

Population Structure and Habitat Use of
BENTHIC FISHES
along the Missouri and Lower Yellowstone Rivers

Volume 2

*Spatial Patterns
of Physical Habitat*

Project Volume



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Population Structure and Habitat Use of Benthic Fishes Along the Missouri and Lower Yellowstone Rivers

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PREFACE

Population Structure and Habitat Use of Benthic Fishes along the Missouri and Lower Yellowstone Rivers

This research is reported in the 12 volumes listed below. Reports are available through the U. S. Army Corps of Engineers, the primary contracting agency for the overall project. Contact: Becky Latka, U. S. Army Corps of Engineers, CENWO-PM-AE, 106 South 15th Street, Omaha, NE 68102, (rebecca.j.latka@usace.army.mil, 402/221-4602) for paper copies or access online in PDF format at: <http://www.nwo.usace.army.mil/html/pd-e/planning.html>. Anticipated date of publication is in (parentheses) for volumes not yet available. Please use the citation format suggested here without the email address when referencing Final Report volumes.

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EXECUTIVE SUMMARY

Unaltered large rivers exhibit predictable patterns of physical (e.g., hydrology, temperature, geomorphology), chemical (e.g., inorganic and organic ions, water quality), and biological (e.g., invertebrate biomass, fish composition) structure and function as they flow from headwaters to the ocean. An ecosystem perspective for rivers requires a basin scale understanding of how climate and geology influence hydrology, morphology, and water chemistry, and in turn how these factors define where fishes and other biota reside.

Impoundment, water withdrawal, flow regulation, channelization, bank stabilization, and levee construction are activities that have modified natural physical habitat of most of the world's large rivers and their floodplains, including the Missouri River. These physical changes have paralleled population declines and shifts in species structure of large river fishes and their food base. Bottom dwelling or benthic fishes are one group in the Missouri River that has exhibited major population declines. Conservation and recovery of Missouri River fishes, and benthic fishes in particular, can be facilitated by a river-wide understanding of physical variables, determining how physical habitat is affected by anthropogenic disturbance, and implementing management actions to improve physical habitat for riverine fishes while maintaining or enhancing other societal benefits.

Research objectives were to: (1) characterize longitudinal patterns of physical variables for the warm-water, riverine portion of the Missouri and lower Yellowstone rivers; (2) evaluate differences in physical variables among and within a hierarchy of spatial scales; (3) relate patterns of physical variables to river management practices, and; (4) provide physical habitat data to integrate with other volumes of this report: fish distribution and abundance (Volume 3) and fish growth, mortality, recruitment, condition, and size structure (Volume 4).

These objectives were accomplished by dividing the mainstem Missouri and lower Yellowstone rivers into a nested set of spatial habitat units. Habitat units included three longitudinal zones (least-altered, inter-reservoir, and channelized) and 27 longitudinal segments within the zones. Segments were defined by geomorphic and constructed features. The diversity of habitats within segments was addressed by sampling six macrohabitats: channel cross-over, inside bend, outside bend, secondary channel connected, secondary channel non-connected, and tributary mouth. Channel cross-overs, inside bends, and outside bends were termed *continuous* macrohabitats, as each occurred in every river bend. These three macrohabitats were grouped into a bend habitat unit for statistical analyses. Secondary channels

connected, secondary channels non-connected, and tributary mouths were not present in every river bend and were termed *discrete* macrohabitats. Sampling physical variables was conducted from about mid July through early October for 3 years: 1996-1998. Fifteen of the 27 river segments were sampled among the three zones and resampled each year.

Nine physical variables were measured: water depth, current velocity, water temperature, turbidity, conductivity, proportion of three substrate particle size classes (gravel, sand, and silt), and geometric mean particle size. River discharge at representative sites during the study was compared to historical discharge to assess trends in river flow. Measurement of physical variables was uniform throughout the river and followed standard operating procedures and statistical sampling protocols. Results were entered into a computerized data base and all project aspects underwent annual quality assurance and quality control.

Most physical variables differed little among years so we did not evaluate temporal patterns. Discharge during the 3-year study was generally above historical levels for most segments, and implies caution in applying results to normal or low-water discharge years.

There was a gradual longitudinal increase in water temperature of 5.5 °C between uppermost least-altered segment 3 and lowermost channelized segment 27. Abrupt temperature decreases of between 6.0 and 8.5 °C were observed in segments immediately downriver from Ft. Peck Lake and Lake Sakakawea. Lewis and Clark Lake had no significant effect on river water temperature below Gavins Point Dam. Temperature differed less among macrohabitats than among segments, but mean temperatures of secondary channels (connected and not-connected) and tributary mouths were often ≥ 1.0 °C warmer than in bends for some inter-reservoir segments. Tributary mouths were between 0.7 and 2.6 °C colder than macrohabitats in bends for all channelized river segments.

Reduction of water temperature was the most significant change observed at the segment scale. We applied the Serial Discontinuity Concept, which generalizes how dams affect upstream-downstream shifts in biophysical patterns and processes, to predict the magnitude of approximately mid-July to early-October temperature depression in the inter-reservoir zone and the longitudinal upstream shift in temperature. Temperature depressions of 9.2 and 8.5 °C were estimated for Missouri River segments below Ft. Peck and Garrison dams, respectively. The water temperature in segment 7, below Ft. Peck dam, was more appropriate to a location >910 km upriver.

A similar pattern was observed in turbidity among segments, except turbidity was also reduced in segment 15, below Gavins Point Dam. Tributary discharge in

the inter-reservoir zone generally increased turbidity, whereas tributaries in the lower channelized zone reduced turbidity. Turbidity in secondary channels, particularly those not connected to the main channel, was often lower than macrohabitats within bends.

Conductivity averaged among bend, secondary channel connected, secondary channel non-connected, and tributary mouth habitat units was lowest in least-altered segments (mean: 476 $\mu\text{S}/\text{cm}$) and increased significantly due largely to tributary inflow in the inter-reservoir zone (mean: 705 $\mu\text{S}/\text{cm}$). Yellowstone River discharge reduced Missouri River conductivity, whereas it increased Missouri River turbidity. The large volume of inflow from tributaries, particularly downriver from Kansas City, Missouri, reduced channelized zone conductivity (mean: 662 $\mu\text{S}/\text{cm}$) compared to inter-reservoir segments.

Water depth in bends increased longitudinally from least-altered to channelized segments (e.g. mean depth of 1.3 m in segment 3 to 4.5 m in segment 17). The order of water depths in habitat units from deepest to shallowest was bend > tributary mouth > secondary channel connected = secondary channel non-connected, and the pattern within bends was: channel cross-over = outside bend > inside bend.

Current velocity in bends was greatest in channelized segments, reaching a mean of 1.3 m/s in segment 19 below the Platte River, Nebraska. The high to low rank order for velocity among habitat units was bend > secondary channel connected > secondary channel non-connected = tributary mouth. Often no current was recorded in secondary channel non-connected and tributary mouth macrohabitats. Water velocity in channel crossover and outside-bend macrohabitats was generally much higher than observed in inside bends.

Geometric mean particle size in continuous macrohabitats was largest in channelized segments, except that the most upriver least-altered segment (3) had the largest mean particle size of any segment. Gravel contributed 51% of the gravel-sand-silt total in segment 3, whereas sand dominated in channelized continuous macrohabitats. Mean particle size in continuous macrohabitats was lowest in inter-reservoir segments. Particle sizes were largest and about equal in channel-crossover and outside-bend macrohabitats. Secondary channels non-connected and tributary mouths exhibited the smallest geometric mean particle sizes, dominated by silt.

These general patterns were further described and statistically corroborated by a series of 21 planned segment contrasts where five types of zone and segment groups (e.g., comparing segments above and below reservoirs) were evaluated by analysis of variance for each physical variable.

Principal components analysis provided a visual sum-

mary of how physical variables collectively defined the previously described relationships among zones, segments, and macrohabitats. Segments in the inter-reservoir zone had lower temperature and turbidity, but higher conductivity than segments in least-altered or channelized zones. The channelized zone exhibited highest temperature and turbidity, as well as deepest water and highest current velocity. Channel cross-over and outside-bend macrohabitats within bends had the deepest water, fastest current velocity, and largest mean particle size. Tributary mouths were relatively warm and turbid in some segments, whereas non-connected secondary channels were primarily shallow, low velocity habitats with fine substrates. Connected secondary channels did not show a consistent distribution among physical variables compared with other macrohabitats.

Our analysis yielded the most comprehensive and robust synthesis of physical habitat assembled for the warm-water Missouri River and its largest tributary. It showed that environmental and anthropogenic factors interacted to produce the physical patterns observed at zone, segment, and macrohabitat scales. Temperature, turbidity, and conductivity differences were greatest at zone and segment scales. Latitude, catchment physiography, regional climate, and regional runoff were the primary environmental determinants of spatial patterns reported for these variables, whereas, impoundment, flow regulation, and channelization were the principal anthropogenic factors. Differences in depth, velocity, % sand, % silt, and geometric mean substrate size were greater among macrohabitats within segments than among segments. Channel geomorphology, hydrology and channelization were the dominant environmental and human influences on these variables.

Six conclusions and recommendations follow from our results.

1. Spatial scale was an important feature explaining differences in physical variability in the Missouri and lower Yellowstone rivers. Temperature, turbidity and conductivity were primarily large spatial-scale variables (zone: $\geq 1,000$ km; segment: ~ 30 - ~ 200 km), although turbidity and conductivity were affected by tributaries at a smaller spatial scale. Differences in depth and velocity were more important at smaller spatial scales (≤ 10 km) and substrate particle size varied at both large and small spatial scales. Management actions to normalize water temperature and turbidity along the Missouri River will be more successful if regionally applied at the zone and segment scales through re-regulating flow and sediment releases from impoundments. Normalizing depth and velocity can be more

effectively accomplished at a local scale by enhancing natural channel geomorphology within river bends.

2. Tributaries ameliorated effects of impoundment and hypolimnetic cold-water releases on temperature depression and turbidity in the Missouri River. Management actions to restore some semblance of pre-regulation flow, temperature, and turbidity regimes of the Missouri River need to recognize the role of maintaining or restoring free-flowing tributaries, i.e. incorporate a watershed perspective into river management.

3. Segments with numerous secondary-channel and tributary macrohabitats showed a wider range of most physical variables than segments with reduced macrohabitat diversity (e.g., low macrohabitat diversity in upstream channelized segments). Number of tributaries per segment is fixed, but connected and non-connected, secondary channels can be increased in the channelized zone where they were historically abundant by restoring a more natural braided channel morphology through a combination of passive and intensive habitat rehabilitation techniques. Seasonal connecting and disconnecting of these recreated secondary channels with the main channel can be enhanced by modifying water release schedules from reservoir dams to better mimic the pre-regulation flow regime.

4. A regression model of temperature on segment midpoint kilometer provided initial guidelines to re-establish more normal water temperatures in river segments below Ft. Peck Lake and Lake Sakakawea between approximately mid July and early October. The technique applied here could be refined to predict more normal summer water temperatures to enhance food resources and growth rates of pallid sturgeon and other imperiled and recreational warm-water fishes.

5. Spatial patterns in physical variables reflect natural environmental (i.e., latitude, regional climate, active-channel geomorphology, etc.) and anthropogenic (i.e., impoundment, flow regulation, channelization, etc.) determinants. Management actions to improve physical habitat need to distinguish between these two sources of variability, capitalize on the capacity for self-repair inherent in large rivers, and

implement restoration actions at the appropriate spatial scale(s).

6. Patterns of physical variables among zones, segments, and macrohabitats provide a template to assess differences in distribution, abundance, growth, mortality, recruitment, condition, and size structure of benthic fishes. These topics will be considered in subsequent volumes in the Missouri River benthic fishes study.

Keywords: habitat hierarchy, longitudinal patterns, Missouri River, physical habitat, serial discontinuity, spatial scale, Yellowstone River

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INTRODUCTION

Physical habitat is recognized as an overarching determinant of the distribution and abundance of aquatic organisms in flowing waters (Poff and Ward 1990; Allan 1995; Petts and Amoros 1996). So important is physical habitat as a template for indigenous riverine fishes that the most serious fishery management and conservation problems often result from actions which have altered the hydrological regime, sediment transport, and geomorphology of rivers (Welcomme et al. 1989; Bayley and Li 1992; National Research Council 1992).

Unaltered rivers exhibit predictable patterns of hydrology, geomorphology, and biological structure and function as they flow from headwaters to the ocean (Hynes 1975; Vannote et al. 1980; Ward 1989). A biophysical perspective of rivers requires understanding how climate and geology influence river hydrology, chemistry, and morphology and how these factors in turn define biological patterns and processes. Geology influences erosiveness of parent material within the drainage basin and thus watershed soils and topography, chemical load to tributaries, river-bed composition, etc. Minshall et al. (1985) and others (e.g., Whitton 1975; Schumm 1977; Frissell et al. 1986; Calow and Petts 1992) summarize how climate affects the type and density of vegetation within a catchment. Precipitation, vegetation, topography, and soils interact to affect runoff and erosion and collectively produce the pattern of streams within a drainage network and the sediment yield to these streams and rivers. The spatial and temporal distribution of these physicochemical forces coupled with the evolutionary history of riverine flora and fauna provides a template for characterizing and interpreting composition, abundance, and distribution of aquatic organisms along the unaltered river continuum.

Dams and impoundments create physical barriers to longitudinal migrations of fishes and alter flow, temperature, and turbidity of riverine reaches below them (Petts 1984; Ligon et al. 1995; Graf 1999). Regulation of river discharge affects water temperature, velocity and depth, modifies downstream habitat structure and substrate composition, and alters the intrinsic intra- and inter-annual flow dynamics upon which native fish and wildlife depend (Poff et al. 1997; Richter et al. 1997). Flood-control levees disconnect the river from its floodplain, thereby impeding lateral exchange of nutrients, organic matter and biota, including fish spawning, feeding, and overwintering migrations (Brookes 1988; Sparks 1995; Roux and Copp 1996). Channelization and bank stabilization reduce in-channel habitat complexity and alter flow patterns and sediment loads. These alterations of physical habitat are most pervasive on large rivers of the developed world since they have been subject to long-term human use (Dynesius and Nilsson 1994; Johnson et al. 1995). Consequences of

alterations in physical habitat are declines in populations and shifts in species composition of large river fishes (Schlosser et al. 1991; Bayley and Li 1992; Stanford et al. 1996; Strange et al. 1999).

The Missouri River has yielded immense societal benefits from transportation, irrigation, hydroelectric power production, municipal and industrial water supply, and reservoir recreation (Ferrell 1993). However, meeting these needs and providing flood protection to floodplain infrastructure has resulted in degradation and loss of channel and floodplain habitats and imperilment of native biological resources (Hesse 1987; Hesse et al. 1989; Schmulbach et al. 1992; Galat et al. 1996). Bottom-dwelling or benthic fishes are one group that has been particularly affected by development of the Missouri River hydrosystem. Over 20 species are currently listed as rare, threatened or of special concern by various organizations (Whitmore and Keenlyne 1990, Galat and Zweimüller 2001). While only one fish (pallid sturgeon, *Scaphirhynchus albus*) is currently listed as federally endangered, an additional eight species (lake sturgeon*, *Acipenser fulvescens*; blue sucker*, *Cycleptus elongatus*; western silvery minnow*, *Hybognathus argyritis*, plains minnow*, *H. placitus*; sturgeon chub*, *Macrhybopsis gelida*; sicklefin chub*, *M. meeki*; flat-head chub*, *Platygobio gracilis*, and paddlefish, *Polyodon spatula*; benthic fishes are identified with an asterisk*) are proposed or considered possibly appropriate for listing by the U. S. Fish and Wildlife Service (i.e., Category 1 or 2, U. S. Fish and Wildlife Service 1994). Many of these fishes depend on a complex of channel habitats, including tributaries, to meet their essential life functions of reproduction, feeding and overwintering (Galat and Zweimüller 2001). Geomorphic and flow modifications may be the major causes for declines of these and other Missouri River fishes (see previous references).

After decades of river degradation, local and international programs are now underway to improve the ecological integrity or health of rivers (Gore 1985; National Research Council 1992; Gore and Shields 1995; Sparks 1995; Stanford and Ward 1996; Karr and Chu 1999; Jungwirth et al. 2000), including the Missouri River (Galat and Rasmussen 1995; Galat et al. 1998; U.S. Fish and Wildlife Service 1999). Promoting river health requires shifting degraded physical, chemical, and biological components of river ecosystems towards a *normalized* state. Stanford and Ward (1996) define *normalization* as what is possible in a natural-cultural context as opposed to striving for pristine conditions which are difficult, if not impossible to define or achieve, at least for entire catchments.

Management, conservation, and normalization of native large river fish community structure, their

habitats, and the societal resources they provide necessitates a river-wide understanding of: (1) patterns of physical variables which affect composition and distribution of fish assemblages; (2) how physical habitat is affected by anthropogenic stressors, and; (3) what remedial actions can be undertaken to enhance physical habitat for riverine fishes that are compatible with other user benefits. Our goal is to address these topics for physical habitat relevant to benthic fishes at the scale of the entire warm-water Missouri River.

