

## River alteration and niche overlap among three native minnows (Cyprinidae) in the Missouri River hydrosystem

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The influence of physical and hydrologic stabilization on habitat niche overlap among three native cyprinid species: flathead chub *Platygobio gracilis*, sicklefin chub *Macrhybopsis meeki* and sturgeon chub *Macrhybopsis gelida*, in riverine segments of the Missouri and Yellowstone Rivers in western North Dakota and eastern Montana, was evaluated. Collectively the three species exhibited higher niche overlap in quasi-natural river segments than in segments highly altered by a mainstem dam based on relatively high percentages of individuals in quasi-natural river segments that were classified correctly, according to species, in discriminant function analyses of resource use, compared to lower percentages of individuals classified correctly in the altered river segments. The lower niche overlap in altered river segments resulted primarily from the lower overlap between flathead chub and the remaining species; this appears to be related to a decline in the diversity of natural habitats and conditions that provided a wide range of habitat conditions suitable for all three species. Results from this study suggest that selective segregation and habitat changes, rather than interactive segregation and competition, is probably the mechanism responsible for the pattern of habitat use and niche overlap among the three species in the altered segments.

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Key words: dams; flathead chub; niche overlap; sicklefin chub; sturgeon chub.

### INTRODUCTION

Studies of habitat use have proven valuable in interpreting patterns of resource partitioning among fishes (Sala & Ballesteros, 1997; Childs *et al.*, 1998; Gray & Stauffer, 1999; Davis, 2001). In streams, the stability of the physical and biological components of the environment strongly influences resource partitioning among fishes (McNeely, 1987). Patterns of environmental stability in streams can be formed by a variety of natural (*e.g.* fire) and anthropogenic (*e.g.* dams) disturbances. Anthropogenic disturbances, if severe enough, can have pronounced effects on these systems by either increasing or decreasing

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environmental stability (Golladay *et al.*, 1987; Polatera & Beisel, 2002). For example, livestock grazing often reduces stability in flow and other stream characteristics because of increased surface runoff due to soil compaction and reduced plant coverage adjacent to the stream (Platts, 1991). Dam construction, however, can have the opposite effect by creating more stable environmental conditions through flow changes that alter downstream fluvial integrity (Heinz Center, 2002).

High environmental variability, particularly in stream flow, has been linked to high niche overlap among stream fishes (McNeely, 1987). Stream minnows (Cyprinidae) in unstable, highly variable habitats may function as opportunists whose niches vary in size and structure in response to environmental changes. For example, Harrell (1978) and Matthews & Hill (1980) have shown that minnows varied in habitat use and exhibited greater niche overlap in streams characterized by high environmental variability than in streams characterized by low environmental variability, where competition reduced the degree of overlap in resource use.

Hutchinson (1957) published an important work on the niche concept. He described the ecological niche as an abstract n-dimensional space that defines a hypervolume where every point corresponds to a state of the environment that would permit a species to exist indefinitely. He further distinguished between fundamental and realized niches: the former represents the total range of environmental conditions that a species could occupy and the latter is that portion of the fundamental niche occupied after interaction with other species. An interpretation of Hutchinson's (1957) niche concept was provided by Aarssen (1984) where he differentiated between potential and available niches of a species, both of which are pre-interactive, and its realized or post-interactive niche. The potential niche is 'a theoretical hyperspace of 'places' where a species could leave descendants defined by all resource requirements and environmental tolerances (of the species), but without biotic interactions'. The available niche is 'a 'place' (or set of places) in nature that is a sub-set of a species' potential niche. This is roughly equivalent to habitat and represents the real space where a species could theoretically leave descendants if there were no biotic interactions with other species'. The available niche is similar to the concept of habitat described by Odum (1971) and others (Whitaker *et al.*, 1973; Whitaker, 1975; Andrewartha & Birch, 1984) as habitable place or suitable environment: an environment or set of environments meeting a species' ecological requirements and tolerances in which the species could, but need not actually, live. The realized (post-interactive) niche is a 'real 'place' in nature where the species can leave descendants in spite of continued interaction with other species' (Aarssen, 1984). In this paper, the terms niche and habitat are analogous to the realized niche and the habitat concepts proposed by Aarssen (1984) and Odum (1971), respectively.

Habitats in the present study provided a framework for examining and interpreting patterns in resource use among ecologically similar minnows in the upper Missouri River system; patterns of habitat use were examined to determine how habitat changes influence niche overlap among these minnows. Portions of the Missouri River have seen major physical and hydrologic disturbance resulting in habitat degradation and reduced habitat diversity (Hesse *et al.*, 1989; Hesse & Sheets, 1993). These changes are greatest in the lower Missouri River between

Sioux City, South Dakota and St Louis, Missouri, where the river has been channelized for commercial navigation. The upper Missouri River, in contrast, is less altered than the lower river, but some segments have been extensively modified. Certain segments (*e.g.* between Fort Peck Dam, Montana and Lake Sakakawea, North Dakota) are highly altered from mainstem dams, reservoirs and bank stabilization projects, whereas others (*e.g.* above Fort Peck Reservoir in Montana) are relatively free-flowing with few anthropogenic disturbances. Flow variability is lower in upper Missouri River segments below mainstem dams than in river segments upstream of these impacts (Galat & Lipkin, 1999). These river segments exhibited near identical flow variability before river regulation began in the 1930s. The difference in other environmental characteristics can be quite pronounced among upper river segments (Galat *et al.*, 2001).

In the upper Missouri and lower Yellowstone Rivers, three cyprinid species, the flathead chub *Platygobio gracilis* (Richardson), sicklefin chub *Macrhybopsis meeki* (Jordan & Evermann) and sturgeon chub *Macrhybopsis gelida* (Girard), have been shown to interact ecologically and overlap to varying degrees in their resource use (Werdon, 1992; Grisak, 1996; Everett, 1999). It was hypothesized that in the upper Missouri River system, physical and hydrologic stabilization in altered segments would result in lower resource and habitat use overlap among these ecologically similar fishes than in more natural and variable river segments.

## MATERIALS AND METHODS

### STUDY AREA

Cyprinid habitat use and niche overlap were examined in three Missouri River segments and in one Yellowstone River segment. The first segment of the Missouri River (MR1; Fig. 1), located above Fort Peck Dam, extends 111.8 km from Sturgeon Island [river km (rkm) 3141.8] to its lower boundary of Beauchamp Coulee (rkm 3029.9). The second Missouri River segment (MR2; Fig. 1) is located in eastern Montana below Fort Peck Dam, and extends 191.5 km from Wolf Point, Montana (rkm 2737.5) to the mouth of the Yellowstone River (rkm 2546.0). The third Missouri River segment (MR3; Fig. 1) is located in western North Dakota and extends 48.3 km from the mouth of the Yellowstone River (rkm 2546.0) to the headwaters of Lake Sakakawea (rkm 2470.3). The Yellowstone River segment (YR1; Fig. 1) extends 114.3 km from Intake Diversion Dam, near Glendive (rkm 114.3) in eastern Montana, to its mouth where it meets the Missouri River (Yellowstone River rkm 0.0) in western North Dakota.

