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Differences in species composition and feeding ecology of catostomid fishes in two distinct segments of the Missouri River, North Dakota, U.S.A.

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Synopsis

In 1997 and 1998, we sampled the Missouri River, North Dakota to determine if anthropogenic disturbances had influenced catostomid species composition and feeding ecology. We compared two distinct river segments, the Missouri River between the mouth of the Yellowstone River and Lake Sakakawea (the Yellowstone–Sakakawea segment (YSS)), a moderately altered segment and the Missouri River between Garrison Dam and Lake Oahe (the Garrison–Oahe segment (GOS)), a highly altered segment. The segments exhibited greatly different sucker communities. Bigmouth buffalo, *Ictiobus cyprinellus*, smallmouth buffalo, *Ictiobus bubalus*, and river carpsucker, *Carpiodes carpio*, represented 94% of the sucker catch in the YSS, whereas in the GOS, white sucker, *Catostomus commersoni*, and longnose sucker, *Catostomus catostomus*, constituted 98% of the sucker catch. In the YSS, high zooplankton densities led to greater sucker zooplanktivory and food niche overlap than in the GOS. Intense anthropogenic disturbances to the GOS are associated with the differences in sucker species composition, prey density and composition, and sucker feeding ecology between the two segments.

Introduction

Catostomid fishes include about 70 species of relatively large, chiefly North American fishes commonly known as suckers (Helfman et al. 1997). These cypriniform fishes are predominately bottom dwelling and possess specialized lips and pre-maxillaries which allow them to feed effectively on a variety of invertebrate organisms. Suckers generally inhabit unpolluted waters and can be found living under a variety of riverine and lake conditions, but most species generally cannot tolerate extensive modification of their habitats (Smith 1979).

Impoundment of rivers through damming has frequently led to changes in native fish ecology and abundance in rivers below dams (Miller 1959). Declines in the abundance and changes in the ecology of native species following river regulation have been documented in many large, turbid rivers, such as the Missouri (Hesse et al. 1989). In the Missouri River, the decline of many native species and the concomitant increase in non-native species coincided with mainstem dam construction that began in the 1930s and ended in the 1960s (Hesse et al. 1989). The sucker community in the Missouri River was once very diverse with many of its species very abundant throughout much of the river. It appears, however, that numbers of most native suckers have been reduced substantially in river reaches below mainstem Missouri River dams (Funk & Robinson 1974).

Despite the historical widespread distribution of sucker species in the Missouri River, the feeding ecology of these fishes has received little attention. Detailed knowledge of food habits for a fish assemblage can give valuable insight into inter-specific interactions, niche dimensions, food resource partitioning, and the trophic status of individual species (Litvak & Hansell 1990, Gray et al. 1997). Discovering and understanding these components of feeding ecology is key to proper management and conservation of suckers in the Missouri River. Our objectives were to: (1) contrast sucker community composition during summer in two riverine upper Missouri segments in North Dakota one a quasi-natural river segment and the other heavily influenced by a mainstem dam; and (2) determine if anthropogenic disturbances influence aspects of sucker feeding ecology (food habits, feeding strategy, and food niche overlap) in these same river segments.

Study area

North Dakota contains two inter-reservoir segments of the Missouri River within its state boundaries. One segment extends from the Yellowstone–Missouri River confluence (Missouri River km (rkm) 2 546.0) near the North Dakota–Montana border to its lower boundary of Lake Sakakawea (rkm 2 470.3) and hereafter is referred to as the Yellowstone–Sakakawea segment (YSS) (Figure 1). The second segment extends from Garrison Dam (rkm 2 235.4) in south-central North Dakota to its lower boundary of Lake Oahe (rkm 2 051.9) near the North Dakota–South Dakota border and hereafter is referred to as the Garrison–Oahe segment (GOS) (Figure 1).

Different habitat characteristics and flow regimes characterize the two segments. The YSS is free-flowing with 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 is characterized by high main channel turbidity, no major shoreline development, and few revetment banks (rip–rap). The lack of shoreline development and revetment banks allows the main river channel to meander naturally which creates a diversity of off-channel habitats. The GOS, in contrast, exhibits 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. Furthermore, the dam regulates

