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Fish community structure in the Missouri and lower Yellowstone rivers in relation to flow characteristics

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Abstract

Human alteration is commonplace among large rivers and often results in changes in the flow regime which can lead to changes in fish community structure. We explored the features of fish community structure, morphological characteristics, functional composition, and life-history attributes in relation to six unique flow regimes in the Missouri and lower Yellowstone rivers where we found significant differences in community composition and abundance. The clearest pattern was the distinction between the channelized portion of the river below the mainstem reservoirs and all other parts of the Missouri and lower Yellowstone rivers due to a marked reduction of species richness above the reservoirs. We also found morphological, functional, and life-history differences among the flow units, with the inter-reservoir communities consisting of slightly more generalist characteristics. Our results suggest some relation between flow and fish community structure, but that human alteration may have the strongest influence in distinguishing community differences in the Missouri and lower Yellowstone rivers.

Introduction

Many abiotic factors, ranging from water quality to habitat availability, have been identified as influential factors in defining aquatic communities in lotic systems (e.g., Bain et al., 1988; Angermeier & Schlosser, 1989; Rahel & Hubert, 1991). However, flow has been identified as one of the more important driving variables used to describe aquatic communities in smaller order streams because it can have a strong effect on many other abiotic factors (Poff & Allan, 1995). Most of the research linking fish community structure to flow characteristics has been conducted on small streams because they are ubiquitous and easier to sample than larger rivers. The difficulty in collecting data from large rivers has been a limitation, but as restoration and mitigation efforts increase, there is an urgent need to gain an understanding of how aquatic communities are influenced by flow regimes.

Several flow variables have been used to describe the physical environment of streams including flow stability, predictability, and variability (Schlosser, 1985; Statzner & Higler, 1986; Bain et al., 1988; Poff & Ward, 1989; Poff, 1992; Townsend & Hildrew, 1994). These variables have then been used to describe and predict stream community structure and function given the existing set of hydrological conditions (Poff & Allan, 1995). Descriptions of aquatic species assemblages based on physical characteristics stem from refinements of Southwood's (1977) habitat template where the basic premise is that stable environments will support specialist species and highly variable environments will support a more opportunistic species assemblage that can take advantage of resources as they become available (Poff, 1992; Townsend & Hildrew, 1994; Poff & Allan, 1995).

Variability and stability in lotic systems are typically defined by the frequency, timing, and magnitude of changes between high and low flows. This does not mean every flood or drought will influence a species assemblage. Many species have evolved to exploit spring flooding in rivers (Junk et al., 1989) so a clear distinction between the ecological and evolutionary time scale of flow disturbances which influence species assemblages is needed (Poff, 1992). When natural disturbances are relatively predictable (e.g., spring floods), communities will be structured around this phenomenon. Less predictable ecological disturbances immediately change habitat availability which can result in a change in species assemblage; hence, flow extremes having low predictability in a river or stream are more likely to act as ecological disturbances which favors generalist species.

Flows in many larger rivers throughout the world have been altered through various management practices like impoundment and channelization. These management practices are directed toward reducing annual flow variability for flood control and/or maintaining a reliable source of water for navigation, hydropower, irrigation, and consumptive uses. Such changes can result in an altered hydrograph and ultimately a reduction in annual predictability of flows. Unfortunately, the dynamics of biological responses to altered flows are not well understood in larger river systems. However, a possible result is that flow alteration may act in a similar fashion to an ecological disturbance for the existing biological communities, thus compelling structural and functional shifts (Reice, 1994). Therefore, human induced changes in flow, coupled with natural variability, may result in considerably different species and functional assemblages within a river system.

Hydrological changes have been observed along the Missouri River where the flow characteristics have been significantly altered after impoundment and channelization in the mid 1900s (Galat & Lipkin, 2000; Pegg & Pierce, 2002). Pegg (2000) and Galat & Lipkin (2000) reported a large amount of flow variability in the Missouri River due to its large expanse and history of alteration. This variability has resulted in distinct regions differing in a suite of flow characteristics (Pegg & Pierce, 2002) which may, in turn, influence fish communities.

The purpose of this study was to explore characteristics of fish community structure, functional composition, and life-history attributes in relation to flow regimes in the Missouri and lower Yellowstone rivers. Our specific objectives were to (1) characterize the fish species richness and composition, functional composition, and life-history attributes of regions with differing flow characteristics, (2) test for differences in fish communities among portions of the river differing in flow characteristics, (3) examine the pattern of responses in relation to flow regimes associated with human alteration, and (4) examine the hypothesis that fish communities in areas with altered flow regimes exhibit more generalist functional and life-history characteristics than communities from unaltered areas.

Materials and methods

Fish community and flow data

Our data collection and preparation procedures followed two basic steps. First, we collected fish from 15 segments located throughout the riverine portions of the Missouri and lower Yellowstone rivers (Fig. 1) during the late summer and early fall of 1996–1998. The goals of our sampling design were to qualitatively and quantitatively characterize the fish communities throughout the river system, and to enable river-wide comparisons among segments differing in flow, habitat, and other characteristics. Within each segment, six macrohabitat types were sampled, including inside and outside bend, main channel at the cross-over point between bends, tributary mouth, connected side channel, and unconnected side channel. Sampling gears used included boat electrofisher, beam trawl, bag seine, stationary gill net, and drifted trammel net. At least two of these gears were used in each macrohabitat to account for size selective bias inherent within each gear. We attempted to sample five randomly selected replicates of each macrohabitat type in each segment. However, there were minor differences in the number of samples taken among segments due to differing availability of some macrohabitats, especially side channels and tributary mouths. To account for these differences in effort, we adjusted catches to our *a priori* standardized sampling effort within each segment. Complete details and rationale for sampling design, sampling procedures, data processing, and quality assurance are reported in Sappington et al. (1998).