The four segments exhibit differing levels of modification. MR2 is highly altered from its pre-impoundment physical and biological characteristics (Galat *et al.*, 2001). Fort Peck Reservoir has reduced the sediment loading in MR2 causing uncharacteristically clear flows. Furthermore, the dam regulates the downstream hydrograph; hypolimnetic releases maintain cool water temperatures downriver during the summer (Galat *et al.*, 2001). MR3 has a more natural flow regime than MR2 because it is downstream from the confluence of the free-flowing Yellowstone River and MR2. During the present study, main channel water temperatures in MR3 were 3–5° C warmer in summer than those in nearby MR2. MR3 is also characterized by high main channel turbidity, no major shoreline development, and few revetment banks (rip-rap). MR1 and YR1 are less altered than MR2 and MR3. These segments are considered quasi-natural because they have been subjected to few anthropogenic disturbances and are free flowing with near natural hydrographs, main channel temperatures and turbidities. From 1967 to 1996 flow regulation by Fort Peck Dam resulted in lower flow variability in MR2 and MR3 than in YR1 and MR1 (Galat & Lipkin, 1999).

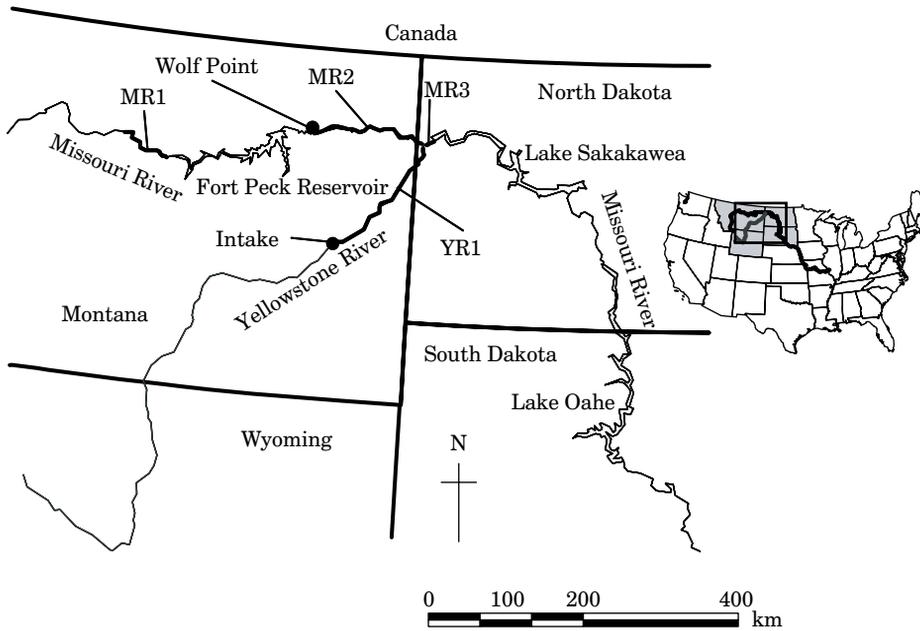


FIG. 1. Map depicting location of study segments in the Missouri and Yellowstone rivers (MR1, Missouri River segment 1; MR2, Missouri River segment 2; YR1, Yellowstone River segment 1; MR3, Missouri River segment 3).

## DATA COLLECTION

The same stratified random sample was used to collect fishes in each of the four study segments. Sampled strata included five habitat types: main channel cross-over, outside bend, inside bend, secondary channel (non-connected) and secondary channel (connected) (Fig. 2). Standard operating procedures were developed that defined habitat characteristics and outlined the protocol for sampling fishes with various gears in each habitat type (Sappington *et al.*, 1998). In each segment, fishes were collected from five randomly selected replicates of each stratum from July to September in 1996, 1997 and 1998. A variety of fish capturing gears was used to sample various depths and velocities

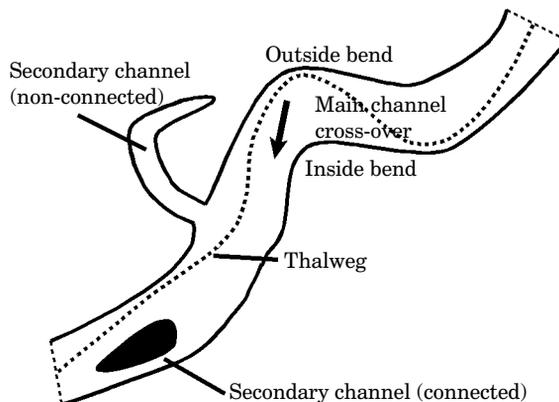


FIG. 2. Location of habitats in a typical Missouri River segment.

within habitats, thereby ensuring accurate description of each species' habitat use. Gear included a bag seine ( $10.7 \text{ m} \times 1.8 \text{ m} \times 1.8 \text{ m}^3$  bag  $\times 5 \text{ mm}$  mesh), benthic beam trawl ( $2 \text{ m} \times 0.5 \text{ m} \times 5.5 \text{ m} \times 3.2 \text{ mm}$  inner bag mesh), trammel net ( $22.9 \times 2.4 \text{ m}$  inner wall  $\times 2.5 \text{ cm}$  mesh, outer wall  $1.8 \text{ m} \times 20.3 \text{ cm}$  mesh), electrofishing boat (Coffelt VVP-15 variable voltage pulsator, 5000 W generator) and gillnet ( $30.5 \text{ m} \times 1.8 \text{ m} \times 1.9 \text{ cm}$ , 3.8, 5.1, 7.6 cm mesh). Each habitat type was sampled with the same gears and effort (three sub-samples for each gear) in each segment. Gear bias was not addressed empirically. A sub-sample was a single gear sample. Adult-sized fishes were identified to species and enumerated in each gear sub-sample. Fish were treated according to 'Guidelines for Use of Fishes in Field Research' (American Society of Ichthyologists and Herpetologists *et al.*, 1988).