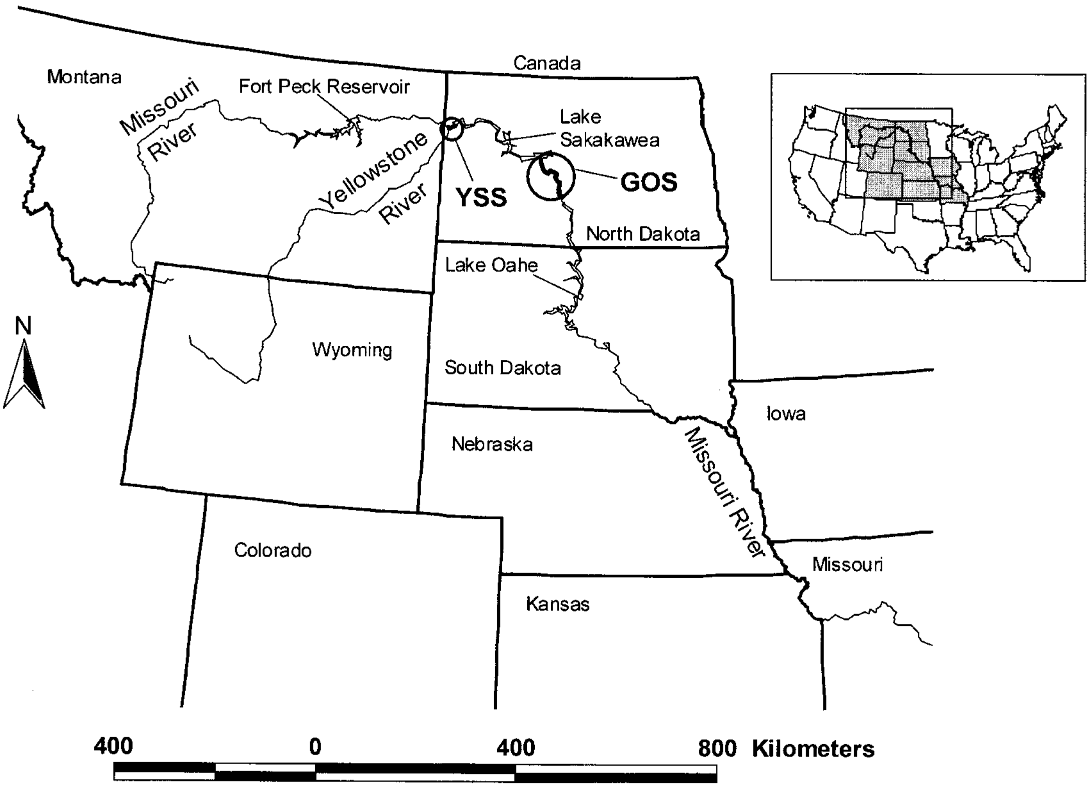

Figure 1. Map depicting study segments and location within Missouri River basin (GOS = Garrison–Oahe Segment, YSS = Yellowstone–Sakakawea Segment).

the hydrograph and 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 is also characterized by numerous revetments and a much higher degree of shoreline development and bank stabilization (25–40%) than the YSS.

Methods

Sucker data collection

We used a stratified random sample to collect suckers in both the YSS and the GOS where the strata were macrohabitat types. These macrohabitats were main channel cross-over, outside bend, inside bend, secondary channel: non-connected, secondary channel: connected, tributary mouth (Figure 2). In both segments, macrohabitats served as sampling units. We collected suckers from five randomly selected sampling units of each macrohabitat type in each segment from June through August in both 1997 and 1998. A variety of fish capturing gears was used that sampled a wide variety of sucker species. These gears were a bag seine (10.7 m long, 1.8 m high, 1.8 m^3 bag, 5 mm mesh), a benthic beam trawl (2 m wide, 0.5 m high, 5.5 m long, 3.2 mm inner bag mesh), a trammel net (22.9 m long, inner wall 2.4 m deep with 2.5 cm mesh, outer wall 1.8 m deep with 20.3 cm mesh), an electrofishing boat (Coffelt VVP-15 variable voltage pulsator, 5000 W generator), a gill net (30.5 m long, 1.8 m high, mesh sizes of 1.9, 3.8, 5.1 and 7.6 cm), and a hoop net (4.8 m in length, 3.7 cm diameter mesh, finger style throat, 7 fiberglass hoops, and a 15.2 m lead attached to the first hoop made of 3.8 cm mesh). A specific set of gears was used in each macrohabitat type with three subsamples of each gear taken at a macrohabitat sampling unit.

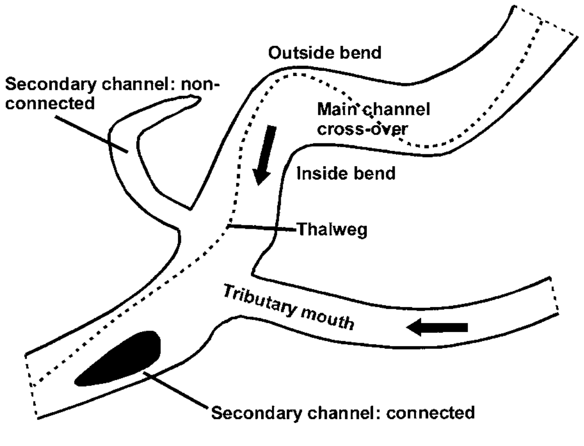

Figure 2. Location of macrohabitats in a typical Missouri River segment.

Benthic and Pelagic invertebrate data collection

We collected benthic macroinvertebrates and pelagic micro- and macroinvertebrates at each fish collection subsample to provide food availability information for the sucker community in each segment. Benthic macroinvertebrates were sampled with a Ponar dredge (22.9 cm^2). Three ponar grabs were taken at each gear subsample location, combined, and placed into a wash bucket that contained a 541 μm sieve screen bottom. The sample was washed and the remaining sediment, debris, and macroinvertebrates placed into a container and preserved with 95% ethanol for lab transport and analysis. In the lab, benthic invertebrates were identified to family if possible. Invertebrate density was expressed as number of organisms per m^2.

Pelagic invertebrates were collected with a Wisconsin plankton net (10.8 cm diameter, 80 μm mesh) fitted with a General Oceanics flow meter. A single tow was taken to survey pelagic invertebrates at each gear subsample. For subsamples with high current velocities (>0.2 m s^{-1}), the boat was anchored and the plankton net was attached to a hangar bar and 22.7 kg sounding weight and suspended near the river bottom with an A55M sounding reel.

For low current velocity subsamples (<0.2 m s^{-1}) the plankton net was attached to a 2 m standard wading rod at the 0.8 total depth mark and deployed for 3 min near the center of the area sampled. In macrohabitats with near zero current velocities, the net was towed by hand or boat for 3 min.

All material was removed from the plankton net and preserved in 95% ethanol. In the lab, pelagic invertebrates were identified in most cases to family. The volume of water sampled by the net was determined using the flow meter. Invertebrate density was expressed as number of organisms l^{-1}.

Sampling of sucker digestive tracts

Only fishes that were large enough to have reached sexual maturity (adult fish) were sampled for food habits analysis. Sexual maturity for each species was determined using lengths provided by Trautman (1957) and Scott & Crossman (1973). Contents were removed from the anterior one-fifth of the digestive tract of each sucker, up to the first bend and preserved in 15% formalin solution. After fixation, we transferred the contents to 95% ethanol until examined.