We consider physical habitat in its broadest sense from a fisheries perspective to include the space occupied by fishes and the features of that space. Physical variables we examined included: water depth, current velocity, water temperature, turbidity, conductivity, and substrate composition.

Objectives were to:

1. Characterize longitudinal patterns of physical variables for the warm-water, riverine portion of the Missouri and lower Yellowstone rivers.
2. Evaluate differences in physical variables among and within a hierarchy of spatial scales.
3. Relate patterns of physical variables to river management practices.
4. Provide physical habitat data to integrate with other volumes of this report: fish distribution and abundance (Volume 3) and fish growth, mortality, recruitment, condition, and size structure (Volume 4).

Eight organizations (referred to hereafter as the Benthic Fishes Consortium) conducted this research and seven sampled different areas of the Missouri and lower Yellowstone rivers. The Benthic Fishes Consortium, [river kilometers (km) each sampled], included the U. S. Geological Survey's Cooperative Research Units at Montana State University (km 3,217-3,029), University of Idaho (km 2,545-2,098), South Dakota State University (km 1,416-1,211), Iowa State University (km 1,191-872), Kansas State University (km 708-402), and the University of Missouri (km 354-0). Montana Department of Fish, Wildlife and Parks sampled km 2,832 to 2,545 on the Missouri River and km 114 to 0 on the Yellowstone River. The eighth participant in the Benthic Fishes Consortium was the U.S. Geological Survey's, Columbia Environmental Research Center. They designed and operated a quality assurance-quality control program, constructed and maintained the data base, conducted statistical analyses, and contributed to overall study design and production of standard operating procedures. See Berry and Young (2001) for additional background on the benthic fishes research project and operation of the Benthic Fishes Consortium.

STUDY AREA

The Missouri River flows 3,768 km from its origin at the confluence of the Gallatin, Madison and Jefferson rivers near Three Forks, Montana, generally east and south to its terminus with the Mississippi River just upstream from St. Louis, Missouri (Figure. 1). It is the longest river in the conterminous United States with a catchment encompassing about 1,327,000 km², or about one-sixth of the conterminous United States. Four physiographic provinces comprise its catchment:

142,000 km² of the Rocky Mountains in the west, 932,000 km² of the Great Plains in the center of the basin, 228,000 km² of Central Lowlands in the north lower basin, and 24,500 km² of the Interior Highlands in the south lower basin (Slizeski et al. 1982). Range of latitude of the Missouri River varies from about 48° 03' N to 38° 47' N (Braaten 2000).

The size of the Missouri River puts it into to a small sub-class of the world's large rivers categorized as *great* rivers (Simon and Emory 1995). Stalnaker et al. (1989) defined large rivers as having an average depth >1 m and requiring that measurements be taken from a boat. Simon and Emory (1995) defined great rivers as hydrologic units with catchments >3,200 km². Other great rivers in the United States include the Mississippi, Ohio, Colorado, and Columbia. The Amazon (South America), Danube (Europe), Mekong (Asia), and Murray-Darling (Australia) are examples of great rivers from other continents. Great rivers are distinctive in that they are few in number, interjurisdictional, comprise the largest component of the continental river resource, and are disproportionately degraded (Gammon and Simon 2000).

The highly regulated Missouri River is divided into three approximately equal length zones. The upper 1,241 km represents a "least-altered" zone relative to the remaining river. Although several mainstem dams and reservoirs are present above Ft. Peck Lake, (e.g., Canyon Ferry, Hauser, and Holter), their usable capacity (ca. 2.7 km³) is only 3% of the downriver mainstem reservoirs. The 1,316-km-long middle or "inter-reservoir" zone was impounded between 1937 and 1963 by six large mainstem reservoirs (total gross volume: 90.7 km³; total average annual discharge: 100.5 km³ yr⁻¹). Flows in the 1,212 km long lower zone are also regulated by upstream reservoirs, although reductions in spring-summer high flows are somewhat offset in lowermost reaches by tributary input (Galat and Lipkin 2000). In addition, channel-floodplain morphology in the lowermost zone from Sioux City, Iowa (km 1,178), to the mouth was altered by channelization, bank stabilization, and levee construction and encompasses the "channelized" zone.

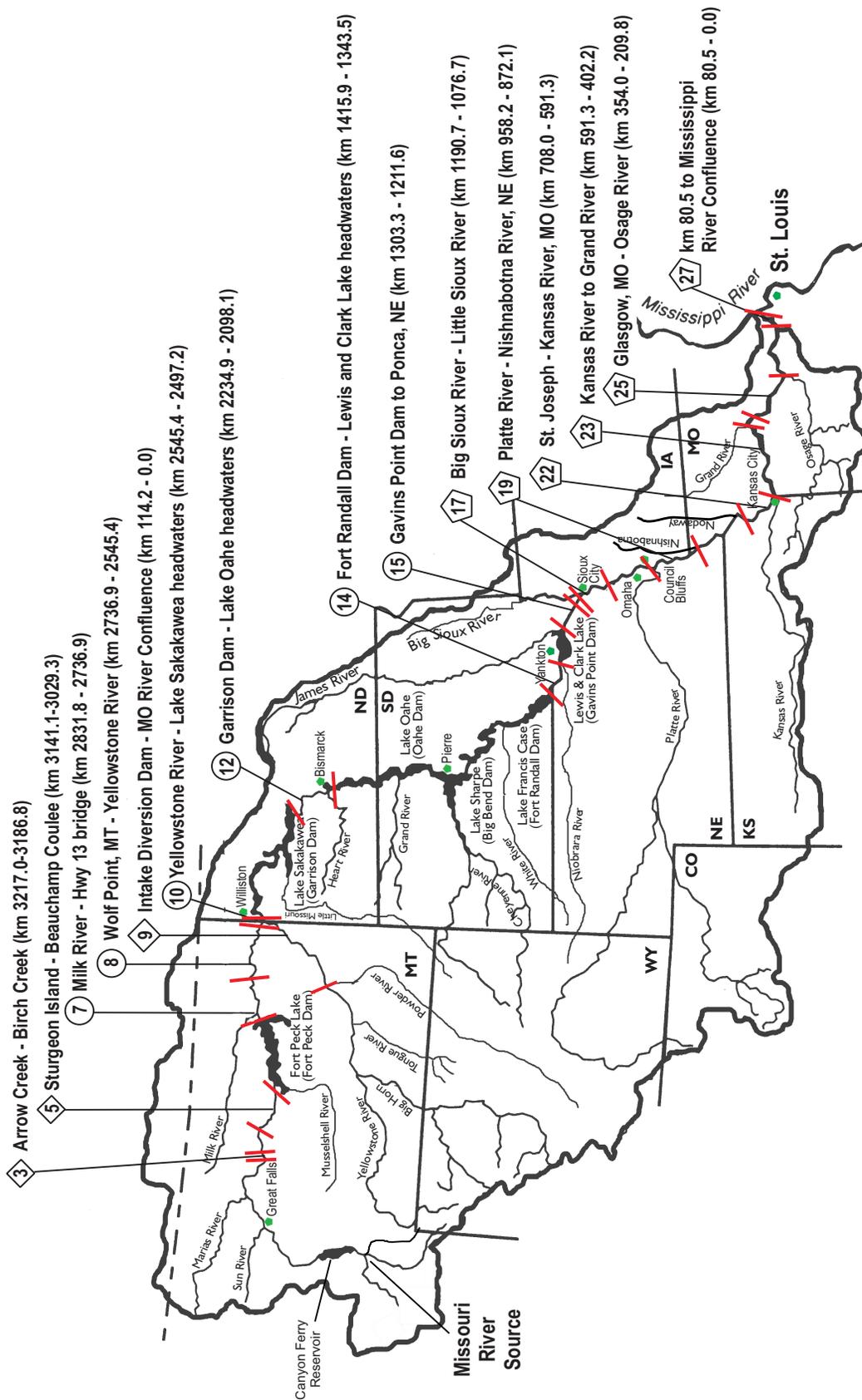


Figure 1. Map of Missouri River basin showing general locations of 15 segments sampled for physical variables from mid-June to October, 1996-1998. Segment numbers within diamonds are in the least-altered zone, numbers in circles are segments in the inter-reservoir zone, and numbers in pentagons are segments in the channelized zone. (map produced by J. Heuser, USGS, CERC).

METHODS

Our goal was to characterize physical attributes of aquatic habitat, using standardized procedures, throughout the warm-water Missouri and lower Yellowstone rivers and to relate patterns to major natural and anthropogenic features. To accomplish this, we developed a hierarchical spatial sampling design for the dominant active-channel habitats present throughout the study area. The active channel includes the main or primary channel and additional channels (secondary, tertiary) that may connect with the main channel during high-flow events.

Spatial Sample Design

Physical variables along the mainstem Missouri River were systematically evaluated by dividing the active channel into longitudinal and lateral patches of varying spatial scales following a hierarchical habitat classification framework (Frissell et al. 1986; Hawkins et al. 1993). Five nested *habitat units* were identified: zone, segment, bend, macrohabitat, and mesohabitat. The Missouri River, exclusive of reservoirs, was first divided into the three **zones** (~10³ km longitudinal scale) described previously: least-altered, inter-reservoir and channelized (Figures 1 and 2). We also included the lower 114 km of the Yellowstone River to its confluence with the Missouri River at km 2,546 as part of the least-altered zone. The Yellowstone is the longest free-flowing, high-quality, large river in the conterminous United States (Benke 1990; White and Bramblett 1993), and has a greater annual discharge than the mainstem Missouri at their confluence (Galat and Lipkin 2000). Each zone was sub-divided into **segments** (ca. 10¹-10² km) based on geomorphic (e.g. tributaries, geology) and constructed features (e.g., impoundments, channelization, urban areas).

Twenty-seven river segments were identified and a subset of 15 sampled throughout the study (Figure 1). Segments within the least-altered zone are hereafter identified in text by underlining, inter-reservoir segments are in **bold** font, and channelized segments are in *italic* font. Segments **6**, *18*, and *21* were sampled only in 1996. Results from these segments are summarized in Appendix Tables, but not otherwise included in analyses. The 15 segments sampled throughout the project approximate the warm-water Missouri River (~83% of its total length), were considered representative of the three zones, and included three least-altered, six inter-reservoir, and six channelized segments (Figure 1, Table 1).

The most apparent and repeatable habitat unit present in large river segments is the crossover-bend, analogous to the riffle-pool sequence in streams (Leopold et al. 1964). River segments were divided into **BENDs** at each thalweg crossover (Figures 2 and 3). We account-

ed for most of the diversity of environmental conditions present within segments and BENDs by sampling representative **macrohabitats** within each. Macrohabitats are smaller areas (10⁻¹-10⁰ km) of visually distinctive, repeatable natural (e.g., channel cross-over, tributary confluence) and man-made (e.g., dike field, revetment) physical features and were defined based on literature (Schmulbach et al. 1981; Cobb et al. 1989; Wilcox 1993; Hesse 1996) and field evaluations.

Three macrohabitats were identified within each BEND (Table 2, Figure 3): inside bend (ISB), outside bend (OSB), and channel crossover (CHXO). These macrohabitats are termed *continuous* as each is present in every BEND of every river segment. Three other representative channel macrohabitats were present in some segments, but not necessarily in a continuous or repeatable fashion within BENDs. These *discrete* macrohabitats were: tributary mouths (TRM), secondary channels connected at both ends to the main channel, termed secondary channels connected (SCC), and secondary channels connected to the main channel at only one end, termed secondary channels non-connected (SCN). Additional macrohabitats unique to a particular segment or a small number of segments that did not fit the descriptors in Table 2, or were sampled in a non-standardized fashion were identified as "WILD". These included dam tailwaters, embayments (e.g., scours, oxbows, vegetated backwaters), and shallow tributary mouths (too shallow for use of a boat). Results from these macrohabitats are not considered here.

Macrohabitats that were particularly complex or contained distinctive subclasses of physical features were further partitioned into **mesohabitats** (<10⁻¹ km, Table 2). This assured that the diversity of physical conditions present within each macrohabitat was also represented in samples. Inside bends were the most complex habitat present in the two rivers. Four distinctive mesohabitats were identified within ISBs: bars (BARS), pools (POOL), steep shorelines (STPS) and channel borders (CHNB). Tributaries were divided into two sizes: large (LRGE) and small (SMLL). Two distinctive types of SCCs were also identified: shallow (SHLW) and deep (DEEP) (Table 2). Not all mesohabitats were present in every ISB, TRM, or SCC of each segment.

Physical variables were sampled within this nested hierarchy using a stratified random design. BENDs and macrohabitats were stratified within each segment as previously described (Figure 4). Five replicates of BEND, TRM-LRGE, TRM-SMLL, SCC-SHLW, SCC-DEEP and SCN were selected at random in 1997 and 1998 from the total number present within each segment. Mesohabitats in TRM and SCC macrohabitats were not identified in 1996 so only five TRMs and SCCs were sampled that year, but 10 of each were sampled in 1997 and 1998 if present. The ISB and OSB

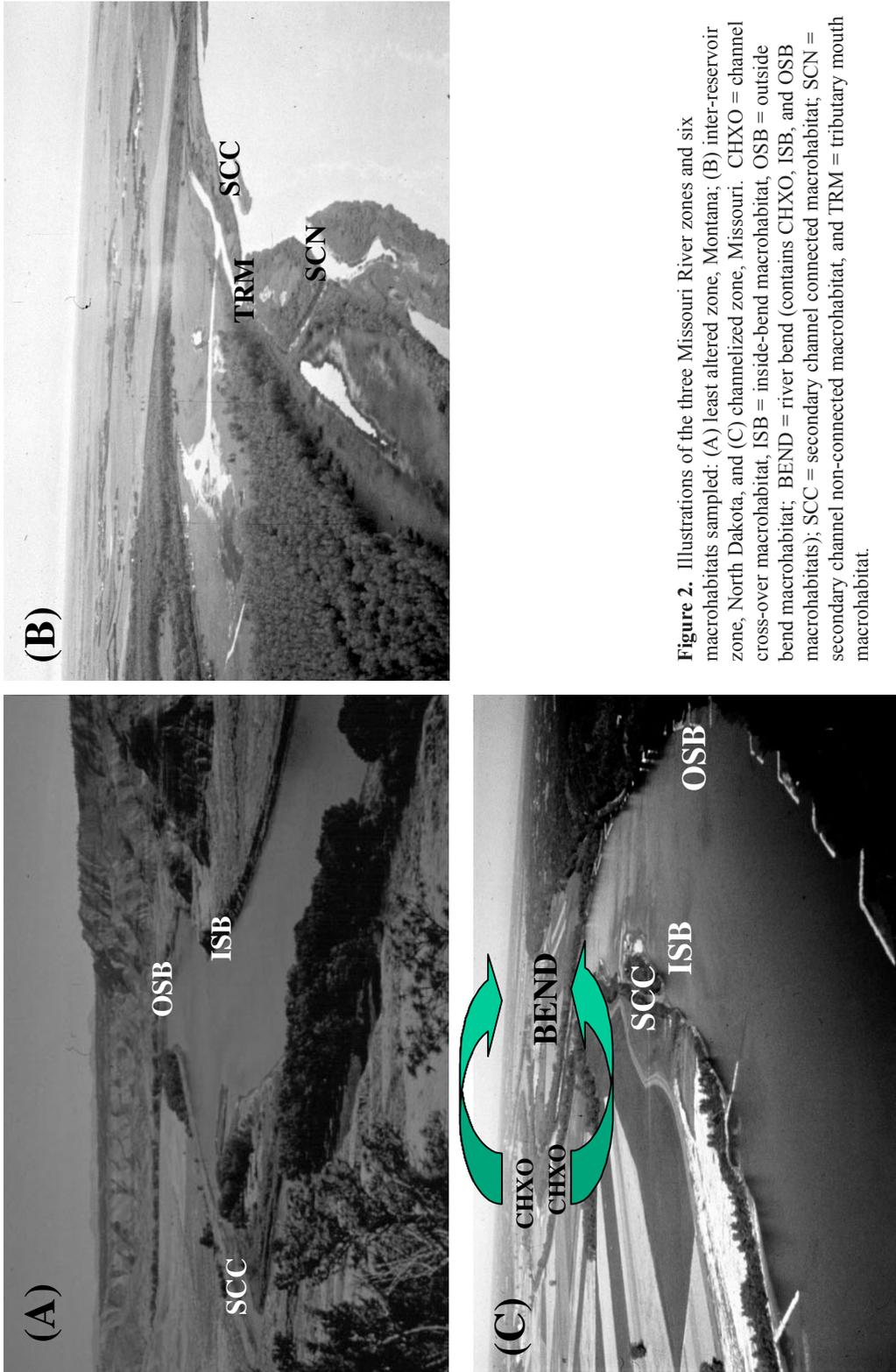


Figure 2. Illustrations of the three Missouri River zones and six macrohabitats sampled: (A) least altered zone, Montana; (B) inter-reservoir zone, North Dakota, and (C) channelized zone, Missouri. CHXO = channel cross-over macrohabitat, ISB = inside-bend macrohabitat, OSB = outside bend macrohabitat; BEND = river bend (contains CHXO, ISB, and OSB macrohabitats); SCC = secondary channel non-connected macrohabitat; SCN = secondary channel non-connected macrohabitat, and TRM = tributary mouth macrohabitat.