Water depth (average depth; m), velocity ( $\text{m s}^{-1}$ ), temperature ( $^{\circ}\text{C}$ ), turbidity (nephelometric turbidity units, NTU) and substratum (%silt, %sand and %gravel) were measured at each sub-sample following the successful deployment and retrieval of fish sampling gears and later used to characterize segments and segment habitats. For an in-depth description of habitats, measurement of habitat physiochemical variables, and fish collection techniques, see Sappington *et al.* (1998). In habitat replicates  $>1.5 \text{ m}$  in depth (deep replicate), a boat was anchored in the habitat and water depth was measured with a Lowrance sonar device to the nearest  $0.1 \text{ m}$ . Current velocity was measured to the nearest  $0.1 \text{ m s}^{-1}$  with a Marsh–McBirney flowmeter (Flowmate model 2000). The probe of the flowmeter was suspended near the bottom with an A55 metric sounding reel and  $22.7 \text{ kg}$  sounding weight. In habitat replicates  $<1.5 \text{ m}$  in depth (shallow replicate), water column depth and water velocity were measured with the aid of a standard wading rod at three points along the gear sampling area. Water temperature was measured with a YSI 30 temperature/conductivity meter. The meter probe was held  $0.5 \text{ m}$  under the water's surface and temperature was measured to the nearest  $0.1^{\circ}\text{C}$ . Turbidity samples were collected *c.*  $0.5 \text{ m}$  below the water's surface and measured (to the nearest  $1.0 \text{ NTU}$ ) with a Hach 2100P turbidity meter. A substratum sample was collected using a hollow iron pipe ( $61.0 \times 10.2 \text{ cm}$ ) that had one end closed. The pipe was dragged the greatest distance sampled by a gear. Pipe contents were categorized (visually) as silt ( $<0.1 \text{ mm}$ ), sand ( $0.1\text{--}2.0 \text{ mm}$ ) and gravel ( $>2.0 \text{ mm}$ ). Later, the geometric mean of substratum size was calculated for each sub-sample (McMahon *et al.*, 1997). An observer's ability to categorize substratum was calibrated periodically using cloth sieves.

## ANALYSES

Distinctiveness of habitats among segments and distinctiveness of fish habitat use among segments were evaluated with multivariate analysis of variance (MANOVA; Johnson & Wichern, 1992). For MANOVA, an interaction term (segment  $\times$  habitat for habitat distinctiveness and segment  $\times$  species for habitat use distinctiveness) served as the independent variable and physiochemical habitat features served as the dependent variable (depth, current velocity, turbidity, temperature, %silt and %sand). MANOVA was used to test the null hypotheses that there was no significant difference in physiochemical characteristics of habitats among segments and there were no differences, across segments, in the physiochemical properties of the habitats of the species.

The equal variance-covariance assumption was checked with the Box test (Box, 1949), and residual plots for each dependent variable were constructed to examine homoscedasticity. Multicollinearity between dependent variables was examined by computing the variance inflation factor. An appropriate transformation, such as arcsine [square root ( $x$ )],  $\log_{10}(x + 1)$  or square root ( $x$ ), was applied to dependent variables that violated any of the assumptions (Hair *et al.*, 1995).

Canonical analysis of variates was used to identify the variables responsible for MANOVA significance (Johnson & Wichern, 1992). Mean canonical variable scores for segment habitats and for species habitat use were plotted to examine segment differences. The data were analysed using the Statistica (Statsoft, 1997) software package.

Categorical data modelling was also used to determine segment and habitat utilization. This procedure was used to test the null hypothesis that habitat use of each cyprinid

species did not differ among the four segments. Through this analysis,  $\log_{10}$ -linear models were fit to functions of species presence (1) and absence (0) frequencies. This analysis used maximum-likelihood estimation of parameters for the models. A  $\chi^2$  was used to test for a significant difference in partitioning of variance among the response functions (presence or absence) (SAS, 1990). Simple effects contrasts were used to further interpret habitat use differences among segments for a species (Kirk, 1995).

Habitat utilization by the three cyprinid species (flathead, sicklefin and sturgeon chub) was also examined by quantifying the relative abundance in each habitat in each segment; this was accomplished by dividing the total number of fish of a species captured in that habitat by the total number of fish of that species captured in that segment. This ratio was computed for each year and then averaged across years to obtain the 3 year average for each habitat.

Niche distinctiveness of each species within each segment was examined by discriminant analysis and classification (Johnson & Wichern, 1992). For discriminant analysis, an omnibus MANOVA was used to test the null hypothesis that no significant difference existed, across segments, in resource use of the species. For the MANOVA, cyprinid species served as the independent variable and resource features (*i.e.* physiochemical variables, *e.g.* depth, velocity and temperature) served as the dependent variable. Species scores on resource features were measurements taken from a habitat sub-sample in which at least one individual of that species was found. Checking of statistical assumptions and transformation of dependent variables for MANOVA followed procedures described for examining distinctiveness of habitats and habitat use among segments. Following a significant MANOVA, Hotelling's  $T^2$  (Johnson & Wichern, 1992) was used to make between species comparisons in the physiochemical properties of their habitats.

For each segment, a discriminant analysis distinguished among groups (minnow species) by weighting and linearly combining independent variables (resource features) into a new variable (canonical variable; also called a canonical function), which gave maximal statistical separation of the groups (minnow species) (Green, 1971). By extracting a second, orthogonal, canonical variable, overlap can be viewed in a plane (Ward & Lubin, 1992). Plots of species scores on the first two canonical variables gave a visual representation of niche overlap among the three cyprinids. Niche overlap was also inferred with classification analysis. Misclassification of a cyprinid species occurred when an individual was similar to another species in its resource use and was assigned incorrectly to that 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 per cent misclassification (Baker & Ross, 1981).

Variability of physiochemical variables within each segment was determined by computing the coefficient of variation (CV) for each variable ( $CV = S\bar{x}^{-1}$ , where  $S$  is the S.D. and  $\bar{x}$  the mean; Zar, 1984). An average CV for the physiochemical variables in each segment was used to make among segment comparisons in variability. Daily discharge data were obtained from the United States Geological Survey webpage ([www.waterdata.usgs.gov/mt/nwis/rt](http://www.waterdata.usgs.gov/mt/nwis/rt)) and used to compute each segment's discharge mean and variability (as expressed by CV) for 12 months and for the 3 month study period (July, August and September) in 1996, 1997 and 1998. These values were then averaged to obtain the 3 year average for each.