The second step in our data preparation process was to group the fish data into appropriate spatial

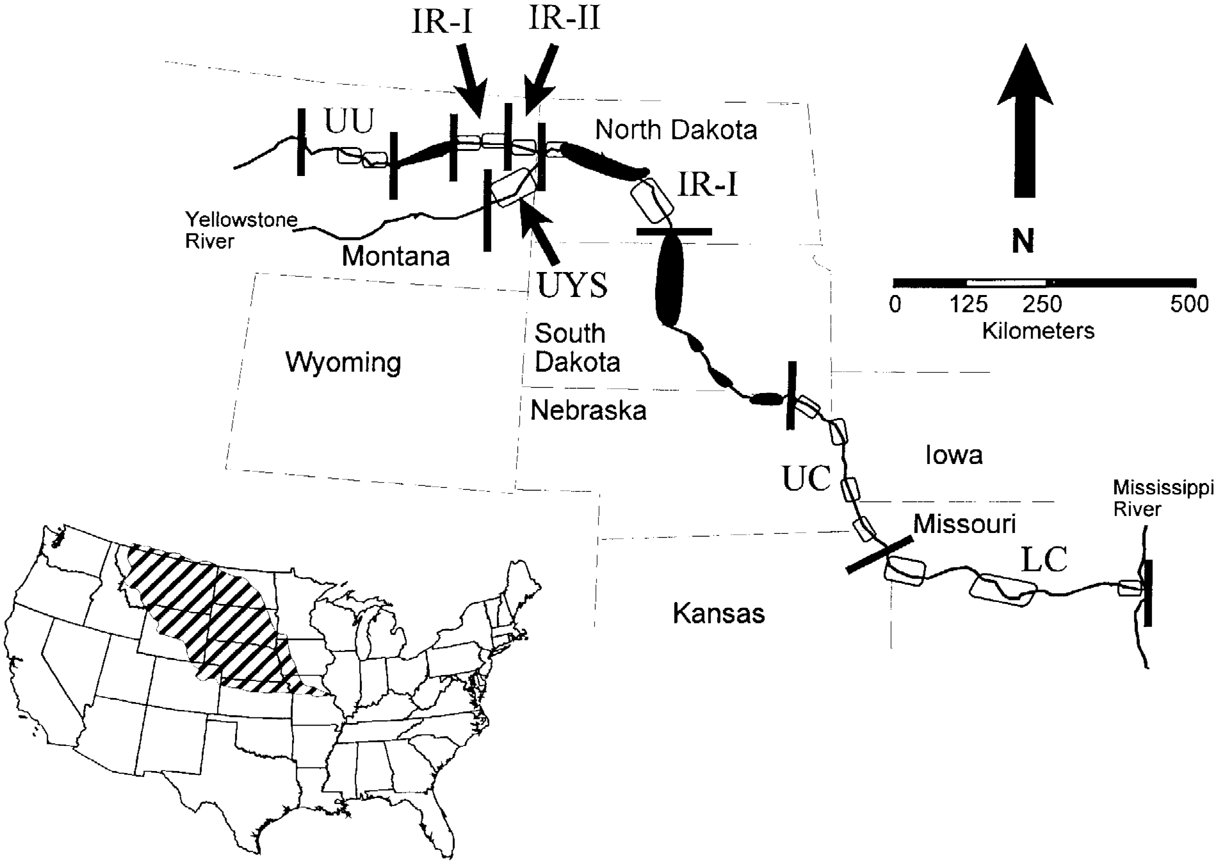

Figure 1. Location of flow variability units on the Missouri and lower Yellowstone rivers. Flow units include Upper Unchannelized (UU), Unchannelized Yellowstone (UYS), Inter-Reservoir I (IR-I), Inter-Reservoir II (IR-II), Upper Channelized (UC), Lower Channelized (LC). Inset shows location of the Missouri River basin within the United States. Open boxes along the rivers indicate location of the 15 segments where fish data were collected.

units that reflected homogeneous flow conditions. To do this, we placed the fish data from each segment into their respective flow regimes that were previously identified in the Missouri and lower Yellowstone rivers by Pegg & Pierce (2002). In their analyses, Pegg & Pierce (2002) used the Index of Hydrologic Alteration (IHA; Richter et al., 1996) to calculate a series of summary statistics from daily mean flow data for each of 15 gauges during the recent, post-alteration period (1966–1996). This 30 year period reflects the management practices and resulting flow regime to which Missouri River fishes have been forced to adapt since completion of the impoundments and channelization projects. These data were then used to identify six distinct flow units exhibiting differing combinations of flow variability and predictability using cluster analysis. Identified flow units included Upper Unchannelized (UU), Unchannelized Yellowstone (UYS), Inter-Reservoir I (IR-I), Inter-Reservoir II (IR-II), Upper Channelized (UC), and Lower Channelized (LC) (Fig. 1; Pegg & Pierce, 2002). The variables that most contributed to delineation among flow units included flow constancy, flow per unit area, and coefficient of variation for annual flows (Pegg & Pierce, 2002). We then categorized the fish data from each segment into their respective flow unit. The number of segments sampled for fish within each flow unit ranged from one to four, so the number of segments per unit was used in our analysis to further standardize the sample effort among the six flow units. The result was an adjusted total catch estimate that reflected equal effort for each flow unit.