Table 1. Location information for Missouri and lower Yellowstone river zones and segments where physical variables were sampled, 1996-1998, and corresponding U. S. Geological Survey (USGS) flow gages. Zones: 1 = least altered, 2 = inter reservoir, 3 = channelized. Reservoir names are also in **bold** and reservoir lengths are approximate. Asterisk (*) indicates USGS gages where river flows were examined.

Zone	Segment	Location	River kilometer			USGS gage location			
			Upper	Lower	Midpoint	Length	Name	Number	km
<u>1</u>	<u>3</u>	Arrow Creek - Birch Creek, MT	3217.0	3186.8	3201.9	30.2			
<u>1</u>	<u>5</u>	Sturgeon Island - Beauchamp Coulee, MT	3141.1	3029.3	3085.2	111.8	*Landusky	06115200	3092
		Ft. Peck Lake	3029.3	2847.9	3120.0	181.4			
<u>2</u>	<u>7</u>	Milk River - Hwy 13 bridge (Wolf Point), MT	2831.8	2736.9	2784.4	94.9	*Wolf Point	06177000	2738
<u>2</u>	<u>8</u>	Wolf Point - above Yellowstone River, MT	2736.9	2545.4	2641.2	191.5	Culbertson	06185500	2618
<u>1</u>	<u>9</u>	Intake Diversion Dam - MO River Confluence, MT	114.2	0.0	57.1	114.2	*Sidney	06329500	47
<u>2</u>	<u>10</u>	Yellowstone River, MT - L. Sakakawea Headwaters, ND	2545.4	2497.2	2521.3	48.3			
		Lake Sakakawea	2469.8	2234.9	2352.4	234.9			
<u>2</u>	<u>12</u>	Garrison Dam - Lake Oahe Headwaters, ND	2234.9	2098.1	2166.5	136.8	*Bismarck	06342500	2115
		Lakes Oahe, Sharpe, and Francis Case	2051.5	1415.9	1733.7	635.6			
<u>2</u>	<u>14</u>	Fort Randall Dam - Lewis & Clark L. Headwaters, SD	1415.9	1343.5	1379.7	72.4			
		Lewis and Clark Lake	1343.5	1303.3	1323.4	40.2			
<u>2</u>	<u>15</u>	Gavins Point Dam, SD - Ponca, NE	1303.3	1211.6	1257.4	91.7			
<u>3</u>	<u>17</u>	below Big Sioux River, SD - Little Sioux River, IA	1190.7	1076.7	1133.7	113.9	*Sioux City	06486000	1164
<u>3</u>	<u>19</u>	Platte River, NE - Nishnabotna River, IA	958.2	872.1	915.1	86.1	Nebraska City	06807000	905

Table 1, continued.

Zone	Segment	Location	River kilometer			USGS gage location			
			Upper	Lower	Midpoint	Length	Name	Number	km
3	22	St. Joseph - Kansas River, MO	708.0	591.3	649.6	116.7	*St. Joseph	06818000	721
3	23	below Kansas River - Grand River, MO	591.3	402.2	496.8	189.1	Waverly	06895500	472
3	25	Glasgow - Osage River, MO	354.0	209.8	281.9	144.2	*Boonville	06909000	317
3	27	km 80.5 - Mississippi River Confluence, MO	80.5	0.0	40.2	80.5	*Hermann	6934500	158

present in each randomly selected BEND and either the up- or down-river CHXO (picked at random) were also sampled. More than five BENDs were always present in each segment and thus, the same BENDs were not necessarily sampled each year. However, many segments contained fewer than 10 TRMs and SCCs or five SCNs. In these instances the entire population of the macrohabitat within a segment was sampled and the same locations resampled each year.

Macrohabitats Sampled Relative to Availability in Segments

We intentionally tried to sample an equal number of each macrohabitat per segment (stratified random design), rather than sample macrohabitats in proportion to their availability (completely randomized design). The latter approach would have resulted in large numbers of continuous macrohabitats, but too few discrete macrohabitats for a robust statistical analysis. In contrast, our sample design yielded a disproportionately large number of rarer macrohabitats relative to their availability in the active channel. Thus, averaging results of stratified random samples among macrohabitats may not have yielded a representative estimate of environmental conditions present within a segment.

Additionally, not all segments contained the number of replicates of discrete macrohabitats set forth in the study design (see **Spatial Sample Design**). Therefore, we report the ratio of the number of replicate discrete macrohabitats sampled per segment over the 3 years relative to the number proposed to sample (SCC = 25, SCN = 15, TRM = 25). Each year we sampled the five replicate BENDs proposed to be surveyed per segment, and the CHXO, ISB, and OSB macrohabitats within each of them. How the number of discrete macrohabitats differed among segments illustrates the relative influence they had on estimates of segment means and variability of physical variables.

We also related the number of macrohabitats sampled to the number of macrohabitats available in each segment to describe this bias in our sample design. The number of macrohabitats available in each segment was determined from multiple sources, including: aerial photographs, USGS 1:24,000 topographic maps, US Army Corps of Engineers Missouri River Hydrographic Surveys, and field observations at the start of each sampling season. We summed mesohabitats within SCC (SHLW, DEEP) and TRMs (SMLL, LRGE), and used the maximum number of each macrohabitat present over the 3-year study as our estimate of *available*. This was done because the number of available SCC and SCN macrohabitats and SHLW and DEEP mesohabitats within SCC varied within and among years for each segment depending on river stage. The number of each

macrohabitat *sampled* was defined as locations where fish collection gear was successfully deployed and this was the number of replicates used in statistical analyses. This criterion was used because we were not always able to collect every physical variable at every macrohabitat over the 3-year study. The number of macrohabitats sampled as a proportion of the number available was calculated as: $\text{sampling/available} = (\text{number of each macrohabitat sampled in 1996-98} / \text{maximum number of each macrohabitat present in 1996-98}) * 100$.

Temporal Sampling Design

Our primary objective was to examine spatial variability

in physical habitats and fish distribution along the Missouri and lower Yellowstone rivers and we attempted to reduce intra-annual temporal variability in habitat conditions by sampling within a short time period. We targeted the mid summer-early autumn (July-October) period because normally: (1) river flows are low and stable during this season, (2) most macrohabitats are present, (3) water is warm and therefore fishes are active, and (4) the majority of age-0 fishes should be large enough to be captured by collection gears. Whereas, this design reduced within-year temporal variability, our results are applicable only to the season examined. Inter-annual temporal variability was

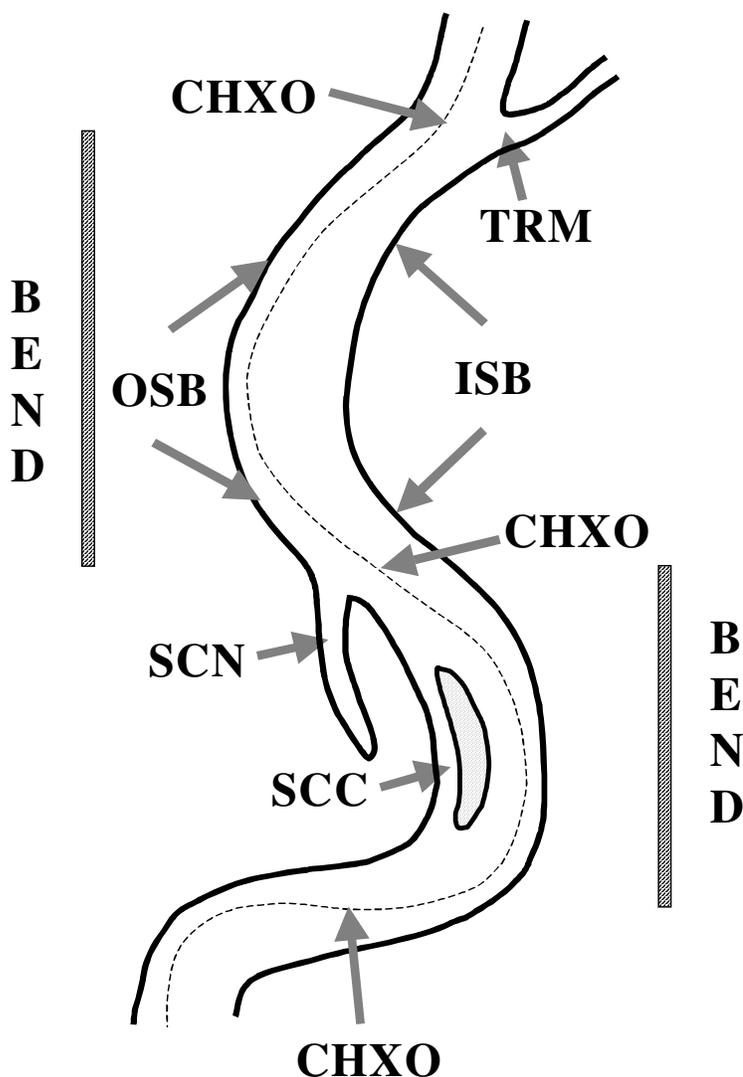


Figure 3. Generalized plan view of Missouri River channel showing outside bend (OSB), inside bend (ISB), and channel crossover (CHXO) continuous macrohabitats within bends (BEND), and secondary channel connected (SCC), secondary channel non-connected (SCN), and tributary mouth (TRM) discrete macrohabitats. Dashed line represents the channel thalweg.

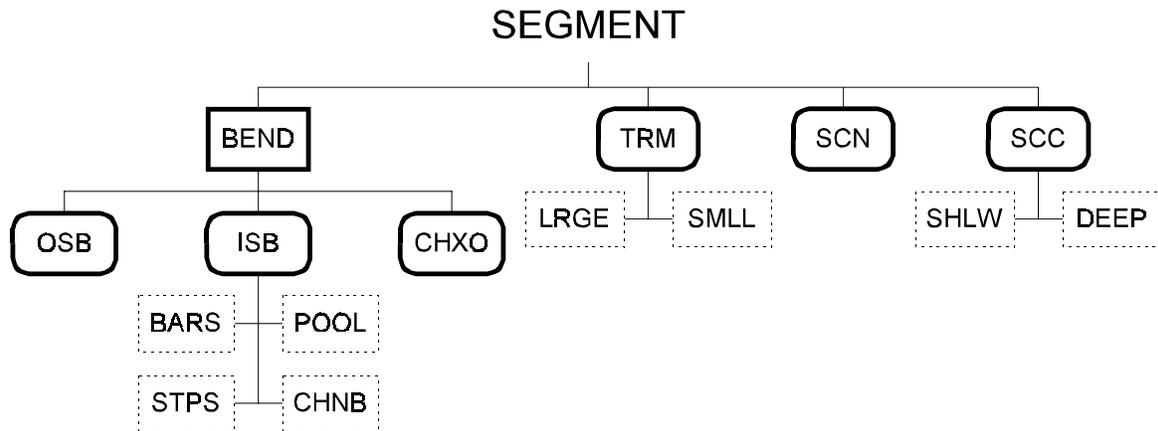


Figure 4. Physical variable sampling hierarchy for all segments within each of three zones (least-altered, inter-reservoir, channelized) along the Missouri and lower Yellowstone rivers. Six macrohabitats (rounded rectangles) were sampled per segment, three within each BEND. Mesohabitats (dotted rectangles) were sampled within complex macrohabitats. See text for definitions of habitat units.

addressed by repeated sampling over 3 years: 1996-1998. BENDs and discrete macrohabitats (i.e., SCCs, SCNs, and TRMs) within a segment were not sampled in any consistent order or longitudinal progression (i.e., upstream to downstream, or downstream to upstream) within or among years to minimize temporal bias.

Physical Variables

Physical parameters were collected at all fish sampling locations to characterize environmental conditions within BENDs and macrohabitats and among study segments and zones in relation to fish habitat use. Physical variables measured were: water depth, current velocity, water temperature, turbidity (as an index of suspended inorganic and organic sediments), conductivity (as an index of total dissolved salts or salinity), and several measures of substrate particle size and composition. Detailed sampling protocols and standard operating procedures were developed and a quality assurance/quality control program established to assure researchers collected physical data in a standardized manner throughout the study area (Sappington et al. 1998).

Water depths ≤ 1.2 m were measured to the nearest 0.1 m using a standard wading rod and when depths exceeded 1.2 m with a A55M sounding reel or a commercial depth finder (e.g., Hummingbird Wide 100). Water velocity to nearest 0.1 m/s was measured with either a Price Type AA or Marsh-McBirney flow meter

following manufacturers instructions. Velocity was measured at 0.6 bottom depth in macrohabitats ≤ 1.2 m deep and at both 0.8 and 0.2 depths in deeper water and averaged to yield a mean water column velocity (Orth 1983). Water temperature ($^{\circ}\text{C}$) and conductivity ($\mu\text{S}/\text{cm}$) were measured with a YSI model 30 SCT meter and probe following manufacturers instructions. Turbidity was measured as NTUs using a calibrated Hach Model 2100P turbidimeter on samples of water collected ~ 25 cm below the surface.

Substrate size composition was determined from substrate samples collected using a Hesse dredge (Sappington et al. 1998). Percent gravel (64-2 mm diameter), sand (2-0.0625 mm diameter) and silt/clay (< 0.0625 mm diameter, hereafter called silt) fractions were estimated visually against sieved standards covering the full particle size range for each fraction (Gordon et al. 1992). Cobble (> 64 mm diameter) was rated as present or absent. When cobble was present, it was classified on a 0-2 scale as incidental (0), dominant (1), or ubiquitous (2). The sum of gravel, sand, and silt always equaled 100% unless cobble was ubiquitous, and then these three size fractions would sum to 0%. Geometric mean particle size was calculated as a measure of central tendency of particle size distribution (Young et al. 1991; McMahon et al. 1996). The geometric mean (D_g) was calculated as: $D_g = D_a^{Pa} \times D_b^{Pb} \times \dots \times D_i^{Pi}$, where D_i = the median of the size range for a given substrate category (i.e., 33 mm for gravel; 1.03

Table 2. Habitat units where physical variables were sampled along Missouri and lower Yellowstone rivers, 1996-1998.

Continuous Macrohabitats within each river bend. At each replicate river bend (channel cross-over to bend to channel cross-over, BEND) within a segment, the outside bend (OSB), inside bend (ISB), and up- or down-river channel cross-over (CHXO, selected at random) was sampled. Results from OSBs, ISBs, and CHXOs within each BEND were averaged to yield a BEND value because these macrohabitats were not sampled independently. Five replicates of each macrohabitat, or mesohabitat (when present) within a macrohabitat, were randomly selected and sampled in each river segment. Means of replicate mesohabitats within a macrohabitat were averaged to yield the macrohabitat value.

Main channel cross-over (CHXO). The center of the main channel where the thalweg crosses over from one concave side of the river to the other concave side (Leopold et al. 1964).

Outside bend (OSB). The concave side of a main channel bend extending from the bankline to the thalweg.

Inside bend (ISB). The convex side of a main channel bend extending from the bankline to the thalweg. Four mesohabitats were identified and sampled when present within ISBs. Results from all mesohabitats sampled within an ISB were averaged to yield a mean value for that ISB.

Bars (BAR): shallow water, gradual slope area extending from the bankline to 1.2 m depth.

Pools (POOL): area immediately downstream from dike or inside bend bar that has formed a scour hole. Depth varied by location, but usually exceeded average main channel depth.

Steep shorelines (STPS): area along inside bend where water depth exceeded 1.2 m within 5 m of the bank and was too deep to effectively seine.

Channel border (CHNB): area between the 1.2 m depth interval and the thalweg, including submerged sand bars.

Discrete Macrohabitats. Each was selected independently within segments and at random if >5 were present. All were sampled when ≤5 replicates of each were present within a segment. Means of replicate mesohabitats within a macrohabitat were averaged to yield the macrohabitat value.

Tributary mouth (TRM). Area in tributary immediately upstream from where it enters the main river channel. Two types of TRMs were identified and sampled and results combined for statistical analyses.

Large tributary mouth (LRGE): terminus of tributary with an average annual discharge $\geq 20 \text{ m}^3/\text{s}$ and/or drainage areas $\geq 2,600 \text{ km}^2$. Tributaries in this class were usually $\geq 30 \text{ m}$ wide and large enough for boats to sample fishes using trawls and drifting trammel nets. Longitudinal distance began at an imaginary line across the downstream limits of apparent shorelines and extended 200 m upstream.

Small tributary mouth (SMLL): terminus of tributary with an average annual discharge $< 20 \text{ m}^3/\text{s}$ and/or drainage areas $< 2,600 \text{ km}^2$. Tributaries in this class were 6.1 to $< 30 \text{ m}$ wide and deep enough to enable boat passage for 45 m upstream from a lower boundary line across the downstream limits of apparent shorelines. Tributaries smaller than SMLL were not sampled.

Secondary channel, non-connected (SCN). Channels blocked at one end by dry land, closing rock dikes, or aquatic vegetation so that water velocity was reduced to near $0 \text{ m}^3/\text{s}$ and movement of fishes was blocked. Area of SCNs extended from a boundary line across the downstream limits of apparent shorelines, upstream to the first water flow impediment.

Table 2, continued.

Secondary channel, connected (SCC). Flowing water channels with less water discharge than the main channel and connected to the main channel at both ends. Upstream and downstream boundaries of SCCs extended from imaginary lines across the upstream and downstream limits of apparent shorelines. Two types of SCCs were identified and sampled, but results combined for statistical analyses.