## RESULTS

### PHYSICAL CHARACTERISTICS OF SEGMENTS AND HABITATS

Below-dam segments MR2 and MR3 had greater depths, lower temperatures and finer substrata than quasi-natural segments MR1 and YR1 (Table I). MR1 exhibited the lowest turbidities among the segments. Velocities for each habitat type were similar across segments. Variability (as expressed by CV) of physiochemical conditions varied among habitats and segments (Table I). Segment rank

TABLE I. Physiochemical characterization [mean, standard deviation (s.d.), coefficient of variation (CV)] of segment habitats

Variable	Habitat																																						
	CHXO (Segments)						ISB (Segments)						OSB (Segments)						SCC (Segments)						SCN (Segments)														
	MR1	MR2	YR1	MR3	MR1	MR3	MR1	MR2	YR1	MR2	MR1	MR3	MR1	MR2	YR1	MR2	MR1	MR3	MR1	MR2	YR1	MR2	MR1	MR3	MR1	MR2	YR1	MR2	MR1	MR3									
Depth (m)	2.3	3.0	2.4	5.3	1.3	1.6	1.6	1.6	1.6	2.5	1.9	3.9	3.9	3.4	3.9	1.2	1.2	1.4	0.9	1.0	0.6	1.4	1.4	1.1	1.2	1.4	0.9	0.7	1.3	0.2	0.6	0.3	0.6						
s.d.	0.8	1.0	0.7	1.9	0.4	0.4	0.4	0.8	1.3	1.5	0.8	1.3	1.3	1.5	1.1	1.2	1.2	0.9	0.7	1.3	0.2	0.6	1.4	1.4	1.1	1.2	1.4	0.9	0.7	1.3	0.2	0.6	0.3	0.6					
CV	35.4	29.8	35.4	29.2	29.7	26.4	26.4	47.9	71.1	39.3	34.4	45.2	27.7	100.4	63.2	78.7	132.9	32.3	39.9	23.8	48.8	39.9	23.8	48.8	39.9	23.8	48.8	39.9	23.8	48.8	39.9	23.8	48.8	39.9	23.8	48.8			
Current velocity (m s <sup>-1</sup> )	0.7	0.8	0.9	1.0	0.6	0.6	0.6	0.5	0.7	0.7	0.7	0.8	0.8	0.7	0.4	0.5	0.4	0.5	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
s.d.	0.2	0.2	0.4	0.2	0.1	0.1	0.1	0.2	0.5	0.2	0.2	0.4	0.4	0.1	0.2	0.2	0.2	0.3	0.3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
CV	31.6	18.9	47.3	22.2	23.1	25.5	44.1	64.5	29.3	24.0	40.8	13.6	44.1	51.9	71.1	90.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	90.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Temperature (°C)	21.7	17.5	22.6	20.6	21.4	17.2	22.7	21.0	21.6	17.5	22.4	20.5	22.5	18.9	22.6	20.5	22.5	18.9	22.6	20.5	22.5	19.4	21.9	21.0	21.0	21.0	22.6	20.5	22.5	19.4	21.9	21.0	21.0	21.0	21.0	21.0	21.0		
s.d.	2.0	2.9	2.7	2.1	2.4	3.1	2.6	2.0	2.0	2.8	2.8	2.7	2.9	3.7	3.1	2.5	3.6	3.9	3.7	3.1	2.5	3.6	3.9	3.2	3.1	3.1	3.1	3.1	2.5	3.6	3.9	3.2	3.1	3.1	3.1	3.1	3.1		
CV	9.1	16.8	12.0	10.4	11.1	17.9	11.6	9.7	9.3	16.1	12.5	13.3	12.9	19.4	13.6	12.4	16.0	19.8	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	
Turbidity (NTU)	23.6	91.0	183.1	349.8	42.2	90.4	168.1	278.6	37.4	89.8	157.3	162.7	21.0	65.4	122.9	122.0	43.0	64.0	102.4	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1	65.1
s.d.	19.5	98.8	260.3	358.2	39.6	95.1	238.4	311.4	39.7	91.9	224.1	107.6	8.8	18.4	225.8	75.5	20.6	59.3	203.5	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0
CV	82.5	108.5	142.2	102.4	93.4	105.2	141.2	111.8	106.1	102.3	142.5	66.1	41.9	28.1	183.7	61.9	47.9	92.1	198.8	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7	47.7
Geometric mean of substratum (mm)	11.2	1.5	11.1	1.4	4.9	0.9	7.1	0.9	10.5	3.6	15.9	4.3	2.5	0.8	8.7	0.8	0.1	0.2	0.2	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.8	0.1	0.2	0.2	0.1	0.2	0.2	0.1	0.2	0.1	0.1	
s.d.	16.0	1.7	10.4	1.1	4.4	0.2	6.7	0.5	10.8	7.5	24.1	9.3	2.4	0.3	8.4	0.8	0.1	0.3	0.4	0.1	0.1	0.3	0.4	0.1	0.1	0.1	0.1	8.4	0.1	0.3	0.4	0.1	0.3	0.4	0.1	0.3	0.4	0.1	0.1
CV	143.2	110.8	93.9	80.4	90.2	21.4	95.3	56.9	103.5	211.3	151.5	97.5	98.4	44.6	96.1	97.5	0.2	157.9	175.0	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4	110.4

CHXO, main channel cross-over; ISB, inside bend; OSB, outside bend; SCC, secondary channel (connected); SCN, secondary channel (non-connected).

from highest to lowest for average physiochemical CV was as follows: YR1 (75.3), MR3 (58.0), MR1 (56.9) and MR2 (52.8).

Mean daily 3 month and 12 month discharge increased down river. MR1 had the lowest mean 3 month discharge ( $294.8 \text{ m}^3 \text{ s}^{-1}$ ) and 12 month discharge ( $318.7 \text{ m}^3 \text{ s}^{-1}$ ). MR3 had the highest 3 month discharge ( $856.5 \text{ m}^3 \text{ s}^{-1}$ ; MR2 =  $397.5 \text{ m}^3 \text{ s}^{-1}$ , YR1 =  $459.0 \text{ m}^3 \text{ s}^{-1}$ ) and 12 month discharge ( $813.8 \text{ m}^3 \text{ s}^{-1}$ ; MR2 =  $375.7 \text{ m}^3 \text{ s}^{-1}$ , YR1 =  $438.1 \text{ m}^3 \text{ s}^{-1}$ ). Variability (CV) in 3 month and 12 month daily discharge was highest for MR1 (3 month = 53.4, 12 month = 65.7) and YR1 (3 month = 65.0, 12 month = 86.5) and lowest for MR2 (3 month = 27.0, 12 month = 30.1; MR3: 3 month = 30.8, 12 month = 43.9).

Within the four segments, main channel cross-over and outside bend habitats tended to exhibit greater depths, velocities and coarser substrata than other habitats (Table I). Secondary channel (non-connected) habitat tended to exhibit lower depths and velocities and finer substrata than other habitats in all four segments. This habitat also had the highest water temperatures. The habitats with the highest and lowest turbidities varied among the segments.