Data analysis

Differences in community structure among the flow units were determined with multi-dimensional scaling

Table 1. Morphological, life-history, and functional characteristics used in the analysis of fish communities in the Missouri and lower Yellowstone rivers. Variables from Winemiller & Rose (1992), Poff & Allan (1995)

Morphological Characteristics	**Functional Characteristics**
Shape Factor (SHP)	Current Preference (CUR)
	1. Fast
Ratio of total length to maximum body depth	2. Moderate
	3. Slow-none
	4. General
Swim Factor (SWM)	
	Tolerance to Silt (SLT)/Turbidity (TRB)
Ratio of minimum depth of caudal peduncle to the maximum caudal fin depth	1. High
	2. Medium
	3. Low
	Substrate (SUB)/Spawn Substrate (SPS)
	1. Cobble
	2. Gravel
Life-History Characteristics	3. Sand
	4. Silt
Mean Clutch Size (MC)	5. General
	6. Vegetation
Mean number of eggs for population at mid-point of latitudinal range	7. Structure (e.g., deadfalls)
	8. Pelagic
Length at Maturity (LM)	Water Column Preference (WC)
	1. Benthic
Total length at maturation (mm)	2. Epibenthic
	3. Pelagiczz Age at Maturity (AM)
	Trophic Guild (GLD)
Mean reported age at maturation (yr)	1. Herbivore
	2. Omnivore
Longevity (LS)	3. General Invertivore
	4. Benthic Invertivore
Maximum reported age in years (yr)	5. Piscivore
	6. Planktivore
Maximum Length (ML)	
Reported maximum total length (mm)	

ordination (MDS) of the species abundance (adjusted total catch) data using a Bray–Curtis similarity matrix. Fourth-root transformations were used to moderate the dominance of extreme abundances. The resulting Bray–Curtis matrix provided only one data point for each unit and year combination. Therefore, we evaluated the significance of these differences using a two-way crossed Analysis of Similarity (ANOSIM2) with no replication (Clarke & Warwick, 1994a, 1994b).

We investigated percent composition of morphological, functional, and life-history characteristics of fish communities within and among the six hydrologic units (Table 1). Most of the data for these analyses were previously compiled by Winemiller & Rose (1992) and Poff & Allan (1995). However, data were not previously summarized for some species, so we compiled them from published literature and classified them following Winemiller & Rose (1992) and Poff & Allan (1995).

Most variables listed in Table 1 are self-evident and have been adequately defined elsewhere (Winemiller & Rose, 1992). However, two lesser known variables are shape factor, and swim factor. Shape factor is the ratio of total length to maximum body depth. A high ratio indicates an elongate body shape which implies better swimming ability in swift current. Swim factor is the ratio of the minimum depth of the caudal peduncle to maximum depth of the caudal fin. Low ratios imply the capability of strong, prolonged swimming (Poff & Allan, 1995). The complete data set for all species collected from the Missouri and lower Yellowstone rivers is available upon request from the authors.

We evaluated life-history differences of fish communities among units by weighting each morphological, functional, and life-history characteristic value by the adjusted total catch for each species and unit combination. The overall characteristic score for each unit was then the average score for all species present in the unit, weighted by their relative abundance. We chose to weight by abundance under the assumption that abundant species probably had characteristics well suited to those areas and that not weighting the scores (essentially using presence/absence data) could be influenced by missing or rare species that would have a proportionately larger effect. This then provides an overall assessment of community trends for a given morphological, functional, and life-history characteristic within each flow unit. Where applicable, we then used analysis of variance (ANOVA) to test for differences among units.

Results

Our MDS analysis of Bray–Curtis similarities indicate differences in fish community structure and abundance among the six flow units (Fig. 2). Dimension 1 clearly separates the channelized units from all other units, and also provides some separation between the UC and LC units to some degree. Of the most abundant species collected (Appendix I), we found strong negative correlations ($P \leq 0.05$) of abundances with dimension 1 for seven species. Contributing to this marked difference between the two lower and four upper flow units were high abundances of flathead catfish *Pylodictis olivaris*, gizzard shad Dorosoma cepedianum, red shiner *Cyprinella lutrensis*, and river shiner *Notropis blennius* in the two lower units (Fig. 2). Significant correlations for dimension 2 were largely based on species that were most abundant in the upper four flow units where abundances for longnose suckers *Catostomus catostomus* and white suckers *Catostomus commersoni* were negatively correlated and sicklefin chub *Macrhybopsis meeki* abundances were positively correlated. These results suggest that dimension 1 was best at delineating large-scale, longitudinal differences among fish communities; whereas, dimension 2 effectively separated fish communities in the upper, unchannelized and inter-reservoir units.