Secondary channel, connected, shallow (SHLW): average depth ≤ 1.2 m

Secondary channel, connected, deep (DEEP): average depth > 1.2 m

mm for sand; and 0.03 mm for silt), and P_i is the power of the proportion the substrate category represented in the sample. Cobble was only considered in geometric mean calculations when it was ubiquitous, since its proportional makeup of substrate was not estimated. When cobble was ubiquitous (index of 2) the geometric mean was assigned a value of 101.6 mm, the diameter of the Hesse sampler.

One or more measurements of each physical variable were made each time a gear was deployed to sample fishes (Table 3). Additionally, multiple samples (hereafter termed *subsamples*) were collected by some fish gears and one or more gears were deployed in each replicate mesohabitat and/or macrohabitat examined per segment (Table 4, see Sappington et al. 1998 for details). This yielded a variable number of physical habitat measurements among macrohabitats (Tables 3 and 4), segments, and zones.

River Discharge

Flow patterns for the Missouri and lower Yellowstone rivers during the 1996 through 1998 study years were compared with the pre-study, post flow-regulation period of 1967 to 1995. Our objective was to determine if river flows during study years were representative of the 28 year post flow-regulation interval, exclusive of the study period. Median monthly discharges for eight U. S. Geological Survey gaging stations within representative river segments of each zone (Table 1) were compared against the 25th and 75th percentiles of the 1967 to 1995 period. We calculated the percent of months per year and percent of months for the approximate sampling period for each of the study years (1996-1998) when median monthly discharge was above the 75th percentile or below the 25th percentile of the 1967-1995 reference period. This approach follows the Indicators of Hydrologic Alteration (IHA) method developed by Richter et al. (1996) for evaluating hydrologic variability among time periods.

Statistical Analyses

Two types of statistical analyses were performed on physical variables: Analysis of Variance (ANOVA) and Principal Components Analysis (PCA). Analysis of variance was used to test for significant differences in individual physical variables (i.e., a univariate test) among spatial (zone, segment, BEND/macrohabitat) and temporal (year) scales and to examine interactions among these scales (e.g., the effect of segment on BEND/macrohabitat, year on segment, etc.). We also used ANOVA to test if significant differences in individual physical variables occurred among specific groups of segments (i.e., planned segment contrasts) or BENDs and macrohabitats. Segments were grouped in relation to natural system features or aspects of river regulation. Principal Components Analysis is a multivariate ordination technique which graphically displays objects (e.g. segments, BENDs/macrohabitats) as points along several axes of reference. Principal Components Analysis differs from ANOVA in that it summarizes in 2-3 dimensions (axes) most of the variability present in a large number of descriptors (i.e., physical variables) and provides a measure of the amount of variance explained by these few independent principal axes (Legendre and Legendre 1998). Principal Components Analysis provides a graphical representation of the relative positions of points representing zones, segments, BENDs or macrohabitats in a multidimensional space composed of relevant combinations of physical variables. However, PCA, does not enable the rigorous hypothesis testing and output of significance levels afforded by ANOVA. The two statistical techniques are complimentary in that ANOVA yields a robust analysis of each physical variable independently within and among spatial and temporal scales of interest, while PCA enables visualization of relationships among spatial scales for all physical variables at once.

Raw physical habitat data had to be collapsed to the within year, within segment, and within macrohabitat level by averaging before ANOVA or PCA analyses could be conducted. Varying numbers of physical

habitat subsamples were collected at gear, mesohabitat, and macrohabitat levels and necessitated use of a hierarchical approach for calculating means. Averaging was conducted so each subsample had the appropriate level of influence on the resulting means. We first calculated the mean when multiple measurements for physical variables were obtained at each location where a fish collection gear was deployed within a mesohabitat subsample (Tables 3 and 4). These individual *gear means* were then averaged for all gears deployed within each mesohabitat subsample. Next, we averaged *mesohabitat means* within each macrohabitat replicate per segment. This averaging method was also applied in those macrohabitats without mesohabitats (i.e., CHXO, OSB, SCN). After producing means for each macrohabitat replicate, channel crossover (CHXO), inside bend (ISB), and outside bend (OSB) physical variable means were averaged within each replicate BEND to produce one mean for each BEND replicate. This was necessary because CHXO, ISB, and OSB macrohabitats were not selected independently of each other (i.e. all three were sampled at each bend). The final set of BEND and macrohabitat means (i.e., one for each BEND, TRM, SCC, and SCN replicate) for each physical variable within each segment were used in all statistical analyses (Figure 4). Additionally, we examined CHXO, ISB, and OSB macrohabitats within BENDs using procedures described under *Analysis of Variance*.

Macrohabitat means for each physical variable were

analyzed for constancy and normality of error variance using SAS/LAB software as part of SAS (SAS 1992). This software tested constancy of variance of residuals from the three-way analysis of variance (ANOVA) model (i.e., year, segment, BEND/macrohabitat) with two-way and three-way iterations using chi-square goodness-of-fit tests between predicted and residual values. The software then suggested appropriate transformations as necessary to obtain constant variance. The following transformations were made on physical variable macrohabitat means: depth, square root; velocity, $\log_{10}(x + 1)$; temperature, $x^{1.5}$; turbidity, \log_{10} ; conductivity, square root; proportion of gravel, sand, and silt, arcsin square root; geometric mean substrate size, \log_{10} . After these transformations, about one-half of the constancy of variance and normality assumption violations were eliminated. The remaining violations, though significant, were often the result of <10 outliers and were only somewhat large for conductivity and proportion of gravel. Furthermore, many of the significant assumption violations still present after transformation were more the result of our power to detect differences due to the large number of observations in the data set as opposed to any real departure from the assumptions inherent in the statistical tests used to analyze the data. After transforming the data, we continued with parametric analyses of all habitat variables based on the effectiveness of our transformations and the robustness of

Table 3. Design of number of measurements for each physical variable per subsample for each fish collection gear deployed in macrohabitats or mesohabitats in segments of Missouri and lower Yellowstone rivers. See Table 4 for number of replicate fish collection gear samples taken in each macrohabitat and mesohabitat and Table 2 for full names of habitat acronyms.

Physical habitat variable	Fish collection gear				
	Drifting trammel net	Benthic trawl	Bag seine	Stationary gill net	Electrofishing
Depth	1	1	3	1 ISB-POOL 3 SCN, 3 TRM-SMLL	1
Velocity			same as depth		
Temperature	1	1	1	1	1
Turbidity	1	1	1	1	1
Conductivity	1	1	1	1	1
Substrate	1	1	1	1	1

ANOVA when violations of the assumptions are not extreme (Snedecor and Cochran 1980, Milliken and Johnson 1984, and Neter et al. 1996). Additionally, when sample sizes are equal or almost equal, as they were in this study, F tests are still effective when variances are not constant (Milliken and Johnson 1984).

Means and standard deviations (± 1 SD) of *transformed* physical variables were plotted in figures for segments, BENDs, and macrohabitats. The Y-axis (physical variable) scale was also transformed (note spacing of tic marks on figures is not uniform), but tic values were back transformed for clarification.

Analysis of Variance

Statistical analyses for each physical variable included a three-way ANOVA with main effects of year, segment, and BEND/macrohabitat (fixed factors) and four inter-

action terms: year x segment, year x BEND/macrohabitat, segment x BEND/macrohabitat, and year x segment x BEND/macrohabitat. This analysis was performed for two models. First, continuous macrohabitats CHXO, ISB, and OSB, were pooled into the BEND habitat unit, and BENDs were grouped with the discrete macrohabitats SCC, SCN, and TRM into what will be referred to hereafter as the BEND-SCC-SCN-TRM model. Second, physical variables were compared only for the continuous macrohabitats CHXO, ISB, and OSB present within BENDs. This ANOVA will be referred to as the CHXO-ISB-OSB model. We looked for significant results in the TYPE III sums of squares (i.e., sums of squares for an effect after all other effects have been accounted for) in the three-way ANOVA. The TYPE III sums of squares gave us a conservative estimate of the variance accounted for by a factor and its interactions

Table 4. Design of number of subsamples for each fish collection gear deployed in macrohabitats or mesohabitats in segments of Missouri and lower Yellowstone rivers. All physical habitat variables were sampled at each gear subsample. See Table 3 for number of physical variable sub-samples taken at each gear replicate and Table 2 for full names of habitat unit acronyms.

Macrohabitat-mesohabitat	Fish collection gear				
	Drifting trammel net	Benthic trawl	Bag seine	Stationary gill net	Electrofishing
BEND					
CHXO	3, segments 3-15 2, segments 17-27	3, segments 3-15 2, segments 17-27			
BEND					
ISB-BARS			3		
BEND					
ISB-CHNB	3	3	3		
BEND					
ISB-POOL				2	
BEND					
ISB-STPS					3
BEND					
OSB	3, segments 3-15 2, segments 17-27	3, segments 3-15 2, segments 17-27			3
SCC-DEEP	3	3	3		2
SCC-SHLW			3		
SCN			3	1	2
TRM-LRGE	3	3			2
TRM-SMLL				1	2

and thus, a conservative test of significance. The conservative nature of the TYPE III sums of squares is that any factor or interaction would have a higher sums of squares if tested alone without adjusting for any of the other factors or interactions. We used $P \leq 0.05$ as the criterion for a significant result.

The three-way ANOVA permitted us to identify statistically significant differences in physical variables due to effects of geographic (segment) and geomorphic (macrohabitat) space, time (year), and interactions among these three main effects. We applied decomposition of variance to identify which of these effects for each physical variable were most important to explaining the overall variance observed (Wiley et al. 1997). The proportion of the corrected total model sum-of-squares (SS_{total}) that was contributed by the Type III partial SS ($SS_{partial}$) for each main effect and interaction was calculated as $SS_{partial}/SS_{total}$ where $[SS_{total} = (SS_{year} + SS_{segment} + SS_{macrohabitat} + SS_{year*segment} + SS_{year*macrohabitat} + SS_{segment+macrohabitat} + SS_{year*segment*macrohabitat}) + SS_{error}]$. When these proportions were $\geq 10.0\%$ of total model variance we considered them to be of ecological significance.

ANOVA segment contrasts. Our study design yielded over 5.5 million possible segment contrasts for each of the nine physical variables sampled in the 15 segments each year. We selected for analysis a subset of 21 planned contrasts for 11 segment combinations (A-K) for each of the nine physical variables (Table 5). These comparisons highlighted contrasts with the most management interest relative to defining natural environmental differences between regions of the two rivers and addressing how impoundment, flow regulation, and channelization affected physical variables. Questions defining these differences were grouped into five categories of planned contrasts (letters in parentheses denote the contrast ID in Table 5):

1. Do the least-altered Missouri River (segments 3, and 5) or the Missouri River below Ft. Peck dam, but above the Yellowstone River (segments, 7 and 8), differ from each other or from the lower Yellowstone River (segment 9)? (upper Missouri River - lower Yellowstone River comparisons, A-C)
2. Are least-altered (segments 3, 5, 9), inter-reservoir (segments 7, 8, 10, 12, 14, 15), and channelized (segments 17, 19, 22, 23, 25, 27) zones different from each other? (3-zone comparisons, D)
3. Do physical variables differ between segments above and below reservoirs? (reservoir related comparisons, E-I)

4. Does partitioning the least-altered zone into its Missouri (segments 3, and 5) and Yellowstone (segment 9) river segments and considering segment 15 below Lewis and Clark Lake as unique (it is the only inter-reservoir segment without a downriver reservoir) alter differences in physical variables compared with segments grouped in the three-zone contrast? (5-zone comparisons, J)
5. Does the upper channelized Missouri River differ from the lower channelized Missouri River? (Channelized river comparisons, K)

Experiment-wise error rate for each of these planned comparisons was controlled by using a Bonferroni adjusted P-value for the acceptable level of significance: $0.05/21 = \leq 0.0024$.

Planned contrasts resulted in 189 physical variable x segment groups to examine for statistical significance. Variance decomposition was again employed to highlight physical variables that contributed a meaningful amount to the total variance observed among significantly different planned segment contrasts. We selected $\geq 2.0\%$ of total variance for each planned contrast as ecologically relevant. This level was used, rather than the $\leq 10\%$ selected previously for the overall ANOVA models, to discern smaller differences among physical variables at the segment and BEND/macrohabitat scales.

ANOVA BEND/macrohabitat contrasts. Similar methods and criteria for analyses were used to compare physical variables among BENDS and discrete macrohabitats (all segments combined) as described above for segments. Comparisons were among BENDS, SCCs, SCNs, and TRMs. Continuous CHXO, ISB, and OSB macrohabitats within BENDS were contrasted in a second set of comparisons.

Principal Components Analysis

Principal Components Analysis (PCA) was applied to six of the nine physical variables measured to illustrate if combinations of physical variables discerned patterns among selected zones, segments, and BENDS/macrohabitats. Principal components analysis was conducted independently among BENDS and discrete macrohabitats (BEND, SCC, SCN, TRM) and also for continuous macrohabitats (CHXO, ISB, OSB) within BENDS, including all segments and years. Data were averaged over years as ANOVA variance decomposition indicated the effect of year was minor relative to the spatial scales. The six habitat variables used in the PCAs were: water depth, current velocity, water temperature, turbidity, conductivity, and geometric mean of substrate sizes. Proportions of gravel, sand, and silt were not included in PCAs because the geometric mean

Table 5. Summary of planned segment contrasts for Missouri and lower Yellowstone river physical variables. The question asked was: is there a statistically significant difference between mean depth, velocity, temperature, turbidity, or percentage of substrate size class between or among segments grouped in each of the contrasts? Segments in the least-altered zone are above the six Corps of Engineers mainstem reservoirs and are identified by underlining. Inter-reservoir segments are below or between the mainstem reservoirs and are identified in **bold** font. Segments in the channelized portion of the lower Missouri River are in *italic* font. MOR = Missouri River, YSR = Yellowstone River; segments are in the Missouri River unless indicated otherwise. See Table 1 for river kilometers each segment includes.

Contrast ID	Segments contrasted	Description and purpose of segment contrasts
Upper Missouri River - lower Yellowstone River comparisons		
A	<u>3, 5</u> vs. <u>2</u>	Least-altered MOR vs. least-altered lower YSR. How different are the least-altered sections of each river studied?
B	<u>3, 5</u> vs. 7, 8	Least-altered MOR vs. inter-reservoir MOR below Ft Peck Dam to YSR. What is the influence of Ft. Peck Lake on upper Missouri River segments above YSR?
C	<u>2</u> vs. 7, 8	Least-altered lower YSR vs. inter-reservoir MOR below Ft Peck Dam to YSR. Do upper Missouri River segments affected by Ft. Peck Lake differ from the nearby un-impounded lower Yellowstone River?
3-zone comparisons		
D	<u>3, 5, 2</u> , vs 7, 8, 10, 12, 14, 15 vs. <i>17, 19, 22, 23, 25, 27</i>	Least-altered zone segments vs. inter-reservoir zone segments vs. channelized zone segments. Are the three river zones different?
Reservoir related comparisons		
E	<u>5</u> vs. 7	Least-altered above Ft. Peck Lake (Sturgeon Island to Beauchamp Coulee) vs. inter-reservoir below Ft. Peck Dam to Milk River. Do Missouri River segments above and below Ft. Peck Lake differ?
G	10 vs. 12	Inter-reservoir MOR from YSR to L. Sakakawea headwaters vs. inter-reservoir, Garrison Dam to Lake Oahe headwaters. Do Missouri River segments above and below Lake Sakakawea differ?
F	7, 8 vs. 10	Inter-reservoir MOR below Ft Peck Dam to YSR vs. inter-reservoir MOR from YSR to L. Sakakawea headwaters. Does inflow from the Yellowstone River ameliorate the influence of Ft. Peck Lake on the Missouri River?
H	14 vs. 15	Inter-reservoir, Ft. Randall Dam - Lewis & Clark Lake headwaters vs. inter-reservoir, Gavins Point Dam-Ponca. Do Missouri River segments above and below Lewis & Clark Lake differ?
I	15 vs. <i>17</i>	Inter-reservoir, Gavins Point Dam-Ponca vs. first channelized river segment, Big Sioux River-Little Sioux River. How different is the river segment immediately below Lewis & Clark Lake from the first channelized river segment?

Table 5, continued.