To quantify prey eaten by suckers, foregut contents of individual fish were diluted in 50–1 000 ml of water and suspended with a magnetic stir bar. Three separate 2 ml subsamples were taken with a plunger-type subsampler and placed in a counting chamber. If a stomach could not be effectively subsampled, the entire contents were analyzed. All invertebrates in each subsample were enumerated using a dissecting scope (7–45× magnification) and identified to family whenever possible. Surface area, volumetric, and gravimetric methods were examined for quantifying prey importance. The three methods produced similar results, however, we used the less time-consuming surface area method.

We determined the relative importance of food categories by counting the number of intersections on an ocular grid that was covered by individuals of each food category (Minckley et al. 1970). We quantified the surface area of partially digested aquatic insect larvae, such as Chironomidae, using regression equations derived from a regression of surface area on head capsule width (Hyslop 1980). All other food items were measured with the ocular grid and missing portions estimated visually.

Analysis

We quantified the species richness and diversity of zooplankton and benthic invertebrate prey populations in sucker habitats. Species richness was determined by counting the number of each prey category in a sample and then averaging across all samples in a macrohabitat sample unit. Richness values obtained in macrohabitat sample units were then averaged to get the segment average. Prey diversity was quantified with the reciprocal of Simpson's index D (Hill 1973).

$$D = \sum p_i^2 \text{ (i = 1, \ldots, s prey categories)}$$

where D is Simpson's index, p_i is the proportion of prey category i in the community, and $\sum p_i = 1.0$.

Prey diversity was quantified with the equation:

$$1/D = \text{prey diversity}$$

where 1/D is the reciprocal of Simpson's index which varies from 1 to s, the number of prey categories in the sample. The diversity of prey types was determined at each subsample within a macrohabitat sample unit. The subsample diversities were then averaged to obtain the prey diversity within the sample unit.

We used ANOVA to examine differences for prey diversity, richness, and density between the GOS and YSS habitats. Segments served as treatments (YOS and GOS) and years (1997 and 1998) served as blocks. Zooplankton and benthic invertebrate density, richness, and diversity served as dependent variables. Prey density, richness, and diversity values were $\log(y + 1)$ transformed to handle non-normality.

Food habits were quantified with several indices. The percent surface area (%A) of each food category was determined for each fish species. In addition, the percent of occurrence (%F), and percent number (%N) were determined for each category for each species of sucker. The equations used were:

$$\%A = (Q_i/Q_t) \times 100, \quad Q_t = \sum_{(i=1)} n * Q_i$$

$$\%N = (B_i/B_t) \times 100, \quad B_t = \sum_{(i=1)} B_i$$

$$\%F = (O_i/O_t) \times 100, \quad O_t = \sum_{(i=1)} O_i$$

where Q_i is the surface area composed by prey i, Q_t is the total surface area of all digestive tract items in the entire digestive tract sample, n is the number of individual prey of a prey type in the digestive tract sample, B_i is the digestive tract content number composed by prey i, B_t is the total digestive tract content number of all digestive contents in the entire sample, O_i is the number of suckers with prey i in their digestive tract, and O_t is the total number of suckers with digestive tract contents.

Linear least-squares regression was used to test the null hypothesis that there was no linear relationship between prey density at capture sites and relative abundance of prey in sucker stomachs. The relative abundance of prey was determined for each sucker and compared with regression analysis against prey density at each capture site. Prey relative abundance served as the response (Y) variable and prey density (pelagic prey = number l^{-1}; benthic invertebrate prey = number m^{-2}) served as the predictor (X) variable. This analysis was conducted separately for zooplankton (Cladocera and Copepoda) and chironomid larvae in both the YSS and the GOS. Prey relative abundance values were arcsine (square root (y)) transformed to handle possible non-normality.

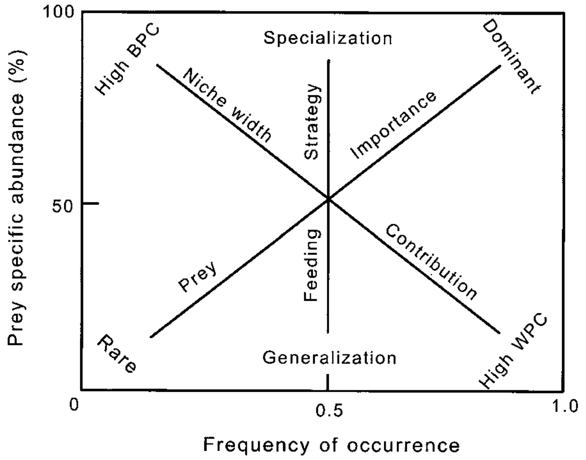

Figure 3. Explanatory diagram for interpretation of feeding strategy, niche width contribution, and prey importance (modified Costello method, Amundsen et al. 1996). BPC = between phenotype component to niche width, WPC = within phenotype component to niche width.

A modification of the graphical Costello method (Amundsen et al. 1996) was used to examine prey importance, feeding strategy, and components of niche width. Feeding strategy is defined as the degree of specialization or generalization by suckers on various prey taxa (Costello 1990). Prey-specific abundance was plotted against frequency of occurrence on a two-dimensional graph (Figure 3). Prey-specific abundance is the percentage a prey taxon comprises of all prey items in only those predators with prey i in their stomach:

$$P_i = \left(\sum S_i \Big/ \sum S_{ti}\right) \times 100$$

where P_i is the prey-specific abundance of prey i, S_i the stomach content (surface area) comprised by prey i, and S_{ti} the total stomach content in only those suckers with prey i in their stomach.