We also found a strong negative correlation ($r = -0.95$; $P < 0.01$) of species richness to dimension 1 suggesting that these two groups were separated on the basis of several species that were absent upstream of the UC unit. Coefficient of variation for annual flow, used initially to identify the flow units, was positively correlated with dimension 2 ($r = 0.81$; $P = 0.05$) suggesting a potential response between the fish communities within inter-reservoir and unchannelized units. Although there were differences in community composition among years within units, among-unit differences were generally greater than within-unit differences. We also performed a separate MDS analysis on the four upper most hydrologic units to further identify relations among units, but the ordination was

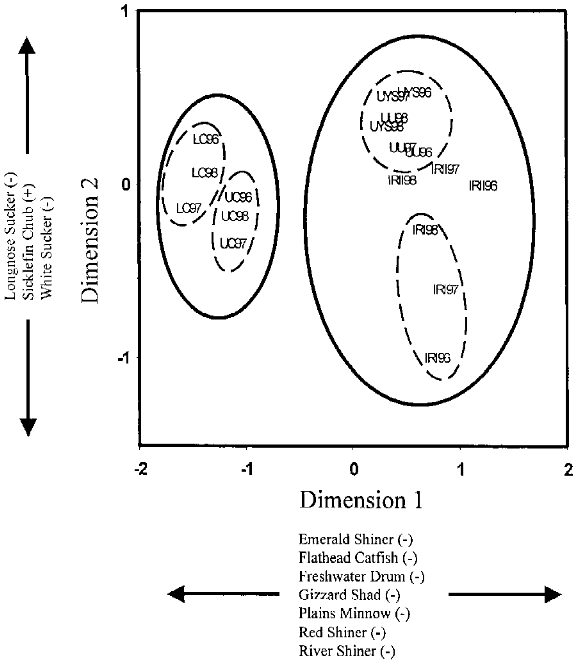

Figure 2. MDS ordination of fish community data by flow variability unit in the Missouri and lower Yellowstone rivers (stress = 0.05). This stress value indicates that the ordination provides excellent representation of the data. Each alphanumeric data point represent the flow variability unit acronym shown on Figure 1 and the year of collection. Solid lines encompass group-average Bray–Curtis similarities of $\geq$60% and the dashed lines encompass similarities $\geq$70%. Species whose abundances were significantly correlated ($P < 0.05$) to each dimension are included. Signs in parentheses indicate direction of correlation.

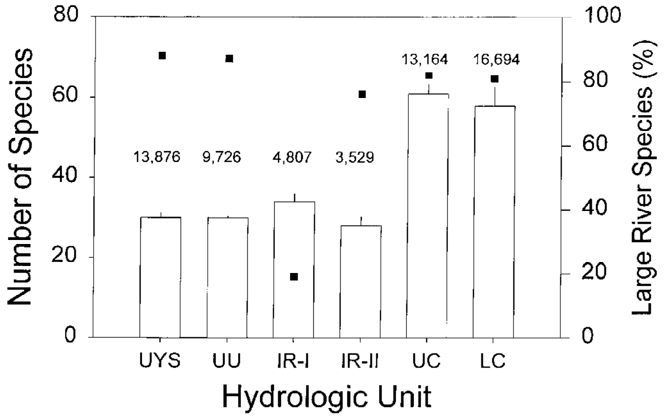

Figure 3. Mean species richness (bars) and percent composition of large river species (Pflieger, 1989) (squares) for each flow variability unit in the Missouri and lower Yellowstone rivers from Figure 1. Hydrologic units are generally arranged upstream (left) to downstream (right). Numbers above each bar are adjusted total sample sizes.

Table 2. Fish community Bray–Curtis similarity (%) among and within flow variability units in the Missouri and lower Yellowstone Rivers. Data analyzed were adjusted species abundances collected in 1996–1998. Within-unit similarity compares the communities among years. See text for description of flow variability units

	UYS	UU	IR-I	IR-II	UC	LC	Within-Unit Similarity
Unchannelized Yellowstone (UYS)	100						78
Upper Unchannelized (UU)	74	100					84
Inter-Reservoir I (IR-I)	56	60	100				72
Inter-Reservoir II (IR-II)	67	69	64	100			69
Upper Channelized (UC)	46	47	43	42	100		79
Lower Channelized (LC)	43	42	34	37	71	100	76

nearly identical to the analysis using all data and is not presented here.

Our ANOSIM2 test for fish community differences showed a significant hydrologic unit effect ($r = 0.92$; $P < 0.01$) which supports the ordination differences identified in Figure 2. However, we did not detect any year effects ($r = 0.20$; $P < 0.96$). Since we could demonstrate no significant year effects on the abundance and species composition of the fish community, we focused further analyses on the general morphological, functional, and life history differences among the six flow units by combining all three years of data.

We collected 106 species, exclusive of hybrids, throughout the course of the 3 year study. The mean number of species collected in each hydrologic unit was fairly constant throughout the upper two thirds of the river, with a marked increase in the two channelized units (Fig. 3). Bray–Curtis similarities within each unit were relatively high (>65%) over the three years of study (Table 2). However, among-unit comparisons showed varying degrees of similarity. Generally, units found in close geographic proximity had higher similarities than did units separated by larger distances. Fish communities from the upper and lower extremes had a similarity of less than 45% among the UU and LC units. Likewise, the inter-reservoir units were typically most dissimilar compared to all other units (Table 2). The percent composition of Pflieger's (1989) large river species was typically over 80% of the standardized total catch throughout the Missouri and lower Yellowstone rivers excluding the inter-reservoir units (Fig. 3). Percent composition of large river species was lowest in the inter-reservoir units, especially the IR-I unit, where the composition of large river species was 20%.