Contrast ID	Segments contrasted	Description of segments grouped and contrast
5-zone comparisons		
J	<u>3</u> , <u>5</u> , vs. <u>9</u> , vs. 7, 8, 10, 12, 14 , vs. 15 vs. <i>17, 19, 22, 23, 25, 27</i>	Least-altered MOR segments vs. least-altered lower YSR segments vs. inter-reservoir segments above Gavins Point Dam vs. inter-reservoir segment below Gavins Point Dam vs. channelized zone segments. Subdivides the 3 zones into 5 zones by adding two contrasts to: (1) assess the influence of least-altered lower Yellowstone River segment <u>9</u> independent of least-altered Missouri River segments <u>3</u> and <u>5</u> , and (2) isolate the effect of the only inter-reservoir segment without a downriver reservoir (15) from the five inter-reservoir segments located between reservoirs.
Channelized river comparisons		
K	<i>17, 19, 22</i> vs. <i>23, 25, 27</i>	Channelized, Big Sioux River to Kansas City vs. channelized, Kansas City to mouth. Are there differences between upriver channelized Missouri River segments and channelized segments farther downriver from reservoir flow regulation where tributaries are large and numerous?

particle size provided an average of these classes. The transformed version of each of the six variables was used in the PCAs so that the data were multivariate normal, facilitating interpretation of results (Johnson and Wichern 1992). Eigenvectors of the correlation matrix (i.e., weighting factors of original physical variables) were used to compute the principal components (PCs), which give the position of the zones, segments or BENDs/macrohabetats with respect to the new system of coordinates. We focused on the first three principal components because there were initially only six variables in the analysis yielding a 50% reduction in the number of variables used to represent the data. The amount of total variance each of the first three principal components contributed was also computed. Pearson correlation coefficients were calculated for each of the six physical variables against the first three PCs to estimate the strength of the relationship between them (i.e., loadings). Physical variables with correlation coefficients ≥ 0.50 were considered the descriptors of greatest contribution to each PC space. Bivariate plots were constructed to illustrate the distribution of zones (segments and macrohabitats combined), BEND and discrete macrohabitats (BEND, SCC, SCN, and TRM; zones and segments combined), continuous macrohabitats within BEND (CHXO, ISB, OSB; zones and segments combined), and macrohabitats within selected segments for PC1 vs PC2 and PC1 vs PC3.

RESULTS

Physical variables were sampled from 1,191 macrohabitats over the three zones, 15 river segments, and 3 study years. Beginning and ending dates of sampling for the seven consortium members (organizations) ranged from Julian day 169 (18 June 1998) to Julian day 302 (28 October 1996, Figure 5). The majority of samples were collected in August and September. Median sample date among organizations and years ranged from Julian day 216 (4 August) to 251 (8 September, Figure 5) and the median sample date for all organizations and years was Julian day 234 (22 August). Although, variability in start, end, and duration of sampling periods occurred, it showed no consistent pattern among organization or year and therefore unlikely introduced any bias in time-dependent physical variables (e.g. temperature).

River Discharge

Flow at the eight Missouri and lower Yellowstone river gaging stations was above the pre-study 28 year reference 75th percentile discharge for many months during the year, and particularly during the study period (Table 6). Nineteen-ninety-seven was the highest flow year with 75- 100% of months between July and October exceeding the 1967-1995 75th percentile discharge at all gages. Flow within segments **7** and segments **12-27** also exceeded the 75th percentile pre-study period for 3 to 4 of the months between July and October in 1996.

Discharge was within the 25-75th pre-study range for most gages and months during 1998, except for segments 22-27 when it was often above the 75th percentile (Table 6).

Macrohabitats Sampled Relative to Availability in Segments

The number of macrohabitats present in a segment was dependent on climate (e.g., dry vs wet), channel-flood-plain geomorphology, and segment length. Segment length ranged from 30.2 km (3) to 191.5 km (8)

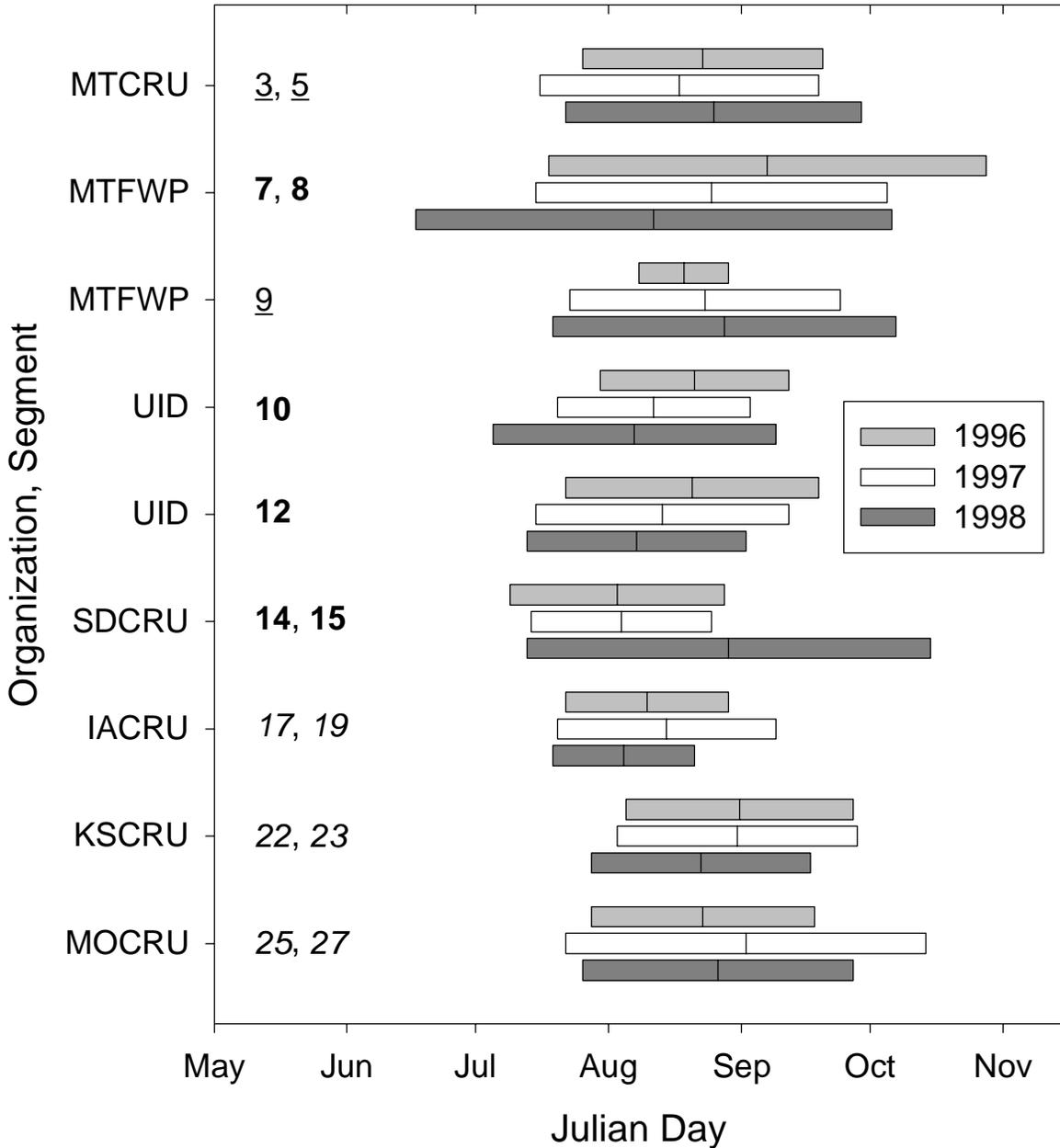


Figure 5. Physical variable sampling intervals for Missouri and lower Yellowstone rivers, 1996-1998. Vertical line in each box is the median sample date for each year. Organizations: MTCRU = Montana Cooperative Research Unit; MTFWP = Montana Fish, Wildlife and Parks; UID = University of Idaho; SDCRU = South Dakota Cooperative Research Unit; IACRU = Iowa Cooperative Research Unit; KSCRU = Kansas Cooperative Research Unit; MOCRU = Missouri Cooperative Research Unit.

Table 6. Median (50th percentile) annual (Jan-Dec) and July-October Missouri and Yellowstone river discharge (m^3/sec) at selected gaging stations for each of the 1996-1998 study years relative to the 25th, 50th, and 75th percentile discharges for the 1967-1995 pre-study period. Percent of months per year or per July-October during study years when median discharge was greater than the 1967-1995 75th percentile ($\% >75th$) and less than the 1967-1995 25th percentile ($\% <25th$) are shown.

Gage/interval	1967-1995 Percentile			50th Percentile		
	25th	50th	75th	1996	1997	1998
Landusky, MT, segment 5						
Jan-Dec	2,321	3,155	4,034	3,715	4,219	3,044
% >75th				25	33	8
% <25th				0	0	8
Jul-Oct	648	903	1,198	833	1,183	1,204
% >75th				0	75	25
% <25th				0	0	0
Wolf Point, MT, segment 7						
Jan-Dec	2,674	3,350	4,398	4,659	4,888	3,054
% >75th				58	42	0
% <25th				0	8	17
Jul-Oct	821	1,064	1,453	1,641	2,031	1,032
% >75th				100	75	0
% <25th				0	0	0
Sidney, MT, Yellowstone River, segment 9						
Jan-Dec	2,862	3,936	5,269	4,795	6,418	3,878
% >75th				33	83	8
% <25th				0	0	8
Jul-Oct	790	1,219	1,717	1,269	2,036	1,473
% >75th				0	100	0
% <25th				0	0	0
Bismarck, ND, segment 12						
Jan-Dec	6,480	7,966	9,691	10,422	12,180	7,578
% >75th				50	58	0
% <25th				8	17	0
Jul-Oct	2,079	2,563	3,262	4,098	5,650	2,409
% >75th				75	100	0
% <25th				0	0	0
Sioux City, IA, segment 17						
Jan-Dec	8,816	9,977	12,373	14,925	19,951	11,133
% >75th				92	100	33
% <25th				0	0	0
Jul-Oct	3,580	3,973	5,027	6,188	7,550	3,750
% >75th				100	100	0
% <25th				0	0	0

Table 6, continued.

	1967-1995 Percentile			50th Percentile		
	25th	50th	75th	1996	1997	1998
St. Joseph, MO, segment 22						
Jan-Dec	12,345	15,011	18,940	21,569	25,934	18,933
% >75th				83	100	50
% <25th				0	0	0
Jul-Oct	4,647	5,497	6,751	8,357	9,031	5,840
% >75th				100	100	0
% <25th				0	0	0
Boonville, MO, segment 25						
Jan-Dec	14,976	20,041	27,929	29,055	31,523	31,369
% >75th				67	75	83
% <25th				0	0	0
Jul-Oct	5,279	6,780	8,768	10,034	9,736	9,813
% >75th				100	75	75
% <25th				0	0	0
Hermann, MO, segment 27						
Jan-Dec	18,363	26,047	37,530	35,278	37,969	42,450
% >75th				67	50	75
% <25th				0	0	0
Jul-Oct	6,010	7,720	10,436	11,457	10,694	13,272
% >75th				100	75	100
% <25th				0	0	0

(Table 1) and averaged 108.1 km (± 45.1 km SD). Down river inter-reservoir segments and channelized river segments generally had more TRMs/km than least-altered segments. Least-altered and inter-reservoir segments generally contained more SCCs and SCNs per kilometer of channel than channelized segments (Table 7). The number of BENDS (i.e., combined CHXO, ISB, and OSB macrohabitats) was $\geq 0.33/\text{km}$ in segments 3-9 and ranged from 0.04 to 0.26/km in the remaining segments.

The proportion (mean \pm 1SD) of macrohabitats sampled of those available over all segments was lowest for BENDs: $31.3 \pm 27.3\%$, and highest for discrete macrohabitats: SCC: $54.2 \pm 33.6\%$, SCN: $65.1 \pm 38.3\%$, and TRM: $69.8 \pm 29.2\%$ (Table 7). None of the three TRMs present in segment 3 were sampled because their small size prevented access by boat (Table 2), a criterion set at the beginning of the study (Sappington et al. 1998). In contrast, 100% of SCCs, SCNs and TRMs present were sampled from several segments (Table 7).

We were able to sample the targeted number of replicate discrete macrohabitats per segment (sampled/targeted = 1.0) in only 7 of 45 cases because of their rarity or failure to meet design criteria, Figure 6). Consequently, the effect of discrete macrohabitats relative to continuous macrohabitats (i.e. BENDs) on means and variances of physical variables was smaller for some segments (e.g., 3, 17, 19, and 22), and larger for other segments (e.g., 7, 8, 9, 15, and 27, Figure 6). The maximum possible influence (sampled/targeted = 1.0) of all discrete macrohabitats was not observed on physical variables in any segment (i.e., $\text{SCC} + \text{SCN} + \text{TRM} = 3.0$ in Figure 6)

Trends of Physical Variables Among Segments, BENDs, and Macrohabitats

Patterns of physical variables were complex and differed depending on the variable. We first provide a longitudinal summary of physical variables whose differences were greatest among segments: temperature,

Table 7. Segment length, number of BENDs and macrohabitats present/segment, number of BENDs and macrohabitats/km of segment, number of BENDs and macrohabitats sampled/segment and percent of BENDs and macrohabitats present that were sampled. Numbers are totals for three years (1996-1998); divide by 3 to get mean number per year. BEND number equals number of CHXO, ISB, and OSB macrohabitats. See text for how variables were determined.

Segment	Length (km)	Variable	BEND/macrohabitat			
			BEND	SCC	SCN	TRM
<u>3</u>	30.2	Number present	39	18	18	3
		Number/km	0.43	0.20	0.20	0.03
		Number sampled	15	16	1	0
		Sampled/present (%)	38.5	88.9	5.6	0.0
<u>5</u>	118.8	Number present	138	111	15	0
		Number/km	0.41	0.33	0.04	0.00
		Number sampled	15	24	6	0
		Sampled/present (%)	10.9	21.6	40.0	-
7	94.9	Number present	105	99	12	14
		Number/km	0.37	0.35	0.04	0.05
		Number sampled	15	20	12	11
		Sampled/present (%)	14.3	20.2	100.0	78.6
8	191.5	Number present	192	204	60	18
		Number/km	0.33	0.36	0.10	0.03
		Number sampled	15	25	16	12
		Sampled/present (%)	7.8	12.3	26.7	66.7
<u>9</u>	114.2	Number present	141	141	66	3
		Number/km	0.41	0.41	0.19	0.01
		Number sampled	15	24	16	3
		Sampled/present (%)	10.6	17.0	24.2	100.0
10	48.3	Number present	16	22	10	3
		Number/km	0.11	0.15	0.07	0.02
		Number sampled	15	15	10	2
		Sampled/present (%)	93.8	68.2	100.0	66.7
12	136.8	Number present	16	30	12	8
		Number/km	0.04	0.07	0.03	0.02
		Number sampled	15	16	12	8
		Sampled/present (%)	93.8	53.3	100.0	100.0
14	72.4	Number present	36	57	12	18
		Number/km	0.17	0.26	0.06	0.08
		Number sampled	15	20	7	12
		Sampled/present (%)	41.7	35.1	58.3	66.7

Table 7, continued.

Segment	Length (km)	Variable	BEND/macrophabitat			
			BEND	SCC	SCN	TRM
15	91.7	Number present	48	81	8	14
		Number/km	0.17	0.29	0.03	0.05
		Number sampled	15	25	8	13
		Sampled/present (%)	31.3	30.9	100.0	92.9
17	113.9	Number present	81	1	0	21
		Number/km	0.24	<0.01	0.00	0.06
		Number sampled	15	1	0	17
		Sampled/present (%)	18.5	100.0	na	81.0
19	86.1	Number present	63	6	0	16
		Number/km	0.24	0.02	0.00	0.06
		Number sampled	15	6	0	16
		Sampled/present (%)	23.8	100.0	-	100.0
22	116.7	Number present	63	9	4	48
		Number/km	0.18	0.03	0.01	0.14
		Number sampled	15	2	4	19
		Sampled/present (%)	23.8	22.2	100.0	39.6
23	189.1	Number present	84	26	8	48
		Number/km	0.15	0.05	0.01	0.08
		Number sampled	15	15	1	17
		Sampled/present (%)	17.9	57.7	12.5	35.4
25	144.2	Number present	111	27	1	33
		Number/km	0.26	0.06	<0.01	0.08
		Number sampled	15	25	1	19
		Sampled/present (%)	13.5	92.6	100.0	57.6
27	80.4	Number present	51	27	19	12
		Number/km	0.21	0.11	0.08	0.05
		Number sampled	15	25	15	11
		Sampled/present (%)	29.4	92.6	78.9	91.7

turbidity and conductivity. We then report physical variables whose differences were greatest among macrohabitats within segments: depth, velocity, and substrate size (See *ANOVA Statistical Comparisons* for criteria used to define these groups). Means (calculated from transformed data) for BEND (1996-1998) were used as a reference to compare with SCC, SCN, and TRM discrete macrohabitats. Means from CHXOs (1996-1998) were compared with ISB and OSB

macrohabitats within BENDs. See Appendix Tables A1-A9 for a summary of physical variable means for macrohabitats within segments.