Segments also differed in physiochemical properties (MANOVA, d.f. = 72,  $P < 0.001$ ). The canonical analysis of habitats derived five canonical variables, each a composite of physiochemical variables (Table II). The first two variables accounted for *c.* 74% of the habitat differences among segments. Depth exhibited the largest score on the first canonical variable (CV 1) which indicated that this variable was responsible for most of the habitat differences among the four segments (Table II).

Mean scores for CV 1 plotted across habitat types, indicated that main channel cross-over and inside bend habitats in MR3 and outside bend habitats in MR1 were most responsible for between-segment differences in habitats [Fig. 3(a)]. Mean scores were similar for the other four habitat types among the four segments.

## HABITAT USE

A total of 10431 flathead chub (MR1 = 2856, MR2 = 315, YR1 = 6393, MR3 = 867), 416 sicklefin chub (MR1 = 239, MR2 = 52, YR1 = 74, MR3 = 51) and 1360 sturgeon chub (MR1 = 365, MR2 = 133, YR1 = 801, MR3 = 61) was sampled from the four segments. Among the four segments, most flathead chub (67–91%) were captured in inside bend and secondary channel (connected) habitats which tended to exhibit shallow depths and low to medium current velocities. In most segments, sturgeon and sicklefin chub catch were distributed nearly evenly among main channel cross-over, inside bend, outside bend and secondary channel (connected) habitats. Seventy-three to 100% of sturgeon chub and 95–100% of sicklefin chub were captured in these four habitat types. These habitats exhibited a variety of depths and velocities.

Flathead chub tended to be found in habitats with shallower depths, lower current velocities and finer substrata than habitats used by sturgeon or sicklefin chub (Table III). Turbidities and temperatures at capture sites for all three species were similar among the four segments. The three species used finer

TABLE II. Results of habitat  $\times$  segment and species  $\times$  segment canonical analysis of variates performed on physiochemical and habitat use data, respectively

Physiochemical variable	Standardized coefficients			
	Habitat $\times$ Segment		Species $\times$ Segment	
	Canonical variable 1	Canonical variable 2	Canonical variable 1	Canonical variable 2
Depth (m)	1.2512	0.2641	1.0697	0.0631
Current velocity ( $\text{m s}^{-1}$ )	0.5102	0.0859	0.3770	-0.1990
Temperature ( $^{\circ}\text{C}$ )	-0.2534	0.3541	-0.0065	-0.0278
Turbidity (NTU)	0.3316	0.2109	0.0213	1.1115
Per cent sand	0.0924	0.5580	0.0009	0.3298
Per cent silt	0.9586	-1.1201	0.3085	-0.2246
Eigenvalues	0.4022	0.1030	0.1088	0.0114
Relative %	59	15	88	9

Relative %, relative contribution to total dispersion.

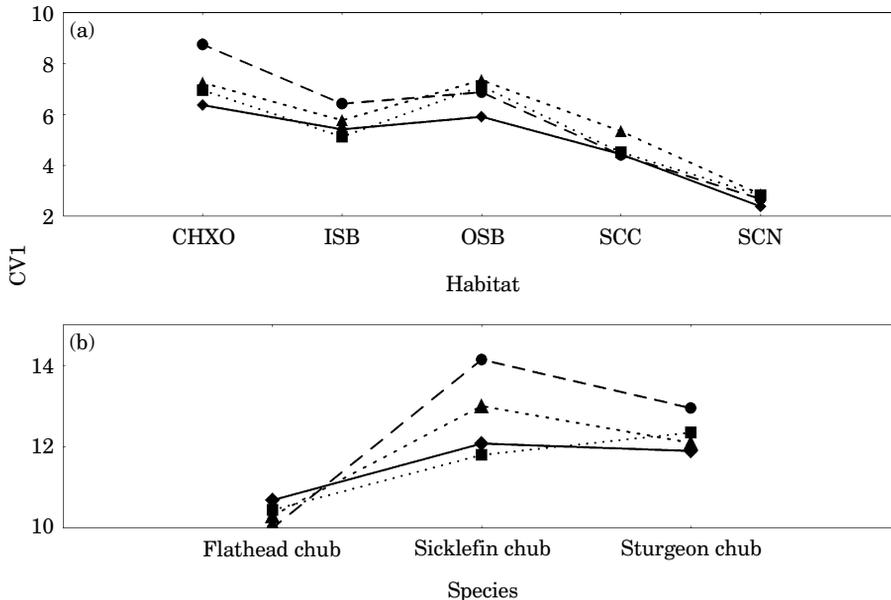


FIG. 3. Plots of mean CV 1 scores across (a) segments [—◆—, MR1; ---▲---, MR2; .....■....., YR1; ---●---, MR3 (see Fig. 1)] and habitats [CHXO, main channel cross-over; ISB, inside bend; OSB, outside bend; SCC, secondary channel (connected); SCN, secondary channel (non-connected)] and (b) segments and species.

substrata, characterized by more sand and less gravel, in MR2 and MR3 than in MR1 and YR1. Sicklefin and sturgeon chub tended to be found in habitats with slightly higher current velocities in MR2 and MR3 than in MR1 and YR1 (Table III).

Habitat use differed significantly among the four segments for flathead chub (categorical data modelling, segment  $\times$  habitat interaction, d.f. = 12,  $P = 0.0038$ ), but not for sicklefin chub (d.f. = 12,  $P = 0.22$ ) and sturgeon chub (d.f. = 12,  $P = 0.61$ ). Use of inside bend, (d.f. = 3,  $P = 0.01$ ), outside bend (d.f. = 3,  $P = 0.0037$ ), and secondary channel (non-connected) (d.f. = 3,  $P = 0.0092$ ) habitats differed among the four segments for flathead chub and were responsible for the significant interaction.

Differences in habitat use existed among the three species among segments (MANOVA, d.f. = 18,  $P < 0.001$ ). The canonical analysis of habitat use derived three canonical variables, each a composite of physiochemical variables (Table II). The first two canonical variables accounted for *c.* 97% of the habitat use differences among segments. Depth exhibited the largest score on CV 1.