Nearly all of the morphological and life-history characteristics differed significantly among units (Table 3). Fish communities from the upper river had significantly higher mean shape factors indicating a more elongate body shape. This was predominantly due to the high abundances of taxa like flathead chubs

Table 3. Mean values for fish community morphological and life-history characteristics from each flow variability unit in the Missouri and lower Yellowstone River identified in Figure 1. Significant differences ($P < 0.05$) using ANOVA among units were detected for each characteristic except life span. Means sharing common superscripts are not significantly different. Numbers in parentheses are standard errors. The units are arranged longitudinally from upstream (left) to downstream (right)

	UYS	UU	IR-I	IR-II	UC	LC
Shape	5.4^{ab}	5.6^{ab}	6.2^{a}	4.9^{b}	4.8^{b}	4.6^{b}
Factor	(0.3)	(0.2)	(0.2)	(0.3)	(0.2)	(0.2)
Swim	0.48^{a}	0.47^{a}	0.55^{b}	0.46^{a}	0.42^{c}	0.41^{c}
Factor	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)
Mean	$35\,333^{a}$	$38\,153^{a}$	$51\,742^{a}$	$165\,098^{b}$	$171\,145^{b}$	$193\,631^{b}$
Cluth	(25 229)	(30 355)	(25 391)	(65 417)	(26 142)	(27 171)
Size						
Length at	150^{a}	140^{a}	321^{b}	209^{ac}	240^{c}	258^{bc}
Maturity	(26)	(26)	(17)	(27)	(16)	(18)
Age at	2.0^{a}	1.7^{a}	4.7^{b}	2.7^{a}	2.2^{a}	2.4^{a}
Maturity	(0.2) (0.3)	(0.2)	(0.3)	(0.2)	(0.2)	
Maximum	389^{ab}	307^{a}	507^{b}	546^{b}	427^{ab}	494^{b}
Length	(4 6)	(44)	(31)	(59)	(40)	(44)
Lifespan	10.3	8.4	11.8	11.8	10.0	11.8
	(1.1)	(1.2)	(0.8)	(1.2)	(0.8)	(0.9)

Platygobio gracilis and *Hybognathus* spp. in the unchannelized and IR-II unit and longnose suckers in the IR-I unit. Swim factor was lowest in the channelized portion of the Missouri River suggesting a large component of individuals capable of prolonged swimming. In these units, gizzard shad were most abundant and had one of the lowest swim factor scores. Age at maturity and length at maturity were both highest in the IR-I unit due to high longnose sucker abundances that had much higher scores for both characteristics than most of the other highly abundant species caught in other units. Mean clutch size was highest in the IR-II, UC, and LC units due to the proportion of river carpsuckers *Carpiodes carpio*, common carp *Cyprinus carpio* and gizzard shad that all have high mean clutch sizes. Maximum lengths showed no clear among-unit trends and average life span did not differ significantly throughout the river system.

Functional characteristics among units also varied considerably (Table 4). We observed marked differences in the proportional composition of the trophic guilds among flow units (Fig. 4a). The upper unchannelized units were dominated by invertivorous (e.g., flathead chubs, sturgeon chubs *Macrhybopsis gelida*) and herbivorous species (e.g., *Hybognathus* spp.) (Table 4; Fig. 4a). Moving downstream, there were several abrupt changes in relative abundance of trophic guilds among flow units. Proportional trophic guild composition changed dramatically between the UU and IR-I units, which are separated spatially by Ft. Peck Reservoir. Herbivores and general invertivores declined precipitously in this transition, whereas omnivores and benthic invertivores increased greatly in proportion. The IR-II unit, located between isolated sections of the IR-I unit, differed from the IR-I unit in having a much larger proportion of general invertivores and a much lower proportion of benthic invertivores. The channelized units showed a dramatic increase in the proportion of planktivores, predominantly gizzard shad.

There were also differences in the proportional composition of current preferences among flow units (Table 4; Fig. 4b). The upper unchannelized units were dominated by species with either fast or moderate water velocity preferences. The transition from the UU to IR-I unit was characterized by a precip-

Table 4. Median values of fish community functional characteristics for each flow variability unit in the Missouri and lower Yellowstone Rivers identified in Figure 1. The number in parentheses represent the 25 and 75 quartiles. The units are arranged longitudinally from upstream (left) to downstream (right)

	UYS	UU	IR-I	IR-II	UC	LC
Trophic Guild	3 (2–4)	3 (2–4)	3 (2–5)	4 (2–5)	4 (2–5)	4 (2–5)
Silt Tolerance	2 (1–2)	2 (1–3)	2 (1–3)	1 (1–2)	2 (1–2)	2 (1–2)
Turbidity Tolerance	1 (1–2)	1 (1–2)	1 (1–2)	1 (1–2)	1 (1–2)	1 (1–2)
Water Column	2 (1–3)	2 (1–3)	2 (1–3)	2 (1–3)	2 (1–3)	2 (1–3)
Current Preference	3 (2–3)	3 (2–3)	3 (2–3)	3 (2–3)	3 (2–3)	3 (2–3)
Substrate Preference	4 (2–5)	5 (2–5)	4 (2–5)	4 (2–5)	4 (2–5)	4 (3–5)
Spawning Substrate	3 (2–6)	2 (2–6)	3 (2–6)	3 (2–6)	5 (2–7)	3 (2–7)

