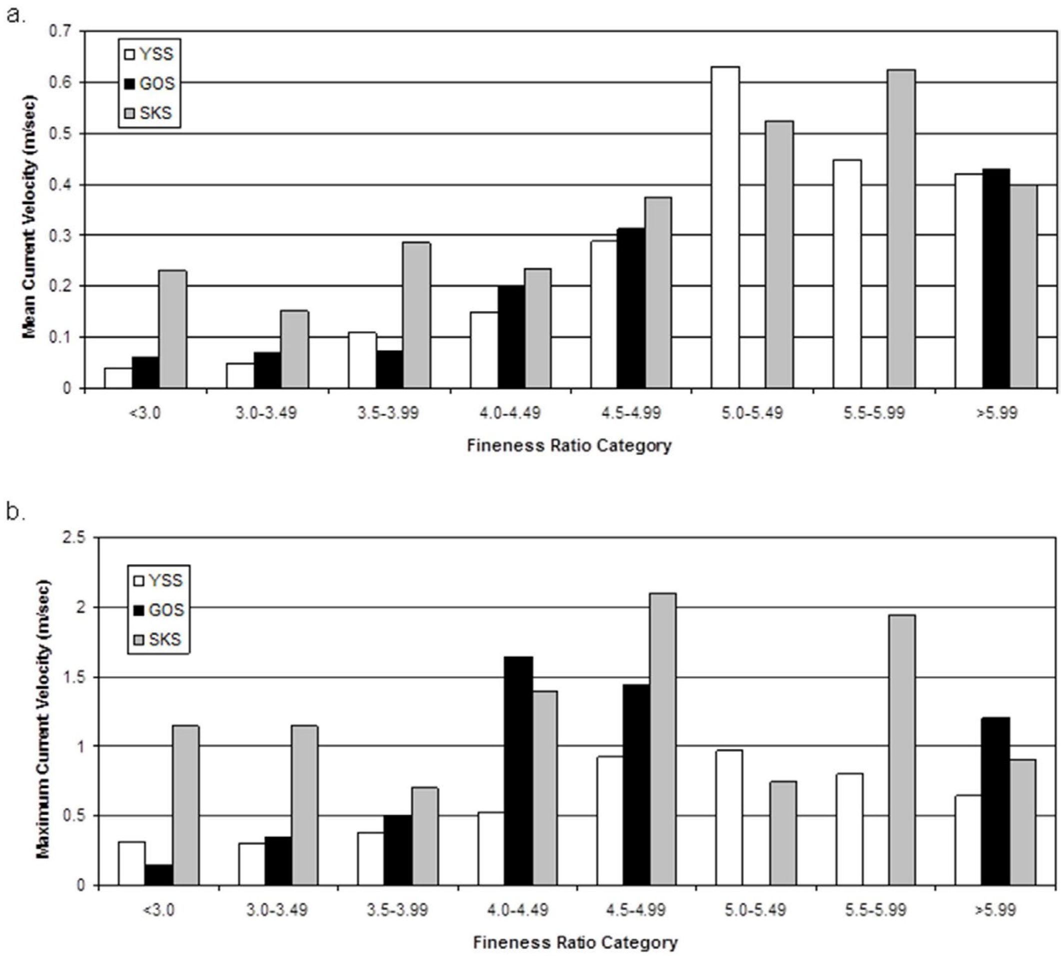

Figure 4. Mean current velocity (a.) and maximum current velocity (b.) used by fineness ratio categories in study segments (YSS=Yellowstone-Sakakawea Segment, GOS=Garrison-Oahe Segment, SKS=St. Joseph-Kansas City Segment).

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