Temperature (Figure 7)

There was a gradual longitudinal increase of 5.5 °C in mean water temperatures during the study period in BENDs between segment 3 (21.5 °C) and segment 27 (27.0 °C). However, superimposed on this increase

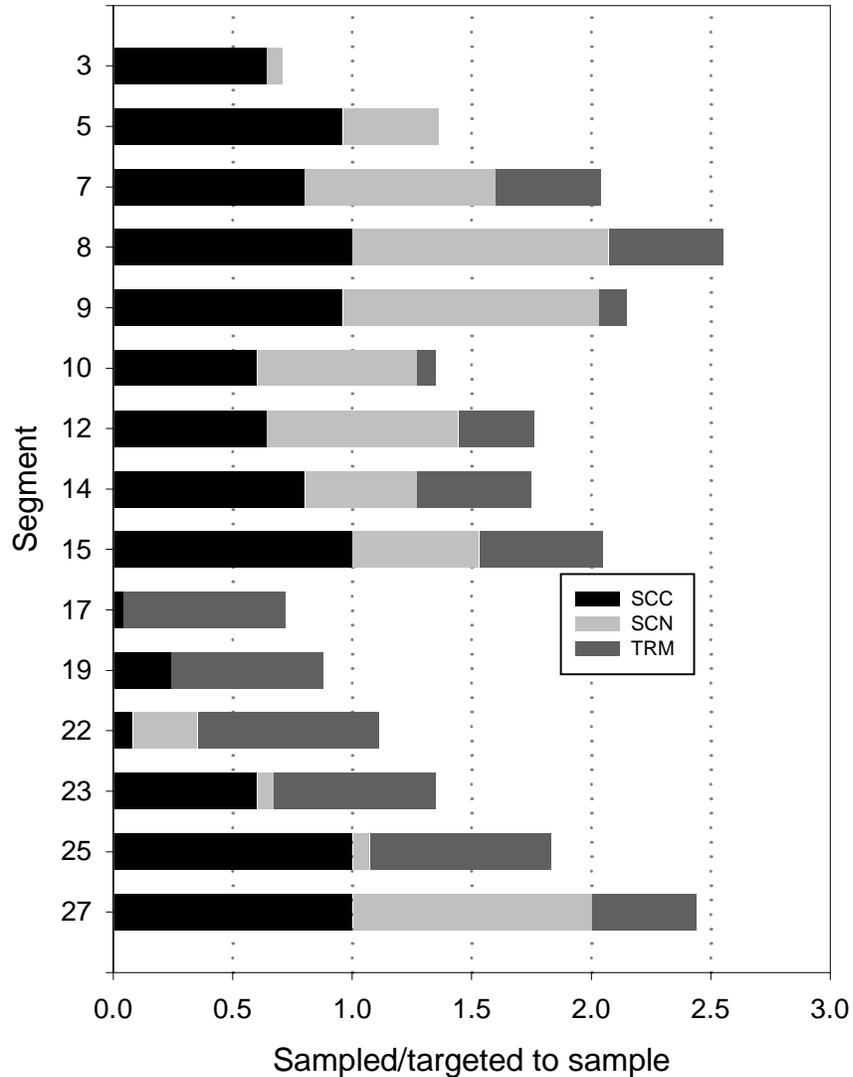


Figure 6. Ratio of number of replicate discrete macrohabitats sampled per segment to the number of replicates targeted to sample per segment over 1996-1998. Discrete macrohabitats include: secondary channel connected (SCC), secondary channel non-connected (SCN), and tributary mouth (TRM).

were abrupt temperature reductions in inter-reservoir segments below upper-basin reservoirs. Mean BEND temperature decreased 8.5 °C between segments 5 and 7, above and below Ft. Peck Lake, respectively, and 6.0 °C between segments 10 (20.8 °C) and 12 (14.8 °C), above and below Lake Sakakawea, respectively.

Temperature differences among macrohabitats averaged over all segments were always <1.0 °C. However, absence of gross temperature differences among macrohabitats was affected by large differences among segments (e.g., longitudinal temperature increases and reservoir related decreases). Mean temperature of SCC and SCN macrohabitats was ≥ 1.0 °C higher than

BENDs for inter-reservoir segments 7 and 8, and also ≥ 1.0 °C higher in TRMs than in BENDs for segments 7, 10 and 12. Tributary mouths were between 0.7 and 2.6 °C colder than BENDs in inter-reservoir segment 15 and in all channelized segments. Temperatures among CHXO, ISB, and OSB macrohabitats within BENDs were within ± 1.0 °C of each other in all but one segment (ISB > CHXO by 1.3 °C in segment 12).

Turbidity (Figure 8)

Mean turbidity in BENDs of least-altered segments 3 and 5 above Ft. Peck Lake ranged from 27 to 29 NTUs, decreased to 17 NTUs below Ft. Peck Lake and then

increased to an average of about 66 NTUs in segment 8. The Yellowstone River was the only tributary sampled in segment 10 and is a TRM-LRGE (Table 6, Sidney gage). It generally discharged highly turbid water (mean: 215 NTU) into the Missouri River (BEND mean: 201 NTU) at the uppermost end of segment 10, about 48 km above Lake Sakakawea. Secondary channels were less affected than BENDs by turbid water influx from the Yellowstone River with SCC's being somewhat clearer (105 NTU) and SCN's (58 NTU) providing the clearest water habitat in segment 10. Mean turbidity in BENDs declined to 8 NTUs in segment 12, below Lake Sakakawea, and to 5 NTUs in segment 14, below Lake Francis Case. Turbidity in SCCs was similar to BENDs, but SCNs were slightly more turbid (9-17 NTU) than BENDs in these inter-reservoir segments.

Mean turbidity in BENDs increased gradually over the 760 km from segment 15 (27 NTU), below Lewis and Clark Lake, to channelized segment 23 (129 NTU) and then nearly doubled to 206 NTU in channelized segment 25. Tributaries sampled from St. Joseph, Missouri (segment 22), to the Missouri River's terminus discharged clearer water (TRM means varied from: 47 to 62 NTU) than recorded in continuous macrohabitats (means varied from: 109 to 206 NTU). This was particularly apparent between segment 25 (mean: 206 NTU) and segment 27 (mean: 128 NTU) where mainstem mean turbidity decreased by 55%. Mean turbidity of SCC and SCN macrohabitats in these segments ranged between 32 and 159 NTUs less than in BENDs, with the greatest difference observed in segment 25. Secondary channels non-connected were less turbid than SCCs in

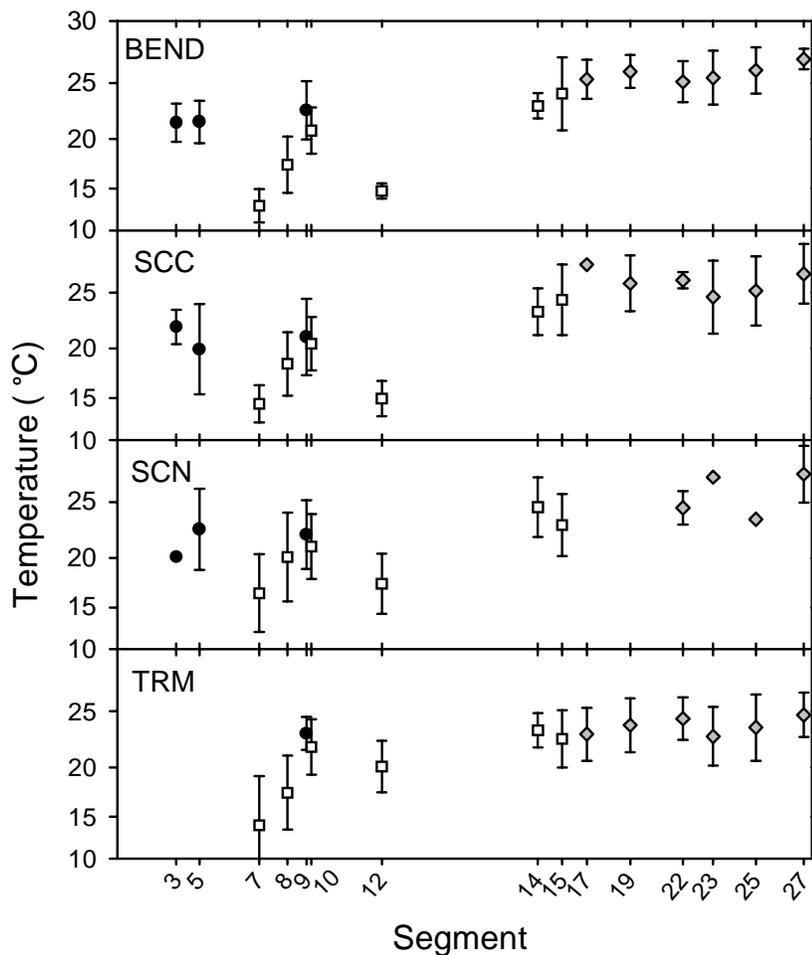


Figure 7. Mean (\pm 1SD) water temperature at BENDs and three discrete macrohabitats within segments of Missouri and lower Yellowstone rivers, 1996-1998. Solid circles: least-altered zone, open squares: inter-reservoir zone, shaded diamonds: channelized zone. Segments are spaced at midpoint km above Missouri River km 0.0. Data plotted are $x^{1.5}$ transformed.

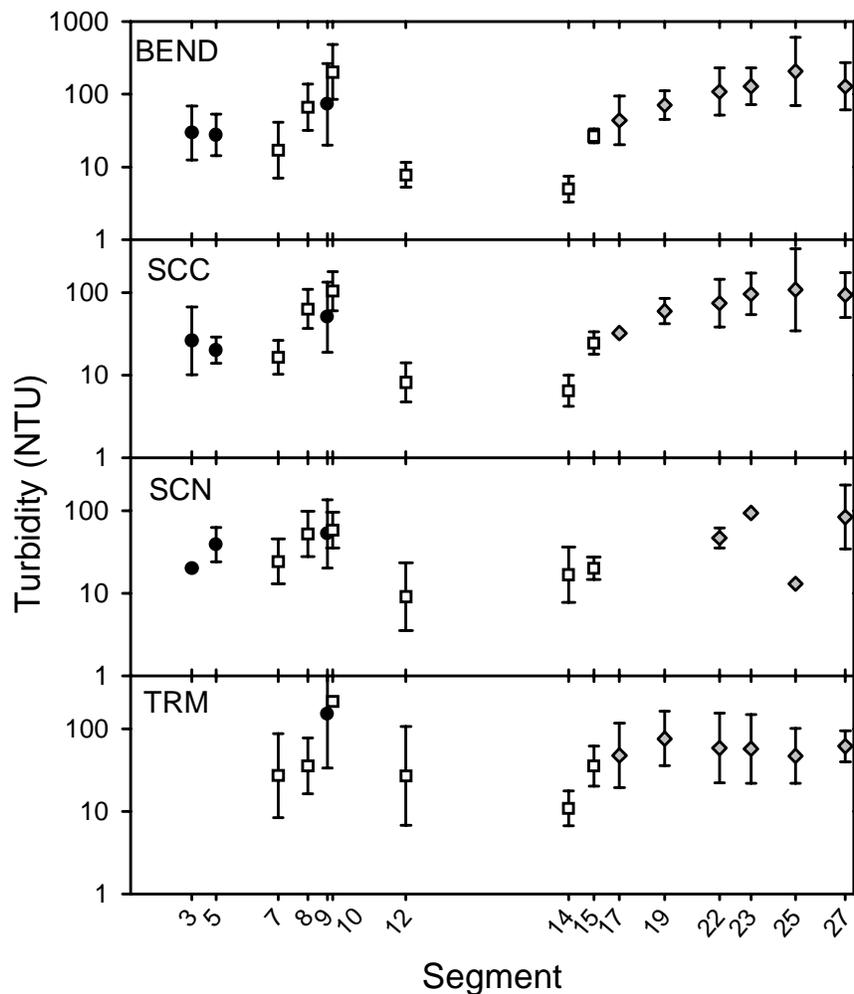


Figure 8. Mean (\pm 1SD) turbidity at BENDs and three discrete macrohabitats within segments of Missouri and lower Yellowstone rivers, 1996-1998. Solid circles: least-altered zone, open squares: inter-reservoir zone, shaded diamonds: channelized zone. Segments are spaced at midpoint km above Missouri River km 0.0. Data plotted are \log_{10} transformed.

segment 22 (mean SCC: 75 NTU, mean SCN: 47 NTU) and especially in segment 25 (mean SCC: 110 NTU, mean SCN: 13 NTU).

Differences in mean turbidity were generally <15 NTU among macrohabitats within BENDs except for segments 10 and 25 where differences were >20 NTU. Channel cross-overs (mean: 210 NTU) were slightly more turbid than ISBs (mean: 178 NTU) or OSBs (mean: 133 NTU) in segment 10 and also in segment 25 (mean turbidity, NTU: CHXO = 226; ISB = 187; OSB = 202).

Conductivity (Figure 9)

Least-altered segments 3 (435 $\mu\text{S}/\text{cm}$) and 5 (402 $\mu\text{S}/\text{cm}$) exhibited the lowest BEND mean conductivity. Missouri River mean conductivity increased below Ft.

Peck Lake to about 600 $\mu\text{S}/\text{cm}$, associated with reservoir evaporation and influx of higher conductivity tributary water in segments 7 (mean: 1,105 $\mu\text{S}/\text{cm}$) and 8 (mean: 830 $\mu\text{S}/\text{cm}$). Tributary inflow of low conductivity water, largely from the high discharge Yellowstone River, (mean BEND: 508 $\mu\text{S}/\text{cm}$, mean TRM: 479 $\mu\text{S}/\text{cm}$) diluted Missouri River BEND conductivity in segment 10 (mean: 469 $\mu\text{S}/\text{cm}$). Tributary inflow of high conductivity water (TRM mean range: 916-1,064 $\mu\text{S}/\text{cm}$) and reservoir evaporation subsequently increased conductivity in inter-reservoir segments 12, 14, and 15 (BEND means: 494, 865, 834 $\mu\text{S}/\text{cm}$, respectively). Channelized river BEND conductivity decreased gradually from segments 17 to 27 (mean: 17 - 827 $\mu\text{S}/\text{cm}$, 27 - 674 $\mu\text{S}/\text{cm}$) with influx of lower conductivity water from several large tributaries (mean

range: 485-662 $\mu\text{S}/\text{cm}$).

Differences in mean conductivity between BEND and SCC macrohabitats were $<50 \mu\text{S}/\text{cm}$. Secondary channel non-connected macrohabitats in segments 8, 9, 10, 14 and 23 exhibited mean conductivities $\geq 100 \mu\text{S}/\text{cm}$ higher than BENDs. Differences in mean conductivity between TRMs and BENDs were variable as described above and often higher or lower by $>150 \mu\text{S}/\text{cm}$ (10 of 15 segments). Variability of TRM conductivity within a segment was also large, as illustrated by the high standard deviation in Figure 9. Differences in mean conductivity among macrohabitats within BENDs were generally less than $50 \mu\text{S}/\text{cm}$.

Water Depth (Figure 10)

A progressive longitudinal increase in BEND mean

depth was observed from least-altered segment 3 (BEND mean: 1.3 m) to channelized segment 17 (BEND mean: 4.5 m). Mean BEND depth varied <0.4 m from segment 17 through segment 27 (mean range: 4.7 - 4.9m). No longitudinal pattern in mean depth was observed for discrete macrohabitats among segments.

BENDs were generally deeper than SCC, SCN, or TRM macrohabitats, often by >1.0 m (Figure 11). Inside bends were the shallowest macrohabitat within BENDs, and CHXO and OSB mean depths were generally similar. Secondary channels (SCC and SCN) were usually the shallowest macrohabitat sampled.

Current Velocity (Figure 12)

Mean BEND current velocity was highest in channelized segments, peaking at 1.3 m/s in segment 19. No

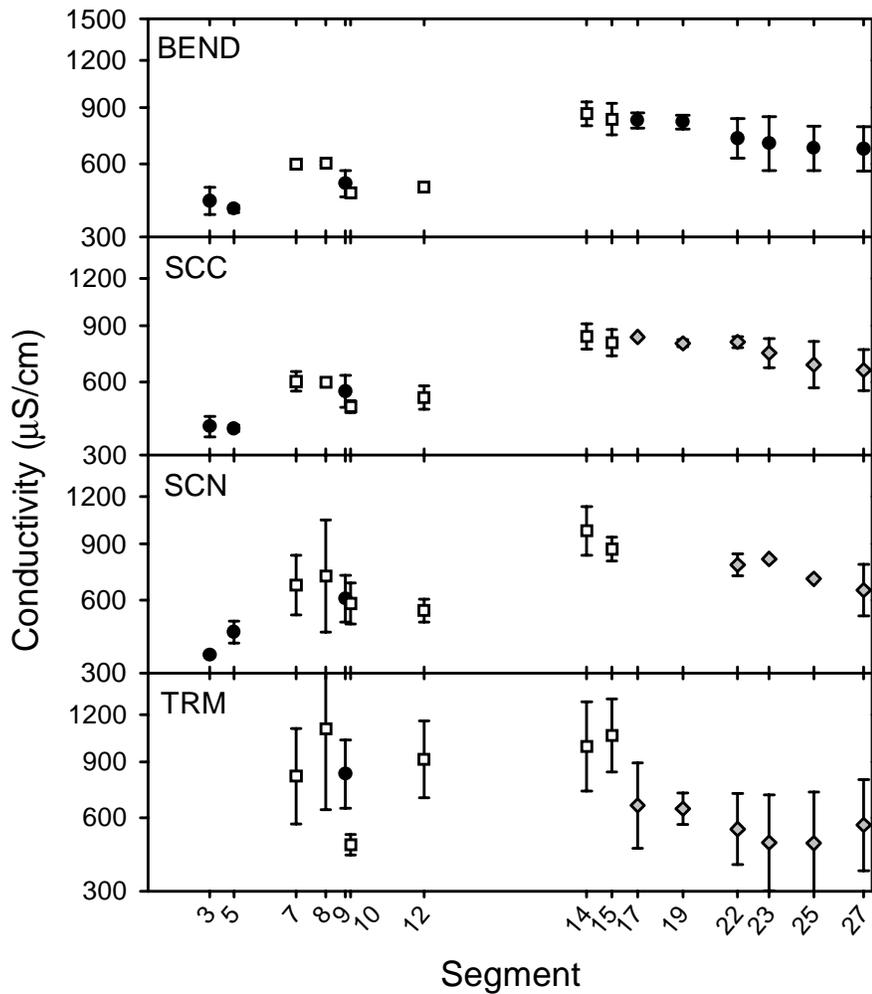


Figure 9. Mean ($\pm 1\text{SD}$) water conductivity at BENDs and three discrete macrohabitats within segments of Missouri and lower Yellowstone rivers, 1996-1998. Solid circles: least-altered zone, open squares: inter-reservoir zone, shaded diamonds: channelized zone. Segments are spaced at midpoint km above Missouri River km 0.0. Data plotted are square-root transformed.