Information about feeding strategy and prey importance of the population can be obtained by examination of distributions of points along the diagonals and axes of the diagram depicted in Figure 3. The percent abundance, increasing along the diagonal from the lower left to the upper right corner, provides a measure of prey importance, with dominant prey at the upper right, and rare or unimportant prey at the lower left. The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization (Figure 3). The predators have specialized on prey types in the upper part of the figure, whereas prey located in the lower portion were eaten more occasionally. Prey points located at the upper left of the diagram would be indicative of specialization of the predator population.

For each sucker species, niche breadth (B) for food items was calculated using the equation of Levins (1968):

$$B = 1 \Big/ \sum P_i^2 \quad (i = 1, \ldots, n \text{ prey types}),$$

and then standardized to express it on a scale from 0 to 1.0:

$$B_A = (B - 1)/(n - 1)$$

where P_i is the proportion of the resource in each category and n is the number of types of prey items. Standardized niche breadth was used to assess the diversity of food items eaten by each catostomid species in a segment.

We tested the null hypothesis of no relationship between sucker food niche breadth (B_A) and prey species diversity (1/D) (there is no linear relationship between sucker food niche breadth and prey species diversity at capture sites) with regression analysis in the GOS and the YSS. Food niche breadth served as the response (Y) variable and prey species diversity served as the predictor (X) variable. This analysis was conducted separately for zooplankton and benthic invertebrate prey.

Multivariate analysis of variance (MANOVA) was used to assess food use differences collectively among suckers in a segment. MANOVA was conducted across species in each river segment to test the null hypothesis of no difference in food resource use among sucker species. Sucker species served as the independent variable and food categories as the dependent variable (percent surface area importance values). The equal variance–covariance assumption was checked with the Box test (Box 1949) and residual plots for dependent variables were constructed to examine homoscedasticity. Multicollinearity between dependent variables was examined by computing the variance inflation factor. Dependent variables (% surface area values) were arcsine (square root (y)) transformed. The data were analyzed using the SAS (SAS Institute 1990) software package.

Following a significant MANOVA, distinctiveness of the food niche among suckers in each river segment was assessed with discriminant analysis. Two components of discriminant analysis were used – canonical analysis of discriminance (CAD) and classification. We used CAD to determine what food categories were important in segregating sucker species and to examine graphically the degree of food niche overlap among sucker species in a segment. We used classification as a quantitative measure of food niche overlap. Misclassification of a sucker occurred because the individual was similar to another species in its food habits and was assigned incorrectly to this species. The more misclassifications that occurred, the more alike the two species were in their resource use (McNeely 1987). Therefore, in this study, niche overlap was treated as analogous to percent misclassification (Baker & Ross 1981). For discriminant analysis, the data were analyzed using the Statistica (Statsoft Inc. 1995) software package.

Results

Sucker community composition

The YSS and the GOS exhibited greatly different sucker communities, with different dominant species. In the YSS, 499 suckers were captured, representing seven species (bigmouth buffalo, *Ictiobus cyprinellus*; smallmouth buffalo, *Ictiobus bubalis*; river carpsucker, *Carpiodes carpio*; shorthead redhorse, *Moxostoma macrolepidotum*; white sucker, *Catostomus commersoni*; longnose sucker, *Catostomus catostomus*; and blue sucker, *Cycleptus elongatus*). Bigmouth buffalo and smallmouth buffalo constituted 8% and 3% of the total fish catch (sucker and non-sucker species), respectively. River carpsucker made up ∼2% of the total fish catch, with the other four species each contributing less than 1% of the total fish catch. Three native species, bigmouth buffalo, smallmouth buffalo, and river carpsucker, represented 94% of the sucker catch in the YSS.

In the GOS 6 217 suckers were captured, representing seven species (bigmouth buffalo, smallmouth buffalo, river carpsucker, shorthead redhorse, white sucker, longnose sucker, blue sucker). Longnose sucker and white sucker, which were rarely sampled in the YSS, represented 76% of the total catch of all fish species and constituted over 98% of the sucker catch in the GOS.

Prey populations

The average zooplankton density for the YSS habitats (251.8 organisms l^{-1}) was approximately 8 times greater than the density of zooplankton in the GOS habitats (32.6 organisms l^{-1}) (ANOVA, $F = 6.80, P = 0.01$). Benthic invertebrate densities were also higher in the YSS (277.0 organisms m^{-2}) than in the GOS (149.6 organisms m^{-2}) habitats (ANOVA, $F = 6.04, P = 0.02$).

Zooplankton richness was similar in both study segments (YSS = 4.02 prey types per macrohabitat sample unit, GOS = 4.14 prey types per macrohabitat sample unit) (ANOVA, $F = 3.09, P = 0.35$), but the YSS habitats had a higher zooplankton diversity ($1/D = 2.21$) than the GOS ($1/D = 1.92$) (ANOVA, $F = 4.27, P = 0.02$). Benthic invertebrate diversities were similar in the YSS ($1/D = 1.08$) and the GOS ($1/D = 1.16$) (ANOVA, $F = 0.98, P = 0.28$), but the GOS (2.15 prey types per macrohabitat sample unit) had higher richness than the YSS (1.60 prey types per macrohabitat sample unit) (ANOVA, $F = 6.45$, $P = 0.0057$).

Food habits

In each of the segments, four species of sucker were captured frequently enough for quantitative analysis of food habits. In the YSS, bigmouth buffalo, river carpsucker, and smallmouth buffalo ate mostly zooplankton. Crustacea, primarily Cyclopoida and Bosminidae, composed over 75% of the number and over 55% of the volume of diets for each of the three species (Table 1). Chironomid larvae also contributed substantially to diets of smallmouth buffalo, constituting ∼18% of the number and 39% of the volume. Shorthead redhorse fed mostly on Chironomid and Trichoptera larvae which accounted for ∼65% of the number and 80% of the volume of diets. The frequency of occurrence of zooplankton crustacea in stomachs was over 95% for bigmouth buffalo, river carpsucker, and smallmouth buffalo (Table 1). Cladocera and Copepoda zooplankton were found in ∼45% of shorthead redhorse stomachs. Chironomid larvae were found in 30% of bigmouth buffalo and river carpsucker stomachs and in 56% and 92% of smallmouth buffalo and shorthead redhorse stomachs, respectively (Table 1).