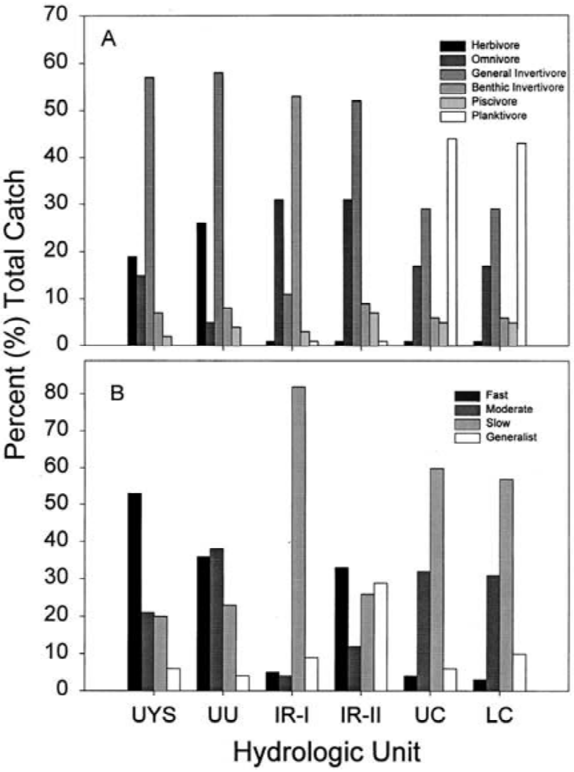

Figure 4. Percent composition for each (A) trophic guild and (B) current preference by flow unit in the Missouri and lower Yellowstone rivers (Figure 1). Percentages were calculated using all data collected over the three years of study. The units are longitudinally ordered from upstream (left) to downstream (right).

itous decline in fast and moderate velocity preferences and a large increase in slow velocity preference. Velocity preferences were fairly even in the IR-II unit with no category accounting for more than 34% of the community. The channelized units had proportional preferences similar to the IR-I unit, with species preferring slow velocity dominating. However, moderate preference was much more prevalent in the channelized unit, accounting for over 30% of the community in both UC and LC units. Species preferring fast current included shovelnose sturgeon *Scaphirhinchus platorynchus*, blue sucker *Cycleptus elongatus*, sicklefin chub and sturgeon chub. The moderate flow preference group was made up largely of walleye *Stizostedion vitreum*, sauger *S. canadense*, and several small cyprinid species like emerald shiner. Deeper bodied species like bigmouth buffalo *Ictiobus cyprinellus*, freshwater drum, and river carpsuckers made up a large proportion of the slow current preference group throughout the river. Common carp, gizzard shad, and goldeye *Hiodon alosoides* were fairly prevalent generalist species.

The proportional composition of substrate preferences were also different among flow units (Table 4). Preference for sand dominated upstream from the reservoirs, and in the IR-II unit (Fig. 5a). Preference for gravel was greater than 40% in the IR-I unit, but well below 20% in all other units. The channelized units were similar with low percentages of gravel and sand preference, and general and pelagic preferences of roughly 40% each. Species preferring gravel substrate included blue suckers and shorthead redhorses *Moxostoma macrolepidotum*; whereas, the most abundant species preferring sand included emerald shiners, *Hybognathus* spp., and many of the other small bodied cyprinids. Substrate generalist species consisted of common carp, channel catfish, and river carpsuckers. The pelagic preference was almost exclusively gizzard shad in the channelized units.

The proportional composition of spawning substrate preference also differed significantly among units, shifting from dominance of gravel, sand, and

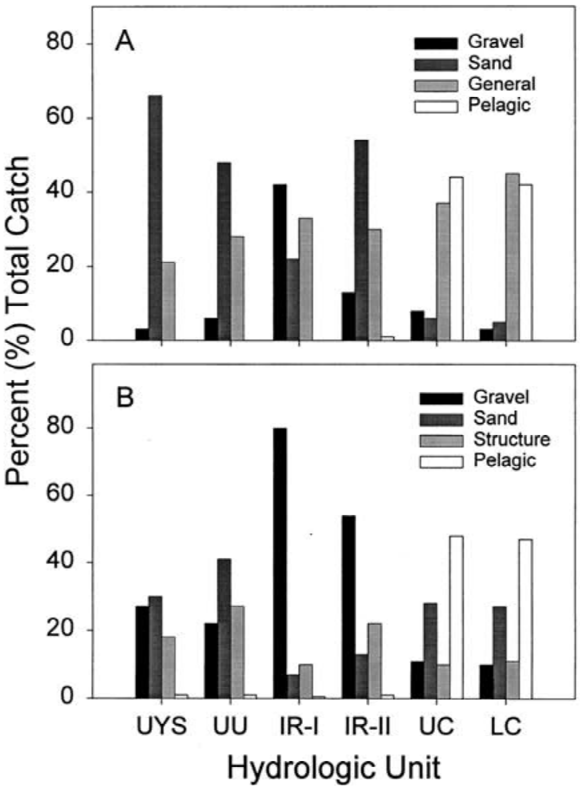

Figure 5. Percent composition for (A) substrate preferences and (B) spawning substrate preferences by flow unit in the Missouri and lower Yellowstone rivers (Fig. 1). Percentages were calculated using all data collected over the 3 years of study. The units are longitudinally ordered from upstream (left) to downstream (right).

structure in the unchannelized units, to dominance of gravel spawners in the inter-reservoir units, to a high percentage of general and pelagic spawners in the channelized units (Table 4; Fig. 5b). The inter-reservoir units had a high proportion of gravel spawners as well. Species preferring gravel spawning substrate included longnose suckers, white suckers, and shovelnose sturgeon. The most abundant species preferring sand included members of the genus *Notropis*, and river carpsuckers. There was also an increase in the preference of underwater structure during spawning in the inter-reservoir and channelized units. The most abundant species preferring this substrate were common carp and channel catfish. We also observed an increase in the proportion of pelagic spawners which consisted mainly of gizzard shad and freshwater drum.