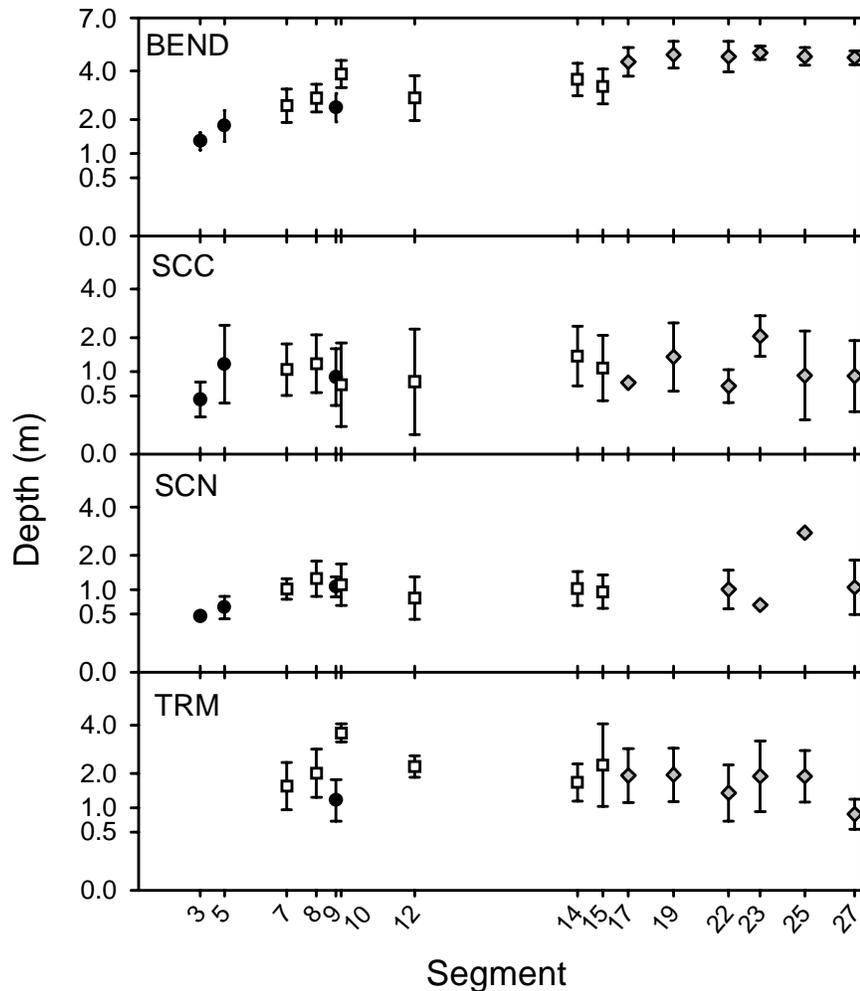


Figure 10. Mean (\pm 1SD) water depth at BENDs and three discrete macrohabitats within segments of Missouri and lower Yellowstone rivers, 1996-1998. Solid circles: least-altered zone, open squares: inter-reservoir zone, shaded diamonds: channelized zone. Segments are spaced at midpoint km above Missouri River km 0.0. Data plotted are square-root transformed.

patterns among segments were apparent in discrete macrohabitats. Mean BEND velocity was generally higher than in SCC, SCN, or TRM macrohabitats (Figure 11). Often no current was recorded in SCN and TRM macrohabitats, although velocity was quite variable within these macrohabitats in the channelized zone as evidenced by the high standard deviation. Velocities were generally similar among CHXO and OSB macrohabitats and higher than in ISBs (Figure 11), except in the channelized zone where CHXO mean velocities ranged from 0.2 to 0.4 m/s faster than in OSB macrohabitats.

Substrate Composition (Appendix Tables A1-A9)

Geometric mean particle size in BENDs was generally

largest in channelized segments (range of means: 9.4-15.0 mm) and also largest in BENDs when compared with SCC, SCN, and TRM macrohabitats among segments (Table 8). However, least-altered segment 3 was distinctive in that it exhibited the largest BEND mean particle size of any segment and also showed a disproportionately large mean particle size in the SCC macrohabitat compared with other segments (Table 8). Mean particle size in BENDs was lowest in inter-reservoir segments (range of BEND means: 1.4-3.3 mm). Geometric mean particle sizes were higher than ISBs and about equal in CHXO and OSB macrohabitats within BENDs of the least-altered zone, whereas average particle size was much greater in OSBs than in CHXOs for channelized segments (Table 8). Secondary

channels non-connected and TRMs exhibited the smallest geometric mean particle sizes over all segments and macrohabitats.

Mean percent gravel in BENDs composed $\geq 10\%$ of substrate size classes in six segments: least-altered segments 3 (51%), 5 (31%) and 9 (36%), inter-reservoir segments 7 (13%) and 12 (12%) below Ft. Peck Lake and Lake Sakakawea, respectively, and channelized segment 19 (18%) below the Platte River (Figure 13). Mean percent gravel in SCCs was 73% (3), 13% (5), and 21% (9) in least-altered segments, but $< 8\%$ in SCCs within other segments (Figure 13). Sand was the dominant BEND substrate size class in all segments, except for segment 3 (mean: 35%), and constituted $\geq 65\%$ of

the three size classes in all but least-altered segments 3, 5, and 9. Mean percent silt was $< 20\%$ of the three substrates in all segments, but varied from 11 to 18 % in segments 3 (12%), 14 (13%), 19 (11%), and 22-27 (18%).

The mean proportion of gravel among macrohabitats was $> 5\%$ in BENDs and SCCs (Figure 14), and all macrohabitats within BENDs contained some gravel. However, sand was the predominant particle size present in BEND and SCC macrohabitats (mean: $> 60\%$), as well as CHXOs, ISBs, and OSBs within BEND. Substrate in SCN and TRM macrohabitats was composed largely of silt (mean: $> 80\%$, Figure 14).

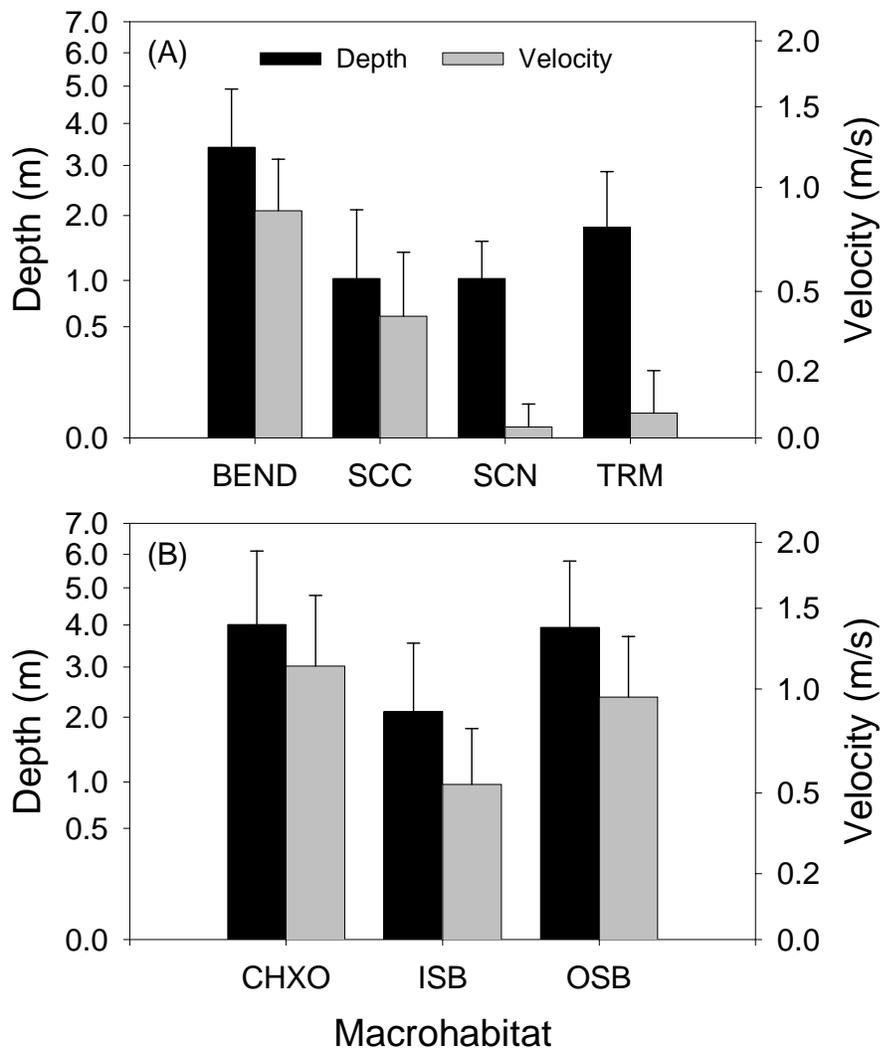


Figure 11. Mean (\pm 1SD) water depth and current velocity in: (A) BENDs and secondary channel connected (SCC), secondary channel non-connected (SCN), and tributary mouth (TRM) macrohabitats; (B) channel cross-over (CHXO), inside bend (ISB), and outside bend (OSB) macrohabitats within BENDs, among segments of Missouri and lower Yellowstone rivers. Depth data are square-root transformed and velocity data are $\log_{10}(x+1)$ transformed.

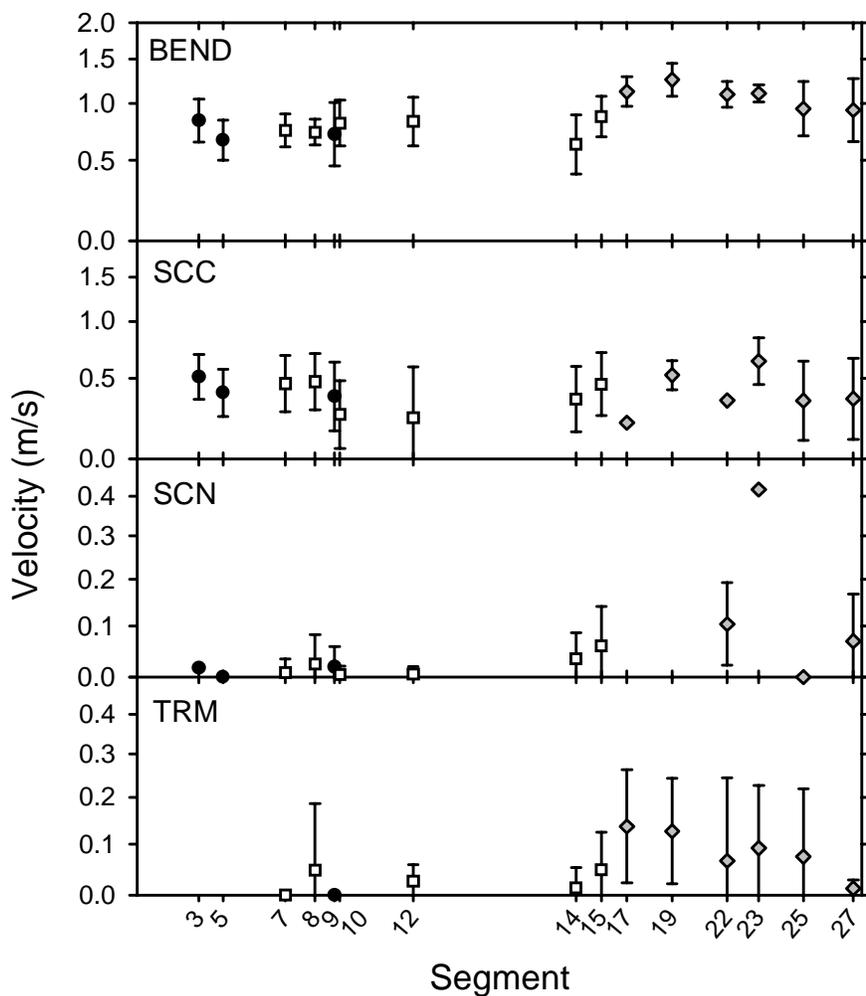


Figure 12. Mean (\pm 1SD) current velocity at BENDs and three discrete macrohabitats within segments of Missouri and lower Yellowstone rivers, 1996-1998. Solid circles: least-altered zone, open squares: inter-reservoir zone, shaded diamonds: channelized zone. Segments are spaced at midpoint km above Missouri River km 0.0. Variable Y-axis scales reflect overall magnitude differences among BENDs and macrohabitats. Data plotted are $\log_{10}(x+1)$ transformed.

ANOVA Statistical Comparisons

As indicated previously, differences in physical variables among segments were examined by nesting BENDs and macrohabitats into two models: a BEND-SCC-SCN-TRM model containing BEND and the discrete macrohabitats, and a CHXO-ISB-OSB model containing only the continuous macrohabitats within BENDs. Each model was analyzed independently. Most of the main and interaction effects for all physical variables were significantly different (3-way ANOVA) due in part to the large sample size and consequent statistical power. However, variance decomposition revealed that only a few effects accounted for most of the variance attributable to the BEND-SCC-SCN-TRM model (Table 9) and also for the CHXO-ISB-OSB model (Table 10).

For example, Table 9 shows that the BEND-SCC-SCN-TRM model accounted for about 75% of the variability observed in water temperature and the Type III partial sums-of-squares for segment contributed about 45%; no other source of variation (i.e., year, BEND/macrohabitat, or any of the four interactions) was greater than 4.4%. Similar results were observed for temperature in the CHXO-ISB-OSB model (Table 10).

Variance decomposition within the BEND-SCC-SCN-TRM model indicated that most physical variables differed at either the segment or macrohabitat spatial scale. For example, Table 9 shows that between about 25% and 45% of the variance for temperature, turbidity, and conductivity was at the segment scale, whereas between about 33% and 50% of the variability in depth, velocity,

% sand, % silt, and geometric mean particle size was at the BEND/macrohabitat scale. Observed variation was about equally divided between segments and BENDs/macrohabitats only for gravel (10.7-11.9%). Conductivity was the only physical variable in the BEND-SCC-SCN-TRM model where any interaction was $\geq 10\%$ (Table 9). Conductivity in macrohabitats was affected by segment location and/or segment differences in conductivity were influenced by macrohabitats.

Results were somewhat different for the CHXO-ISB-OSB model, as segment main effects were largest for turbidity, temperature, conductivity, % gravel, and % sand and macrohabitats dominated only for % silt (Table 10). Both segment and macrohabitat (i.e., CHXO, ISB, OSB) contributed $\geq 10\%$ of total variance for depth, velocity, and geometric mean particle size (Table 10). Segment and macrohabitat interactions were important for velocity and all substrate measures except % gravel.

Differences among physical variables were generally influenced less by year relative to segments and macrohabitats. Year, or the interaction of year and segment, or year and BEND/macrohabitat, accounted for less than 10% of overall variance for all physical variables in the BEND-SCC-SCN-TRM and CHXO-ISB-OSB models. This result indicates that differences in sampling intervals among organizations and years

(Figure 5) had a small effect on results. Statistical analyses were therefore directed at spatial comparisons.

This is not to imply that all physical variable differences among years or interactions between year and spatial habitat units were small or non-significant. For example, turbidity in segment 9 and in several inter-reservoir segments and macrohabitats was 2 to >8 times higher in 1998 than in 1996 and was similarly less in selected channelized macrohabitats in 1997 compared with 1996 or 1998 (Appendix Table A4).

Segment Comparisons: BEND-SCC-SCN-TRM Model

Differences in physical variables among segments for the BEND-SCC-SCN-TRM model include effects of continuous macrohabitats ISB, OSB, and TRM, collectively represented by BEND, and the individual discrete macrohabitats SCC, SCN, and TRM (Table 2). Results of planned segment contrasts from this model provide a composite of physical conditions evaluated among the six macrohabitats.

Upper Missouri and lower Yellowstone rivers (Tables 11 and 12). Comparisons of three segment groups were made for this section of the study area (Table 5, A-C). First, we evaluated if physical variables differed between least-altered Missouri River segments 3 and 5 and least-altered lower Yellowstone River segment 9

Table 8. Averages of geometric mean substrate particle size (mm, calculated from \log_{10} transformed data) for macrohabitats within least-altered, inter-reservoir, and channelized segments of Missouri and lower Yellowstone (9) rivers, 1996-1998. Dash (--) indicates macrohabitat was absent in segment or was not sampled.