In the GOS, shorthead redhorse and white sucker ate mostly chironomid larvae. Chironomids composed over 60% and 85% of the volume of white sucker and shorthead redhorse diets, respectively (Table 1). Longnose sucker fed mostly on a combination of filamentous green algae and chironomid larvae which accounted for over 90% of the volume of food items in the diet. River carpsucker ate mostly zooplankton. Crustacea,

Table 1. Relative abundance (%N), percent surface area (%A), and frequency of occurrence (%F) of prey items in sucker stomachs in the YSS and the GOS (N = number of sucker stomachs with food contents, BM = bigmouth buffalo, RC = river carpsucker, SH = shorthead redhorse, SM = smallmouth buffalo, BK = blue sucker, LN = longnose sucker, WS = whitesucker). %N not reported for AG or DT.

Fish species	N	Other prey items	Index (%)	Prey items*															
				CY	CA	BS	DP	CD	NA	LP	SI	OS	CH	TR	CP	AG	TY	DT	DM
YSS																			
BM	68	2	N	51.3	0.8	29.9	7.8	0.1	0.2	0.5	1.0	<0.1	7.6						
			A	45.2	0.9	25.8	10.6	0.1	<0.1	1.5	0.6	<0.1	13.3						
			F	76.5	11.8	67.6	38.2	5.9	5.9	5.9	2.9	2.9	29.4						
RC	74	2	N	37.0	0.5	38.0	9.2	4.2	1.5	0.6	<0.1	0.7	6.4				1.8		
			A	31.8	0.9	32.9	15.1	3.6	0.6	0.7	<0.1	0.6	11.8				2.0		
			F	86.4	11.4	72.7	59.1	27.3	15.9	2.3	2.3	11.4	29.5				2.3		
SH	42	1	N	11.8		16.7	3.8	2.0					47.2	17.0	1.4				
			A	7.1		5.6	2.8	0.4					57.2	25.2	0.5				
			F	46.2		46.2	15.4	23.1					92.3	53.9	15.4				
SM	92	7	N	51.6	0.9	15.0	2.4	7.8	<0.1	<0.1		1.6	18.2		0.1				
			A	37.6	0.6	11.9	3.6	3.9	<0.1	<0.1		1.1	38.8		0.1				
			F	94.3	13.6	51.1	29.6	39.8	1.1	1.1		14.8	54.6		3.4				
GOS																			
BK	10	0	N				2.8						73.3	5.4	0.9				
			A				2.2						72.8	7.7	0.4	17.0			
			F				16.7						83.3	50.0	16.7	33.3			
LN	74	1	N	0.1	<0.1	<0.1	1.9	<0.1			<0.1		18.0	0.4	0.5				1.9
			A	<0.1	<0.1	<0.1	1.9	<0.1			<0.1		39.9	0.1	1.4	54.2		0.5	1.8
			F	5.6	<0.1	<0.1	3.7	1.9			1.9		94.4	1.9	40.7	90.7		1.9	11.1
RC	84	6	N	47.2	1.5	6.3	4.1	8.5	2.7	<0.1	0.5	1.8	20.3	0.2	0.2				0.2
			A	34.4	2.4	4.7	7.1	4.7	1.2	0.1	0.2	1.1	35.1	0.2	0.1	3.6		<0.1	0.1
			F	89.7	20.6	44.1	35.3	42.7	16.2	<0.1	1.5	23.5	64.7	2.9	4.4	4.4		1.5	1.5
SH	46	1	N	2.5		2.2	0.3	3.5			0.6		80.6	2.8	2.7				
			A	1.1		0.5	0.1	0.5			1.0		87.7	5.9	3.2	<0.1		<0.1	
			F	16.7		8.3	4.2	16.7			4.2		95.8	20.8	4.2	4.2		4.2	
WS	71	3	N	9.2	0.6	1.6	2.2	5.5		1.0	2.1	0.2	44.4	1.0	5.3				2.4
			A	5.4	0.1	0.2	1.3	1.9		0.4	4.5	<0.1	61.8	1.9	6.7	9.8		4.2	1.2
			F	31.0	4.8	7.1	16.7	19.0		2.4	16.7	2.4	92.9	23.8	42.9	23.8		2.4	26.2

*CY = Cyclopoida, CA = Calanoida, BS = Bosminidae, DP = Daphnidae, CD = Chydoridae, NA = Nauplius larvae, LP = Leptidoridae, SI = Sididae, OS = Ostracoda, CH = Chironomidae larvae, TR = Trichoptera larvae, CP = Chironomidae pupae, AG = filamentous green algae, TY = Thysanoptera, DT = organic detritus, DM = diatoms.

primarily Cyclopoida, constituted over 90% of the number and over 55% of the volume of river carpsucker diets (Table 1). The frequency of occurrence for crustacean zooplankton was high in river carpsucker (97%) and white sucker (51%) diets. Chironomid larvae were found in over 90% of longnose sucker, shorthead redhorse, and white sucker stomachs; however, this prey type was found in only 64% of river carpsucker stomachs (Table 1). Food habits information for blue sucker is also included in Table 1.

In both segments, a positive relation was found between the density of chironomid larvae in the environment and the abundance of larvae in fish stomachs ($r = 0.53–0.83, P < 0.05$). This relation, however, did not exist between zooplankton density (number l^{-1}) and the abundance of zooplankton found in fish stomachs ($r = 0.01–0.11, P > 0.05$) in the two segments except for longnose sucker in the GOS ($r = 0.80$, $P < 0.05$).