Mean scores for CV 1, plotted across segments and species, indicated that sicklefin and sturgeon chub contributed the most to intraspecific differences in habitat use between segments. The habitat use of the flathead chub did not vary much from one segment to another [Fig. 3(b)]. Mean canonical scores for the three species were most similar in MR1 and YR1 and least similar in MR2 and MR3 [Fig. 3(b)]. Mean scores for sicklefin and sturgeon chub were similar to each other in all segments, but flathead chub scores were much lower. Thus,

TABLE III. Physiochemical characterization [mean and coefficient of variation (CV)] of flathead, sicklefin and sturgeon chub capture sites

Variable	Species													
	Flathead chub (segment)			Sicklefin chub (segment)			Sturgeon chub (segment)			Sturgeon chub (segment)				
	MR1	MR2	MR3	MR1	MR2	MR3	YR1	YR2	YR3	MR1	MR2	MR3	YR1	YR2
Depth (m)	1.3	1.0	0.9	0.8	0.7	0.8	2.0	3.0	2.4	4.7	1.9	2.6	2.0	3.2
CV	0.3	0.9	0.8	0.7	0.7	0.7	0.7	1.0	0.7	1.5	0.8	1.0	1.2	1.7
Current velocity ( $m s^{-1}$ )	0.5	0.4	0.3	0.2	0.8	0.8	0.8	0.8	0.7	0.9	0.8	0.8	0.7	0.8
CV	0.9	0.2	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.1	0.3	0.3	0.4	0.3
Temperature ( $^{\circ}C$ )	20.4	17.9	22.0	20.7	20.7	17.8	20.7	17.8	21.8	20.7	20.6	18.2	21.8	20.2
CV	3.6	2.6	2.9	2.0	2.4	1.3	2.4	1.3	2.5	0.7	2.8	2.6	2.8	1.7
Turbidity (NTU)	36.7	80.9	146.2	161.2	26.6	62.6	26.6	62.6	172.4	187.7	26.3	85.1	156.9	303.6
CV	50.0	54.3	211.7	146.5	14.9	43.0	14.9	43.0	215.5	117.9	14.7	73.5	202.0	228.6
Geometric mean of substratum (mm)	5.0	0.7	6.5	1.0	5.7	1.1	7.0	1.1	7.0	1.3	5.6	1.6	8.1	2.2
CV	7.8	0.4	8.9	1.9	7.0	0.2	10.7	0.2	10.7	0.6	7.2	2.7	10.5	3.2
Per cent silt	29.8	23.7	33.1	31.6	9.6	1.1	1.6	0.9	9.5	11.1	8.3	11.1	8.3	9.1
Per cent sand	41.7	75.8	40.2	58.5	61.3	97.0	66.6	94.0	62.3	85.2	55.0	81.1	55.0	81.1
Per cent gravel	28.6	0.5	26.7	10.0	29.1	2.0	31.8	5.1	28.2	3.8	36.7	9.8	36.7	9.8

MR1, Missouri River segment 1; MR2, Missouri River segment 2; YR1, Yellowstone River segment 1; MR3, Missouri River segment 3.

sicklefin and sturgeon chub exhibited similar habitat use, whereas the habitats of the flathead chub differed from those of the other two species.

## NICHE OVERLAP

Differences in resource use existed among the three cyprinid species (MANOVA; MR1: d.f. = 12,  $P < 0.001$ ; MR2: d.f. = 12,  $P < 0.001$ ; YR1: d.f. = 12,  $P < 0.001$ ; MR3: d.f. = 12,  $P < 0.001$ ) in each river segment. Between species pairs, resource use differed significantly between flathead chub and both sicklefin and sturgeon chub (Hotelling's  $T^2$ ,  $P < 0.05$ ) in all segments. Resource use differed significantly between sicklefin and sturgeon chub only in MR3. Discriminant analysis of cyprinid resource use in each of the four segments derived two canonical variables, each a composite of the physiochemical categories retained (Table IV). CV 1 accounted for 89–99% of the within-segment differences in resource use among the three species. Current velocity and depth exhibited the largest scores on CV 1 in MR1, MR2 and MR3 with CV 1 accounting for >97% of the between-group variation in each segment (Table IV). YR1 was unique in that depth alone exhibited the largest score on CV 1 and explained only 89% of the interspecific variation in resource use. Further, YR1 also differed from the other segments in that most of the remaining variation (11%; that explained by CV 2) could be attributed to sites in which depth and velocity were negatively correlated (Table IV).

In all three of the Missouri River segments, flathead chub were found more often in shallow, low current velocity sites than were sicklefin and sturgeon chub. Flathead chub used relatively shallow depths in YR1, but did not use sites with lower current velocities than those used by the other two species. Thus, flathead chub consistently used relatively shallow depths. Plots of the scores of the species on the first two canonical variables in these analyses revealed that the three species exhibited a unique pattern of niche overlap in each river segment (Fig. 4). In all segments, however, sturgeon and sicklefin chub exhibited high niche overlap. In addition, flathead chub had lower overlap with the other two species in altered river segments than in quasi-natural river segments.

The species that was most distinctive in its resource use was flathead chub which was correctly classified by resource use >75% of the time in each of the four segments (Table V). Sicklefin chub were rarely classified correctly, based on their resource use, except in MR3 (Table V). The highest niche overlap among the three species was found in MR1 and YR1 in which only 60.1 and 63.1% of individuals were correctly classified, respectively. In MR3 and MR2, the three species exhibited the lowest niche overlap with 84.1 and 70.1% of individuals classified correctly, respectively (Table V). The higher niche overlap in MR1 and YR1 than in MR2 and MR3 may be related to higher overlap between flathead chub and the remaining species. Flathead chub was misclassified (by percentage) as sturgeon and sicklefin chub most often in MR1 and YR1 (Table V). Flathead chub was classified correctly most often in MR3 and least often as sicklefin and sturgeon chub in MR3 and MR2, respectively.

TABLE IV. Discriminant analysis of flathead, sicklefin and sturgeon chub from the study segments. Canonical variables were scores on six physiochemical variables for the three cyprinid species

Physiochemical variables	Standardized coefficients					
	MR1			MR2		
	Canonical variable 1	Canonical variable 2	Canonical variable 1	Canonical variable 1	Canonical variable 2	Canonical variable 2
Depth (m)	0.4960	-0.1005	-0.6300			0.0546
Current velocity (m s <sup>-1</sup> )	0.5631	0.0142	-0.4956			-0.4263
Temperature (°C)	0.0306	-0.8184	-0.0898			0.2237
Turbidity (NTU)	0.0743	-0.0210	0.3109			0.1123
Per cent sand	0.1730	0.5469	-0.0745			1.0705
Per cent silt	-0.3034	0.3949	*			*
Eigenvalues	0.3644	0.0019	1.0253			0.0144
Relative %	99	1	99			1
				MR3		
				YR1		
Depth (m)	0.7737	-0.6576	-0.4771			-0.4599
Current velocity (m s <sup>-1</sup> )	0.0642	1.3555	-0.6914			0.4691
Temperature (°C)	0.0001	0.1261	-0.0224			-0.7037
Turbidity (NTU)	0.0611	-0.3369	0.2315			0.7117
Per cent sand	0.1525	0.2558	-0.3305			-0.3903
Per cent silt	-0.2838	0.5023	-0.1837			-0.0759
Eigenvalues	0.4897	0.0617	2.8946			0.0810
Relative %	89	11	97			3

\*, Per cent silt excluded from analysis due to a high correlation with other variables; relative %, relative contribution to total dispersion; MR1, Missouri River segment 1; MR2, Missouri River segment 2; YR1, Yellowstone River segment 1; MR3, Missouri River segment 3.