Correlation analysis of morphological, functional, and life history characteristics with the individual flow variables used to define flow units revealed few significant relations, suggesting that the among-unit differences cannot be explained in terms of any single defining flow variable. However, along a gradient of increasing hydrologic alteration (from Galat & Lipkin, 2000) that takes several flow variables into account, there were significant decreases in shape factor ($r = -0.88$; $P = 0.05$), age at maturity ($r = -0.96$; $P = 0.01$), and proportion of fast velocity species ($r = -0.91$; $P = 0.03$) and an increase in the proportion of slow velocity species ($r = 0.92$; $P = 0.03$) for all reaches of the river, with the exception of the IR-II unit that was not included in Galat & Lipkin's (2000) analysis.

Discussion

Community structure and abundance

Fish community structure in lotic systems has been evaluated by morphology (Gatz, 1979), functional groups (Grossman et al., 1982) and life-history characteristics (Mahon, 1984). Additionally, Poff & Allan (1995) documented community structure patterns in relation to flow variability and stability in several small streams. While we examined one continuous system where the overall differences in flow characteristics can be subtle, our analyses do provide a similar framework to assess community structure within the Missouri River basin. The clearest pattern in our results was the distinction of communities in the channelized portion of the river below the mainstem reservoirs from all other parts of the Missouri and lower Yellowstone rivers. This distinction was due in large part to the higher species richness found in the channelized portion of the river. Our data also suggest the morphological, functional, and life-history characteristics in the inter-reservoir units consist of more generalist species which supports our prediction of increasing generalists with an increase in the degree of alteration for each flow unit. Species abundance structure also appears different between the two channelized and the upper four flow units (Fig. 2). A possible explanation for differences among these communities is the effect of dams blocking migration. In unregulated rivers, we would expect a gradual increase in species richness moving downstream (Vannote et al., 1980), but when dams are placed on these rivers the physical barriers can impede upstream movements, effectively isolating above-dam communities from their downstream species source pools.

In addition to being barriers to movement, dams change many water quality and habitat characteristics as well (Ward & Stanford, 1983). Water quality parameters such as turbidity and temperature are often changed as water passes through impoundments due to settling sediments and location of water release in relation to thermal stratification of the reservoir. The loss of sediment in released water changes substrate and channel dynamics, frequently resulting in a degraded channel (Hammad, 1972). Further, increased light penetration and exposure of coarse substrates may result in increased autotrophy, with a variety of potential consequences for higher trophic levels (Voelz & Ward, 1991). These processes can essentially reset many biotic and abiotic characteristics, often making the conditions immediately downstream from dams similar to headwater areas. Fish and other aquatic organisms adapted to conditions prior to alteration are then regionally extirpated because they are not well suited to their newly created environment. The result is a loss in species richness and this effect could help explain large differences in richness observed between the inter-reservoir and channelized units.

The inter-reservoir units are most strongly influenced by flow alteration along the Missouri River (Galat & Lipkin, 2000; Pegg, 2000) and changes in morphological, functional, and life-history characteristics were most pronounced throughout this portion of the river. For example, there were no major changes in proportions of any functional characteristic between the two unchannelized units and between the two channelized units (Figs 4 and 5). This means that most of the major changes occurred in the transition into and out of the inter-reservoir units located in the highly impounded middle portion of the river. An artifact of reservoir influences is the introduction or increased abundance of more lacustrine fish populations. The impact of these lacustrine fish species on riverine fish communities is not currently known. However, many of the species found in this part of the river were deeper bodied individuals like freshwater drum and river carpsuckers or slow water velocity preference species like yellow perch *Perca flavescens*, which makes them less adapted to maintaining their position in swift currents associated with spring flows in the upper and lower flow units.

Patterns in tolerance to silt and turbidity are two interesting variables because they have a very different meaning on the Missouri River compared to the small streams where these metrics were first developed. In small streams, silt and turbidity are generally associated with stream degradation (Karr et al., 1986), but prior to alteration the Missouri River was extremely turbid and silt laden (Funk & Robinson, 1974). Presumably, most of the endemic fish species in the Missouri River system would be adapted to and tolerant of silt and turbidity. Our data support this presumption with both metrics indicating that fish communities from all units had fairly high tolerances to both variables (Table 4). Therefore, in the context of the Missouri River system, these two metrics are probably not as valuable in describing differences among communities as they may be in smaller streams or less turbid large rivers.

Predictions based on flow regimes

Pegg & Pierce (2002) concluded that flow regimes in the uppermost and lowermost portions of the river exhibit some similarities. Galat & Lipkin (2000) reported similar results showing the amount of hydrological alteration was lowest in these portions of the river as well. Since we were attempting to identify fish community relationships with flow regime, we might have expected some community similarities among upper and lower portions of the river, mirroring the flow results. We found, on the contrary, a low similarity (Table 2) and quite different functional and life-history patterns (Figs 4 and 5) between the upper and lowermost units so this hypothesis was not clearly supported in a functional sense. However, the percent of large river fishes in each of these units was high suggesting that some integrity in reference to maintaining a riverine community may exist. Unfortunately, data are not available to make pre and post alteration community assessments, so we do not have the ability to quantify long term temporal shifts in community composition. It appears that the community patterns we found reflect a combination of effects: natural river zonation patterns, blockage of migration due to dams, as well as a variety of changes in flow regime and other environmental effects of human alteration.