Feeding ecology

Dominant food resource use patterns differed among the four dominant sucker species in each segment. River carpsucker in both segments and bigmouth buffalo in the YSS had generalized feeding strategies, as indicated by the high frequency of occurrence and the low prey-specific abundance of many food items in their stomachs (i.e., most points located in the lower right portion of the Costello graph, Figures 4 and 5) and their relatively wide food niche breadths (YSS = bigmouth buffalo, $B_A = 0.106$; river carpsucker, $B_A = 0.138$; GOS = river carpsucker, $B_A = 0.106$). Smallmouth buffalo in the YSS exhibited a more mixed feeding strategy, with varying degrees of specialization and generalization of different prey types (Figure 4) and a relatively wide food niche breadth ($B_A = 0.101$).

White sucker and longnose sucker in the GOS, and shorthead redhorse in both segments exhibited specialized feeding strategies where they fed almost exclusively on a few prey types (Figures 4 and 5). Narrow food niche breadths further supported a specialized feeding strategy for these species (GOS = longnose sucker, $B_A = 0.046$; shorthead redhorse, $B_A = 0.013$; white sucker, $B_A = 0.057$; YSS = shorthead redhorse, $B_A = 0.009$).

A positive relation was found between zooplankton diversity in sucker habitats and sucker food niche breadth in both the YSS ($r = 0.49, P < 0.0001$) and the GOS ($r = 0.39, P = 0.0009$). No such relation was found, however, between benthic invertebrate diversity and food niche breadth.

Food use differences existed among sucker species (YSS, MANOVA, Wilk's Lambda = 0.4118, $P < 0.0001$; GOS, MANOVA, Wilk's Lambda = 0.2422, $P < 0.0001$), but not years (YSS, MANOVA, Wilk's Lambda = 0.8252, $P = 0.08$; GOS, MANOVA,

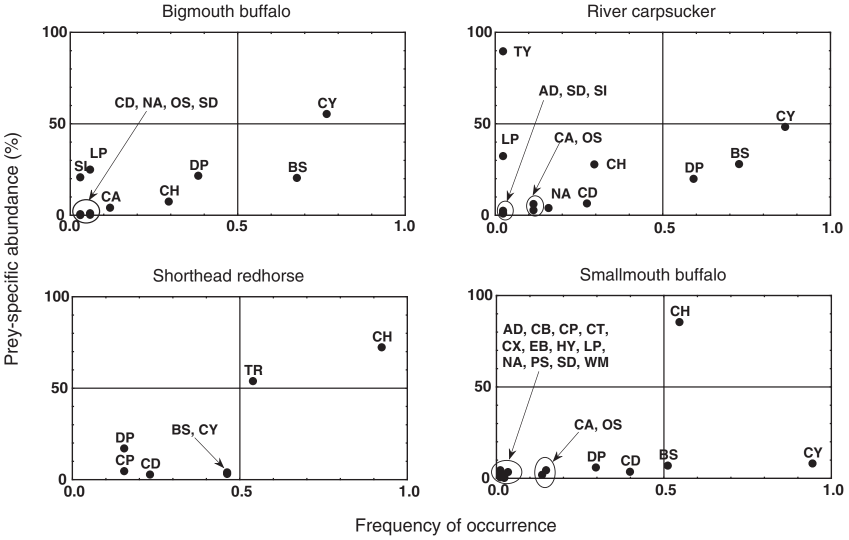

Figure 4. Graphs depicting feeding strategy and prey importance for YSS catostomid species (for explanation of prey code, consult Table 1).

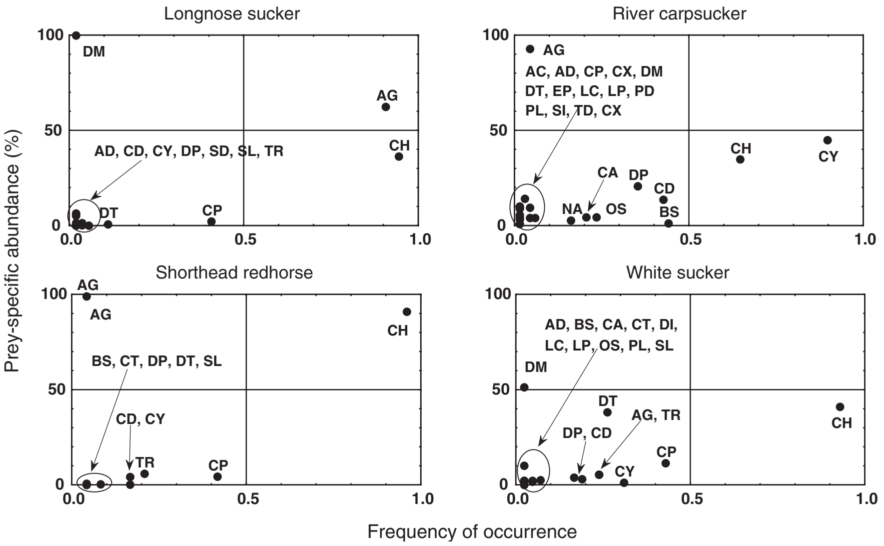

Figure 5. Graphs depicting feeding strategy and prey importance for GOS catostomid species (for explanation of prey code, consult Table 1).

Wilk's Lambda = 0.9364, P = 0.23) in each river segment. No significant interaction was found between sucker species and years in the YSS (MANOVA, Wilk's Lambda = 0.8391, P = 0.06) or the GOS (MANOVA, Wilk's Lambda = 0.8504, P = 0.37).