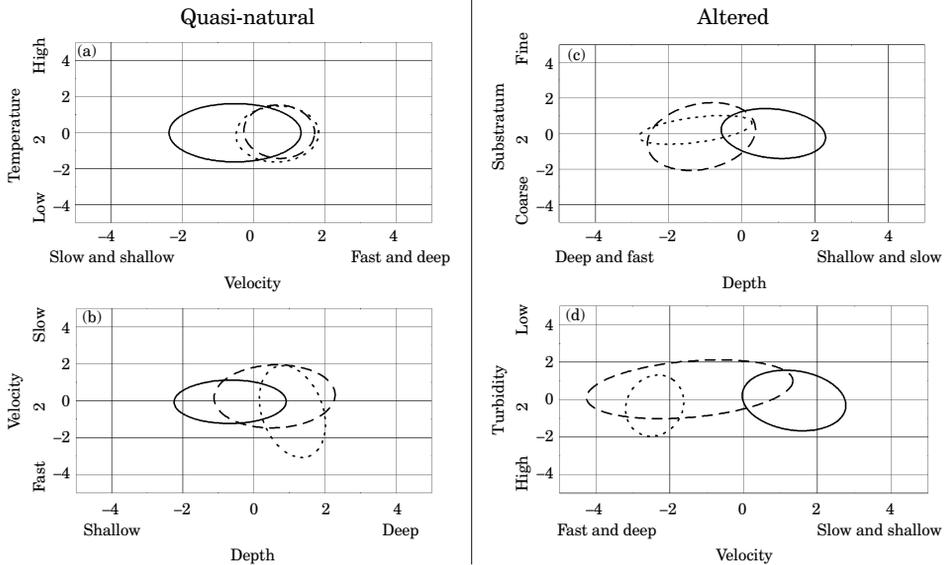


FIG. 4. Ellipses enclosing 70% of observations of each cyprinid species (—, flathead chub; - - -, sturgeon chub) plotted on CV 1 and 2 for (a) MR1, (b) YR1, (c) MR2 and (d) MR3 (see Fig. 1).

## DISCUSSION

Although niche overlap among fishes in relation to environmental features has been studied in small streams (Schlosser & Toth, 1984; McNeely, 1987; Kessler *et al.*, 1995; Welsh & Perry, 1998), few researchers have examined this phenomenon among fishes in large rivers. In addition, few have studied the influence of stream or river alteration on niche overlap. Niche overlap among these ecologically similar fishes was lower in highly altered river reaches: altered segments MR2 and MR3 exhibited lower niche overlap among the three minnows than did quasi-natural segments MR1 and YR1. Based on the variability of physiochemical characteristics and of flow, environmental conditions in MR2 and MR3 were more stable than in MR1 and YR1. Quite often in river systems, more stable environmental conditions result from anthropogenic disturbance, which can homogenize physical, chemical or biological components of natural environments (Hesse & Sheets, 1993; Scott & Helfman, 1997; Bednarek, 2001).

Flow modification is one of the most widespread human disturbances of stream environments (Fraser, 1972; Ward & Stanford, 1983). The flow regimes in many regulated streams and rivers are highly variable and unpredictable; typical seasonal flow variations may occur weekly or even daily, with no regular periodicity (Bain *et al.*, 1988). Conversely, regulation can reduce the variability in flow and other stream habitat characteristics (Ligon *et al.*, 1995; Heinz Center, 2002). The latter, rather than the former, represents the situation in the upper Missouri River (Galat & Lipkin, 1999). In the study area, Fort Peck Dam is the largest and most influential anthropogenic disturbance, and influences the river hydrograph in MR2 and MR3. After closure of Fort Peck Dam in 1940, mean

TABLE V. Classification matrices derived from discriminant analysis with the per cent classified correctly and the per cent classified incorrectly for each species in a segment

	<i>n</i>		Per cent classified correctly			Per cent classified incorrectly		
			Flathead chub	Sicklefin chub	Sturgeon chub	Flathead chub	Sicklefin chub	Sturgeon chub
MR1	208	Flathead chub	84.1	74.1	15.9			
	68	Sicklefin chub	0.0	49.3	50.7	10.0	0.0	11.1
	88	Sturgeon chub	50.0	50.0	50.0	0.0	0.0	85.6
		Total	60.1	88.9	64.9	0.0	7.3	64.9
MR2	134	Flathead chub	88.9	88.9	11.1			
	51	Sicklefin chub	7.3	7.1	85.6	7.3	0.0	11.1
	57	Sturgeon chub	64.9	12.2	64.9	22.9	0.0	85.6
		Total	70.1	76.4	70.1	2.1	7.3	64.9
YR1	196	Flathead chub	76.4	76.4	21.5			
	52	Sicklefin chub	20.9	10.0	69.2	20.8	0.0	10.3
	145	Sturgeon chub	68.3	26.2	68.1	5.5	0.0	36.4
		Total	63.1	96.0	63.1	0.0	4.5	4.0
MR3	101	Flathead chub	96.0	96.0	4.0			
	42	Sicklefin chub	89.7	0.0	10.3	89.7	0.0	10.3
	48	Sturgeon chub	36.4	18.2	36.4	45.4	0.0	36.4
		Total	84.1	18.2	36.4	45.4	0.0	36.4

MR1, Missouri River segment 1; MR2, Missouri River segment 2; YR1, Yellowstone River segment 1; MR3, Missouri River segment 3.

monthly discharge increased from its historical level by as much as  $404 \text{ m}^3 \text{ s}^{-1}$  in February and decreased by as much as  $614 \text{ m}^3 \text{ s}^{-1}$  in June. The dam has also lowered flow variability in below dam river segments (Hesse & Sheets, 1993; Galat & Lipkin, 1999). Variability in daily flow was much lower in below dam MR2 and MR3 than in MR1 and YR1 during this study. During summer, river discharge can fluctuate by as much as 50% over a 7 day period in MR1 and YR1 (United States Geological Survey webpage; [www.waterdata.usgs.gov/nwis-w/mt](http://www.waterdata.usgs.gov/nwis-w/mt)). Flow changes of this magnitude are virtually absent in altered MR2 and MR3 during this time period. Other researchers have also found dams to drastically reduce variability in river flow and other environmental factors (Walker & Thoms, 1993; Ligon *et al.*, 1995). High flow variability has been shown to influence niche relations among fishes in small streams. McNeely (1987) hypothesized that in upstream reaches of an Ozark stream high niche overlap among cyprinids was related to high flow variability and high fluctuation of other environmental variables and that niche overlap was lower in the more environmentally stable lower reaches. Further, McNeely (1987) determined that high environmental stability allowed competition to shape resource use in the absence of high environmental instability. A similar hypothesis was suggested by Schlosser (1982).