Response to flow alteration

An alternative to evaluating riverine fish communities solely on flow variability may be assessment of the degree of alteration to the flow regime as an aggregate descriptor of flow and environmental variability. For example, Zampella & Bunnell (1998) found that fish assemblage changes were associated with gradients of watershed disturbance in New Jersey Pineland streams. On the Missouri and lower Yellowstone rivers, Galat & Lipkin (2000) reported that the degree of alteration was moderate for flows in the unchannelized reaches, high in the inter-reservoir and upper portion of the UC unit, then declined to a more moderate level proceeding downstream. Present flows through the inter-reservoir units have changed immensely in some areas compared to those prior to alteration and typically have very little variation on an annual scale. Comparatively, the natural hydrograph that once typically had periods of high flow in the spring and lower flows in late fall and winter no longer exists (Hesse & Mestl, 1993; Pegg, 2000). Accordingly, by using degree of alteration as a measure of change in flow regimes for each unit as a surrogate to flow variability, we would predict that the inter-reservoir and UC units would consist of more generalists and species not well adapted to the pre-alteration conditions due to their higher degree of alteration. Our results provide some support for this hypothesis because we did find significant decreases in proportion of fast velocity preference and shape factor values, coupled with an increase in proportion of slow velocity preference species with an increased level of alteration. This suggests that species from units with higher degrees of alteration tend to be deeper bodied and not well suited for more natural flow regimes that still exist to some extent in the extreme flow units. This also suggests a shift away from the large river life-history traits such as a large proportion of high velocity preference and high shape factor values found in the nearby unchannelized units. Additionally, the lower percentage of large river species in the inter-reservoir units, especially in the IR-I unit, suggest the inter-reservoir fish communities are not similar to riverine communities found elsewhere in this system, further supporting our hypothesis.

Conclusions

Few studies have assessed the functional organization of fish communities in a large river system as we have done here. Our data provide some evidence that fish communities are linked to flow regimes, but that other, and possibly greater influences including the longitudinal zonation of species, effects of dams blocking migration, and other human alterations likely play a role as well. While there is a continuing concern to identify community patterns as they relate to environmental conditions (Matthews & Heins, 1987), identifying these patterns in a large river system will be a major challenge for river ecologists.

Large river systems are by nature in limited supply, and unfortunately, there remains even fewer unaltered large river systems (Benke, 1990) to use as controls for evaluating the effects of human alteration. The imperative to rigorously evaluate these effects remains, however, and novel approaches (e.g., Simon & Emery, 1995) will be required to overcome the limitations inherent in conventional statistical approaches. Comparison of communities from sites *within* a single river system, as we have done here, will be the only practical approach in many situations. By quantifying how flow conditions currently differ among portions of the river, as we have done previously (Pegg & Pierce, 2002), relating flow conditions to alteration in some portions of the river (Galat & Lipkin, 2000; Pegg, 2000), and demonstrating community differences among these areas, as we have done here, we believe we have demonstrated not only relations of the fish community with flow characteristics, but some likely consequences of human alteration of the Missouri River system.

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Appendix 1. Correlations of adjusted species abundances with dimension scores from the multi-dimensional scaling (MDS) for species comprising $\geq$ 1% of the total catch in the Missouri and lower Yellowstone Rivers. Percent of the total catch are included in parentheses

Species	Dimension 1		Dimension 2	
	r	*P*	*r*	*P*
Gizzard Shad, *Dorosoma cepedianum* (19)	−0.98	<0.01	0.11	0.84
Flathead Chub, *Hybopsis gracilis* (16)	0.38	0.45	0.48	0.33
Emerald Shiner, *Notropis atherinoides* (13)	−0.73	0.10	0.04	0.94
River Carpsucker, *Carpiodes carpio* (6)	−0.52	0.28	0.43	0.39
W. Silvery Minnow, *Hybognathus argyritis* (5)	0.69	0.31	0.11	0.89
Longnose Sucker, *Catostomus catostomus* (4)	0.39	0.44	−0.83	0.04
Plains Minnow, *Hybognathus placitus* (4)	−0.85	0.03	0.11	0.83
Goldeye, *Hiodon alosoides* (4)	0.62	0.18	0.37	0.47
Channel Catfish, *Ictalurus punctatus* (4)	−0.58	0.22	0.47	0.34
Sturgeon Chub, *Macrhybopsis gelida* (3)	0.32	0.54	0.46	0.36
Common Carp, *Cyprinus carpio* (2)	0.23	0.66	0.38	0.46
White Sucker, *Catostomus commersoni* (2)	0.53	0.28	−0.76	0.08
Shovelnose Sturgeon, *Scaphirhynchus platorynchus* (2)	0.16	0.77	0.37	0.47
Freshwater Drum, *Aplodinotus grunniens* (2)	−0.95	<0.01	−0.02	0.96
Red Shiner, *Cyprinella lutrensis* (2)	−0.85	0.03	0.30	0.56
Shorthead Redhorse, *Moxostoma macrolepidotum* (1)	0.65	0.16	0.39	0.44
Quillback, *Carpoides cyprinus* (1)	0.54	0.26	−0.36	0.49
Fathead Minnow, *Pimephales promelas* (1)	0.60	0.21	−0.63	0.18
Sicklefin Chub, *Macrhybopsis meeki* (1)	0.39	0.43	0.75	0.09
Flathead Catfish, *Pylodictis olivaris* (1)	−0.98	<0.01	0.02	0.97
Longnose Dace, *Rhinichthys cataractae* (1)	0.35	0.50	0.45	0.37
Sauger, *Stizostedion canadense* (1)	0.34	0.50	0.46	0.35
River Shiner, *Notropis blennius* (1)	−0.75	0.08	−0.25	0.63