CAD of food habits derived three canonical functions, each a composite of the seven food categories retained in the YSS (Table 2a) and of the nine food categories retained in the GOS (Table 2b). The first two functions accounted for ~97% of the diet differences among the four species in the YSS. Trichoptera and chironomid larvae exhibited the largest scores (standardized canonical coefficients) on the first canonical function (Trichoptera = 0.9515, chironomid larvae = 0.7845). Among the four sucker species in the GOS, the first two functions accounted for ~94% of the diet differences. Filamentous green algae and Cyclopoida exhibited the largest scores (standardized canonical coefficients) on the first canonical function (filamentous green algae = −0.6912, Cyclopoida = 0.4691).

Plots of individual scores on the first two canonical functions resulted in the species separating into two groups in each of the segments (Figures 6 and 7). In the YSS, one group consisted of the three mainly zooplanktivorous fishes and showed the following order of decreasing dependence on large benthic prey and increasing dependence on small pelagic prey: smallmouth buffalo, river carpsucker, bigmouth buffalo (Figure 6). The second group included the benthic invertivorous shorthead redhorse which showed a strong dependence on large benthic prey. Bigmouth buffalo and river carpsucker showed nearly complete overlap in diet, whereas smallmouth buffalo overlapped

Table 2. CAD of catostomid species from the two segments. (a) Standardized coefficients of food categories on the first two canonical functions for the YSS. (b) Standardized coefficients of food categories on the first two canonical functions for the GOS.

Food category	Canonical function I	Canonical function II
(a)		
Cyclopoida	0.1687	0.5377
Bosminidae	0.0460	−0.1540
Daphnidae	−0.0009	−0.2986
Chironomid larvae	0.7845	0.6580
Chydoridae	−0.0104	0.3654
Trichoptera larvae	0.9515	−0.2968
Ostracoda	0.2079	−0.2536
(b)		
Cyclopoida	0.4691	−0.4437
Bosminidae	0.2882	−0.2295
Daphnidae	0.0082	−0.2558
Chironomid larvae	0.0040	−0.0142
Chydoridae	0.3227	−0.2874
Filamentous algae	−0.6912	−0.6664
Chironomid pupae	−0.2023	0.3208
Trichoptera larvae	0.0223	0.2623
Organic detritus	0.0351	0.2068

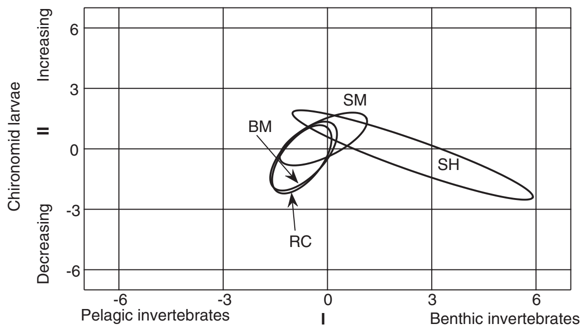

Figure 6. Ellipses enclosing 70% of the individuals of each YSS catostomid species plotted on canonical functions I (I) and II (II) (BM = bigmouth buffalo, RC = river carpsucker, SH = shorthead redhorse, SM = smallmouth buffalo).

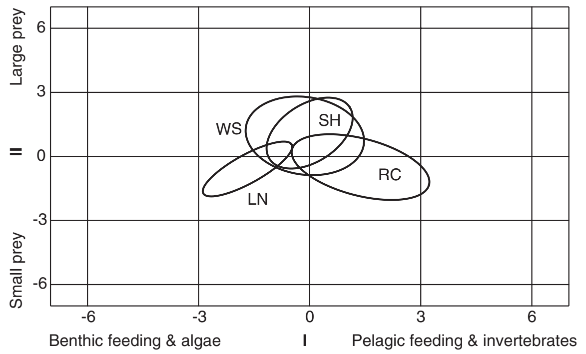

Figure 7. Ellipses enclosing 70% of the individuals of each GOS catostomid species plotted on canonical functions I (I) and II (II) (LN = longnose sucker, RC = river carpsucker, SH = shorthead redhorse, WS = white sucker).

Table 3. Classification analysis of catostomid species from the two segments. (a) Classification matrix for the YSS. (b) Classification matrix for the GOS.

Species	% Classified correctly	Number of cases classified as species			
		BM	RC	SM	SH
(a)					
BM	44.1	30	21	17	0
RC	54.4	20	41	13	0
SM	57.6	16	23	53	0
SH	61.9	0	0	16	26
Totals	54.3	66	85	99	26
(b)					
LN	81.8	60	1	7	6
RC	78.6	1	66	6	11
WS	56.3	10	10	40	11
SH	63.0	1	2	14	29
Totals	70.9	72	79	67	57

BM = bigmouth buffalo, RC = river carpsucker, SM = smallmouth buffalo, SH = shorthead redhorse, LN = longnose sucker, RC = river carpsucker, WS = white sucker, SH = shorthead redhorse.

with these two species as well as shorthead redhorse. In the GOS, three invertivores formed one group and showed the following order of decreasing dependence on filamentous green algae: white sucker, shorthead redhorse, river carpsucker (Figure 7). The second group consisted of the herbivorous and invertivorous longnose sucker which showed a strong dependence on filamentous green algae.

In the YSS, shorthead redhorse was most distinctive in its food habits over 60% of the time (Table 3a). Bigmouth buffalo was the least distinctive species in this segment. In the GOS, longnose sucker exhibited the most distinctive food habits with over 80% of observations classified correctly (Table 3b). White sucker was the least distinctive in its food habits in the GOS. The highest niche overlap was found among sucker species in the YSS in which only 54.3% of individuals were correctly classified (Table 3a). Suckers in the GOS were more distinctive in their food habits than in the YSS with 70.9% of individuals classified correctly (Table 3b). Similar to results obtained with the CAD plots, the high niche overlap in the YSS is related to high food use overlap among bigmouth buffalo, smallmouth buffalo, and river carpsucker as each was frequently misclassified as the other 18–31% of the time (Table 3a). The greater food niche distinctiveness in the GOS appears to be related to the distinct food habits of longnose sucker and river carpsucker which were classified correctly 81.8% and 78.6% of the time, respectively (Table 3b).