Fort Peck Dam and Fort Peck Reservoir also act as a sediment trap, preventing downstream transport of sediment from upper reaches, which has led to downcutting and deepening of the main channel in MR2 and MR3 (Leopold *et al.*, 1964). In the lower Missouri River (*i.e.* from Gavins Point Dam, South Dakota to the Missouri River mouth), reduced sediment transport, resulting from mainstem dam construction, and river channelization have altered channel shape and changed the depth-velocity profile of the river (Hesse & Sheets, 1993). Before mainstem alteration, the channel was an offset V-shape and characterized by a high diversity of depths and velocities. The natural offset V has been converted into a trapezoidal shape, leaving the main channel devoid of intermediate depths and velocities. Transition habitat, located between shallow channel border habitats and deeper main channel habitats at the gradually sloping section of the channel's offset V, is characterized by intermediate depths and velocities. Downcutting below dams, in the absence of channelization, has been shown to simplify river channels (Ligon *et al.*, 1995), thereby reducing the diversity of channel depths and velocities. While changes in channel shape in below-dam upper Missouri River segments are less drastic than in the lower Missouri River, reduced sediment transport in these upper Missouri River segments has probably decreased the amount of transition habitat and thereby reduced the diversity of depths and velocities.

Mean depth and velocity in main channel habitats (inside bend, main channel cross-over, outside bend) were greater in below-dam MR2 and MR3 than in quasi-natural MR1 and YR1. Additionally, the variability of depths and velocities within main channel habitats (as measured by CV; Table I) were generally lowest in MR2 and were lower in the two main channel habitats for MR3 than for MR1 and YR1. This indicates that there has been a loss of transition habitat in the altered river segments. Elimination of transition habitat probably impacts the habitat use by flathead chub the most, forcing it to use only shallow, slow velocity habitat along the river's shorelines, islands and

sandbars. The magnitude of this impact on flathead chub habitat use, as compared to the other two species, may be reflected by the fact that only flathead chub exhibited significant segment-related differences in habitat use. Without transition habitat, the other two cyprinids appear to use deeper and swifter main-channel habitats. This is especially true for the sturgeon chub. Sturgeon chub have shown overlap in habitat use with flathead chub in other studies (Werdon, 1992) and have been shown to use intermediate depths and velocities (Everett, 1999). Sturgeon and flathead chub, and occasionally sicklefin chub, were frequently captured in transition habitat in the lower Yellowstone River, North Dakota, during other, non-study sampling (Welker & Scarnecchia, 2004). Rarely were all three species captured together in deep main channel habitats or shallow channel border habitat.

Resource availability has been shown to influence resource use in stream fish communities (Fausch & White, 1981), and an increase in the variety of habitats and conditions available to organisms has been shown to reduce niche overlap and competition in ecological communities (Giller, 1984). Within segments, most flathead, sicklefin and sturgeon chub were captured in main channel cross-over, inside bend, outside bend and secondary channel (connected) habitat. Analyses for this study indicate that these four habitats in altered MR3 were less similar than in the other three segments. In altered MR2, however, these same habitats were more similar than in the other three segments and the three species in this segment exhibited only the third highest niche overlap. This indicates that the lower niche overlap among species in altered MR2 and MR3 did not result from a greater variety of available habitat conditions than found in MR1 and YR1.

Resource segregation is a major means of coexistence between competing species (Giller, 1984). There is an extensive body of theory, largely untested in natural settings, suggesting that intraspecific aggregation in subdivided habitat can promote the coexistence of interspecific competitors (Morin, 1999). Simple subdivision of the environment without intraspecific aggregation is not effective in promoting coexistence and, on average, sites with dense clumps of one species do not also contain dense clumps of other species. Support for this theory has been provided by Finger (1982) and Taylor (1996) who found that habitat partitioning among fishes in small streams resulted from spatial segregation mediated by interference competition. As far as is known, evidence supporting this theory has not been obtained for fishes in large rivers. Results from this study generally fit this theory.

Nilsson (1967) developed valuable concepts for explaining interspecific partitioning of resources among sympatric populations of fishes. He suggested that resource segregation is interactive ('interactive segregation'), with one species excluding one or more species from certain physical conditions (*e.g.* depths and velocities); interactive competition among species results in niche segregation. In contrast, resource segregation may be selective ('selective segregation'), reflecting species-specific preferences for various physical conditions. In situations where niche segregation is interactive, interspecific competition forces each species to compete only at its 'ecological optimum,' *i.e.* under those conditions to which it is best adapted or where it has some competitive advantage (Hartman, 1965). It is this tendency of species to utilize only their ecological optima that results in segregation during rigorous interspecific interaction. The possibility of

competition among the three minnows in this study, however, can only be speculated. In the absence of high environmental variability, competition among flathead, sicklefin and sturgeon chub in altered Missouri River segments could be responsible for greater resource partitioning and decreased niche overlap. Menge & Sutherland (1987) theorized that in environments characterized by high environmental variability, organisms are regulated directly by environmental stress and competition for space is prevented. Under more-moderate physical conditions, such as those within altered segments of the present study, competition increases as the importance of environmental stress as a community regulatory mechanism declines. Conversely, competition may not be important in organizing niche relations among the three species. Environmental variability is widespread and sufficiently high in many freshwater communities and existing evidence suggests that environmental variability is frequently a stronger organizing force in stream communities than is competition (Grossman *et al.*, 1982, 1998; Schlosser, 1987; Allan, 1995). If variability is sufficiently high in MR2 and MR3, competition may not be a significant factor in organizing niche relations among the three cyprinids. Present-day resource partitioning among flathead, sicklefin and sturgeon chub in these two upper Missouri River segments may simply result from a decline in the diversity of natural habitats and conditions which provided more areas of resource overlap for the three species. Selective segregation and habitat changes, rather than interactive segregation and competition, may be responsible for increased niche distinctiveness among the three species in the altered segments.

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