Discussion

Sucker community composition

Major differences in river physiochemical conditions and habitat in the two segments were associated with the highly dissimilar catostomid communities in the YSS and the GOS. Garrison Dam and Lake Sakakawea have lowered water temperatures, reduced turbidity, and altered natural habitats in the GOS. Conversely, high turbidity, a more shallow and braided main channel, periodic connecting of the main channel with the floodplain, and large backwater habitats characterizes the YSS.

The more natural habitats and physiochemical conditions in the YSS has produced a sucker community dominated by river carpsucker, bigmouth buffalo, and smallmouth buffalo, most of which were captured in several large backwaters. These species have been shown to forage and rear in floodplain river systems that contain large, lacustrine habitats, such as backwaters (Kay et al. 1994), that are characterized by periodic inundation from high run-off (Pflieger 1975). Such floodplain backwaters typified the pre-impoundment middle and lower-Missouri River which was characterized by a sucker community comprised mainly of these three species and others in the genera *Ictiobus* and *Carpiodes* (Funk & Robinson 1974).

Conversely, white suckers and longnose suckers dominated the sucker community in the GOS; these species are most often found in streams and lakes that are characterized by very clear, cool water (Scott & Crossman 1973). The preferred temperature range for longnose sucker is 10–15°C (Brown & Graham 1953) with the upper lethal temperature (50% mortality in 24 h) for this species near 27°C (Black 1953). The preferred temperature range for white sucker was 19–21°C in a Colorado reservoir (Horak & Tanner 1964) and experimental evidence suggests that an optimum summer water temperature for this species is 24°C (Reynolds & Casterlin 1978). Both species also seem to survive best in very clean and clear water (Edwards 1983, Twomey et al. 1984). Water temperatures rarely exceeded 16°C in the main channel and 18°C in off-channel habitats in the GOS, but frequently exceeded 23°C in these habitats in the YSS (Young et al. 1998). Warm water temperatures and high turbidity most likely limited longnose sucker and white sucker numbers in the YSS, whereas cool water temperatures and low turbidity facilitated their high abundance in the GOS.

Minor alterations to river systems have often led to changes in growth (Beamesderfer et al. 1995), habitat use (Pert & Erman 1994), or patterns of recruitment (Crisp et al. 1983) for native species of fish. However, species replacement has occurred in rivers which have sustained more intense anthropogenic disturbances (Martinez et al. 1994). The drastic changes in habitat and physiochemical conditions in the GOS have evidently led to replacement of native sucker species that thrive in river conditions that typified the pre-control Missouri River with species that thrive in systems characterized by cool, clear water.

Feeding ecology and food habits

Collectively, the dominant sucker species in the YSS (bigmouth buffalo, river carpsucker, and smallmouth buffalo) exhibited greater food niche overlap than the dominant species in the GOS (longnose sucker, river carpsucker, white sucker), a result of YSS suckers feeding opportunistically on a dense zooplankton food resource. Opportunistic feeding of this type has resulted in a lack of food resource partitioning among riverine fish species in other systems as well (Martin 1984, Schlosser & Toth 1984). Of the dominant species in the YSS, the bigmouth buffalo is the only species considered to be a strict zooplanktivore (Pflieger 1975), although even this species has been known to feed opportunistically on non-zooplankton prey when these prey items were in high abundance (Tafanelli et al. 1971). River carpsucker and smallmouth buffalo are generally considered to be benthic invertivores (Pflieger 1975). However, like the bigmouth buffalo, these species have been known to feed opportunistically on alternative prey, such as zooplankton, when in high abundance (McComish 1967, Vainio 1973).

Morphological constraints may have led to less zooplanktivory by the GOS sucker species. Longnose sucker, river carpsucker, and white sucker possess adaptations for a benthic existence, such as a subterminal mouth, that may effectively limit the availability of a food resource that is distributed in the water column. However, longnose sucker and white sucker have been shown to be strict zooplanktivores when this resource was abundant (Barton 1980) and zooplankton dominated the diet of river carpsucker in the YSS, another species that usually exhibits benthivorous feeding habits (Brezner 1958). Therefore, the use of this food resource was likely limited by its availability in the GOS, not fish morphology.

The high availability of a diverse zooplankton prey source in the YSS and the low availability of zooplankton and the low diversity of invertebrate prey in the GOS are apparently responsible for segment differences in food niche breadths. Food niche breadth quantifies the diversity or breadth of the food resource gradient utilized by a given species (Siaw-Yang 1988). The dominant sucker species in the YSS fed on a readily available and diverse zooplankton food source. This food resource was also diverse in the GOS, but was of limited importance to suckers because of its low availability. The major dietary component of sucker diets in the GOS was benthic invertebrates which exhibited low diversity.

The mechanisms responsible for the difference in prey densities between segments are unclear. In the Missouri River, dam construction, dredging, and bank stabilization have reduced sediment transport and deposition and virtually eliminated the processes of flooding and meandering of the main channel (Hesse et al. 1989, Hesse & Sheets 1993). Elimination of these conditions has reduced the formation of backwater and wetland habitat and drastically reduced available supplies of carbon in the GOS and other Missouri River segments (Hesse et al. 1988). Changes in carbon supplies and in the availability of off-channel habitats have reduced invertebrate productivity in segments of the Missouri River altered by dams (Berner 1951, Hesse et al. 1988). Invertebrate communities undoubtedly benefit from the natural Missouri River conditions and processes that still exist in the YSS, but are now absent or reduced in the GOS.

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