Segment	BEND	SCC	SCN	TRM	BEND		
					CHXO	ISB	OSB
3	16.2	14.1	0.13	--	14.8	10.8	15.3
5	5.9	0.9	0.06	--	4.9	3.5	5.4
7	2.3	1.3	0.05	0.05	1.9	1.3	3.0
8	1.4	0.6	0.08	0.05	1.2	0.9	1.6
9	5.7	2.2	0.11	0.04	5.4	2.9	7.0
10	1.4	0.5	0.04	0.83	1.2	0.6	1.7
12	3.3	0.5	0.07	0.14	2.3	0.9	6.5
14	2.0	1.1	0.30	0.11	1.0	0.9	2.2
15	3.1	1.4	0.21	0.06	1.4	1.1	4.4
17	11.7	0.1	--	0.10	1.1	5.4	19.8
19	13.6	0.6	--	0.05	2.2	5.4	19.4
22	13.4	0.2	0.04	0.07	1.1	8.8	25.2
23	15.0	0.9	0.03	0.05	1.2	10.9	32.0
25	9.4	0.7	0.05	0.04	1.1	1.3	23.5
27	11.4	0.9	0.30	0.05	1.1	6.5	18.7

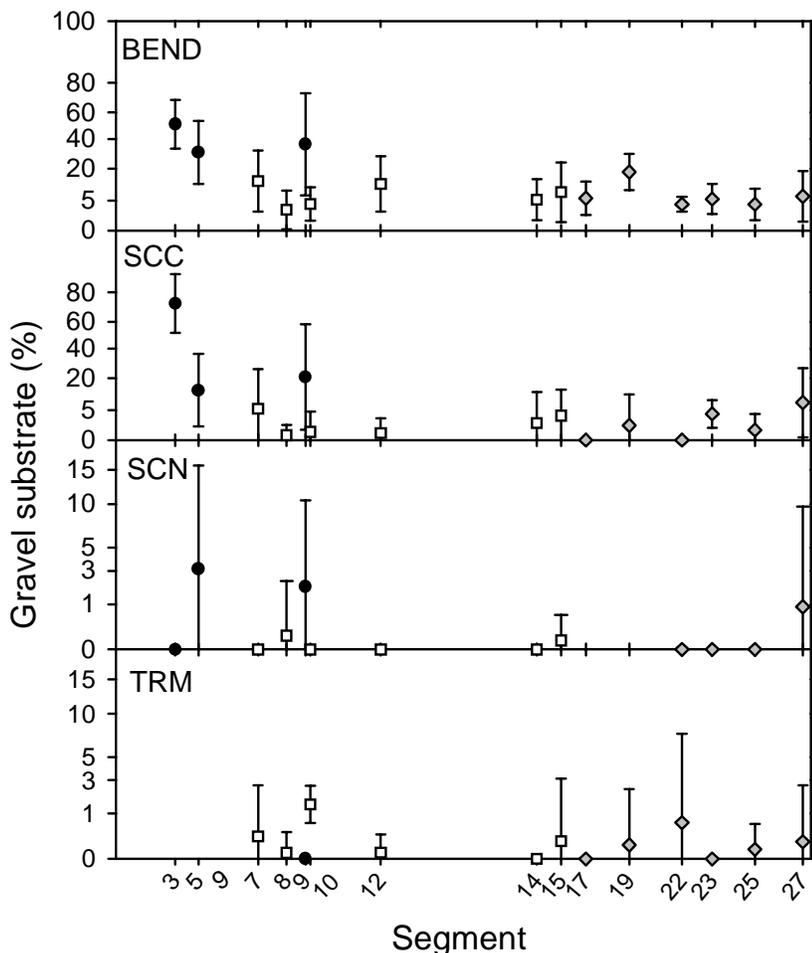


Figure 13. Mean (\pm 1SD) percent gravel substrate at BENDs and three discrete macrohabitats within segments of Missouri and lower Yellowstone rivers, 1996-1998. Solid circles: least-altered zone, open squares: inter-reservoir zone, shaded diamonds: channeled zone. Segments are spaced at midpoint km above Missouri River km 0.0. Variable Y-axis scales reflect overall magnitude differences among BENDs and macrohabitats. Data plotted are arcsin square-root transformed.

(A). Next, we tested if the approximately 142 km of least-altered Missouri River above Ft. Peck Lake (segments 3 and 5) differed from the ca. 286 km of inter-reservoir segments (7 and 8) between Ft. Peck Dam and the Yellowstone River (B). Third, we evaluated if these two inter-reservoir segments (7 and 8) differed from nearby least-altered lower Yellowstone River segment 9 (C).

Current velocity, % gravel, and geometric mean particle size were significantly higher, whereas turbidity and conductivity were significantly lower in least-altered Missouri River segments 3 and 5 than in least-altered lower Yellowstone River segment 9. Turbidity and conductivity differences were most meaningful as they contributed $\geq 2.0\%$ of total variance in the BEND-SCC-SCN-TRM model.

Mean water temperatures during the 3rd year, seasonal sampling period differed little between the two least-altered Missouri River segments above Ft. Peck Lake (3 and 5) and least-altered Yellowstone River segment 9 (0.7°C). However, water temperature averaged between 4.5 and 5.2°C less in the two Missouri River inter-reservoir segments below (7 and 8) than above (3 and 5) Ft. Peck Lake or in the lower Yellowstone River (9). Additionally, water temperature was lower in Missouri River inter-reservoir segments 7 and 8, above the confluence with the Yellowstone River, than in lower Yellowstone River least-altered segment 9. All these differences were significant and accounted for $\geq 2\%$ of overall variance in the contrasts.

Mean percent of gravel (1.4%) in Missouri River inter-reservoir segments 7 and 8, below Ft. Peck dam,

was also significantly lower than in either Missouri River least-altered segments above the dam (33.0%) or in lower Yellowstone River (15.2%) least-altered segment 9. This reduction in amount of gravel resulted in a corresponding increase in proportion of sand and silt and a reduction in geometric mean substrate particle size.

Conductivity was the only non-substrate physical variable to significantly increase when comparing Missouri River segments above and below Ft. Peck

Lake. Mean conductivity rose by 66% comparing inter-reservoir segments 7 and 8 (683 S/cm) with least-altered segments 3 and 5 (411 S/cm).

Three-zone: least-altered, inter-reservoir, and channelized (Table 13). Here we contrasted physical variables over the entire study area divided into three zones: least-altered -- segments 3, 5 and 9, inter-reservoir -- segments 7, 8, 10, 12, 14, and 15, and channelized --

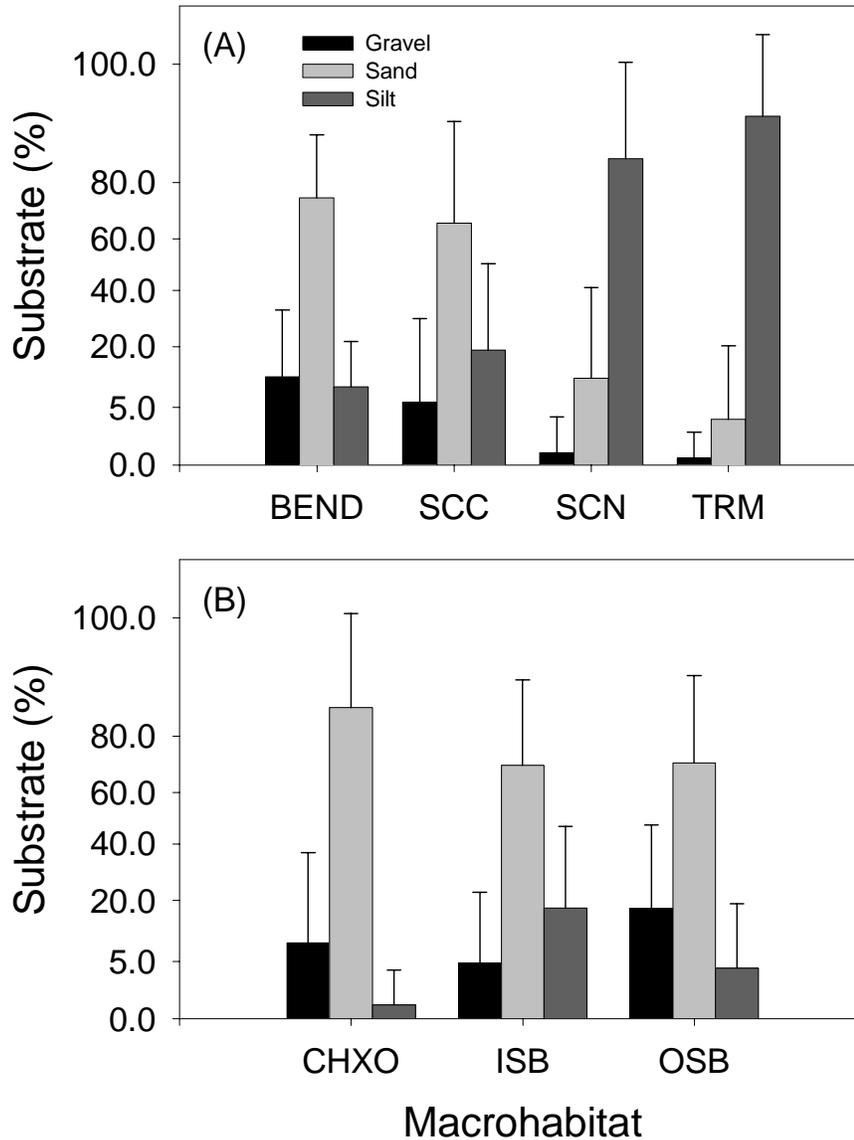


Figure 14. Mean (\pm 1SD) of substrate size classes among segments of Missouri and lower Yellowstone rivers in: (A) BENDs and secondary channel connected (SCC), secondary channel non-connected (SCN), and tributary mouth (TRM) macrohabitats; (B) channel cross-over (CHXO), inside bend (ISB), and outside bend (OSB) macrohabitats within BENDs. Data are arcsin square-root transformed.

Table 9. Variance decomposition for the overall analysis of variance in the BEND-SCC-SCN-TRM model with main effects of year, segment, and BEND/macrohabitat (BEND, SCC, SCN, TRM) and their two- and three-way interactions summarized as percent of the total sum of squares for each of nine physical variables using Type III partial sums of squares. Effects and interactions accounting for $\geq 10.0\%$ of the total variance are shown in **bold**.

Physical variable	Main effects					Interactions		
	Model	Year	Segment	BEND/ Macrohabitat	Year * segment	Year * BEND/ macrohabitat	Segment * BEND/ macrohabitat	Year * segment * BEND/macrohabitat
Depth (m)	71.38	0.30	4.70	33.50	1.36	0.54	8.33	2.42
Velocity (m/s)	83.66	0.01	2.37	50.18	0.83	0.34	3.05	1.55
Turbidity (NTU)	73.78	1.38	29.26	0.80	6.48	0.77	8.02	5.09
Temperature (°C)	75.05	1.16	44.58	0.31	4.41	0.15	3.78	3.29
Conductivity ($\mu\text{S}/\text{cm}$)	73.50	0.14	25.33	0.91	6.24	0.34	20.54	4.20
Gravel (%)	64.19	0.04	10.66	11.93	1.06	0.36	6.60	2.36
Sand (%)	75.96	0.24	4.79	35.16	0.76	0.29	4.85	2.89
Silt (%)	79.36	0.15	2.01	41.53	1.05	0.24	3.98	2.13
Geometric mean (mm)	78.24	0.02	1.88	42.88	1.01	0.26	5.61	2.41

Table 10. Variance decomposition for the overall analysis of variance in the CHXO-ISB-OSB model with main effects of year, segment, and macrohabitat (CHXO, ISB, and OSB) and their two- and three-way interactions summarized as percent of the total sum of squares for each of nine physical variables using Type III partial sums of squares. Effects and interactions accounting for $\geq 10.0\%$ of the total variance are highlighted in **bold**.

Physical variable	Model	Main effects				Interactions			
		Year	Segment	Macrohabitat	Year * segment	Year * macrohabitat	Segment * macrohabitat	Year * segment * macrohabitat	
Depth (m)	80.37	2.48	43.03	25.59	1.82	0.44	4.36	3.18	
Velocity (m/s)	76.40	0.34	15.25	39.56	4.61	0.09	14.22	3.28	
Turbidity (NTU)	79.47	1.93	65.33	0.04	9.78	0.16	0.58	0.88	
Temperature (°C)	83.43	1.32	78.19	0.03	3.00	0.02	0.23	0.41	
Conductivity ($\mu\text{S}/\text{cm}$)	84.71	2.36	75.61	0.19	4.57	0.11	1.08	0.74	
Gravel (%)	50.30	0.36	32.57	6.75	3.67	0.20	3.77	2.83	
Sand (%)	52.60	0.21	24.45	8.07	5.51	0.16	10.27	3.48	
Silt (%)	64.38	0.34	6.13	28.68	6.52	0.26	16.50	5.54	
Geometric mean (mm)	63.95	0.23	22.19	16.38	5.38	0.46	14.40	4.47	

Table 11. Physical variable means (from transformed data) for the BEND-SCC-SCN-TRM model contrasts among six Missouri (MOR) and lower Yellowstone (YSR) river segment groups. Similar suffix letters denote pairwise group contrasts within rows that were not significantly different at $P \leq 0.0024$. Contrasts not significantly different between inter-reservoir segments below Ft. Peck Lake to Yellowstone River and least-altered Missouri River (contrast B, Table 5), or least-altered lower Yellowstone River (contrast C, Table 5) segment groups are denoted by x's and y's, respectively. See Table 5 for description of contrasts.

Physical variable	Segment groups				
	Least-altered MOR	Least-altered YSR	Inter-reservoir below Ft. Peck Lake to YSR	Inter-reservoir w/o segment 15, below Lewis & Clark	Segment below Lewis & Clark Lake
	3, 5	9	7, 8	7, 8, 10, 12, 14	15
Depth (m)	1.1a	1.3aby	1.6y	1.7bc	1.8bcd
Velocity (m/s)	0.50a	0.32by	0.32y	0.32bc	0.43a
Turbidity (NTU)	25.6ax	59.7b	34.6x	25.0ac	26.7abc
Temperature (°C)	21.2a	21.9ab	16.7	18.7	23.8b
Conductivity (µS/cm)	411	569	683	670a	872
Gravel (%)	33.0	15.2a	1.35	1.3b	2.5abc
Sand (%)	25.5a	35.3aby	49.1y	52.0c	3.1bc
Silt (%)	29.1a	35.3aby	43.3y	40.4abc	27.3abc
Geometric mean (mm)	3.15	1.00a	0.34	0.43ab	0.69abc
					Channelized 17, 19, 22, 23, 25, 27

segments 17, 19, 22, 23, 25, and 27. All pairwise comparisons for the nine physical variables among the three river zones were significantly different except for % gravel substrate between inter-reservoir and channelized zones and % silt substrate between least-altered and inter-reservoir zones. The least-altered zone had the shallowest water depths, lowest conductivity, and lowest percent of sand and silt in substrates, but the highest % gravel and geometric mean particle size. The inter-reservoir zone exhibited lowest water velocity, turbidity, water temperature, % gravel substrate, and geometric mean particle size. Segments in the channelized zone had the deepest water, highest turbidity, and highest % silt substrate. Water depth (Figure 10), turbidity (Figure 8), water temperature (Figure 7), conductivity (Figure 9), and % gravel substrate (Figure 13) were physical variables that showed the most important differences among the three zones based on variance decomposition. Turbidity and temperature differences between inter-reservoir and channelized zones explained 12.5 % and 14.3 %, respectively, of overall variance. Between 7.9 % and 12.5% of total variability in conductivity and % gravel was observed between the least-altered and the other two zones.

Reservoir related (Table 14). Differences in physical variables in the segment directly above and the segment immediately below Ft. Peck Lake (5 vs 7, E), Lake Sakakawea (10 vs 12, G), and Lewis and Clark Lake (14 vs 15, H) were evaluated. Also, we tested for differences between the combined inter-reservoir segments below Ft. Peck Lake to the Yellowstone River (7 and 8) and the inter-reservoir segment below the Yellowstone River (10, F). Lastly, we compared inter-reservoir segment 15, below Lewis and Clark Lake with the first channelized river segment (17, I).

Mean water depths were not significantly different between segments above and below any of the reservoirs compared (exclusive of the tailwater area). Current velocity, % gravel, and % sand differed significantly in one inter-reservoir comparison each, but none contributed $\geq 2\%$ of total variance among contrasts. Water temperature, conductivity, and turbidity were physical variables showing the most significant differences in Missouri River segments above and below Ft. Peck Lake and above and below Lake Sakakawea. There was no significant difference in water temperature or conductivity above and below Lewis & Clark Lake.

Mean water temperature decreased 6.5 °C between segments 5 and 7, above and below Ft. Peck Lake, respectively. Missouri River regained lost heat by the time it reached segment 10, above Lake Sakakawea (20.8 °C), then mean temperature decreased 4.4 °C in segment 12 below Garrison Dam (Figure 7). Percent of

total variance for the segment 10 and 12 contrast was $< 2.0\%$ in the BEND-SCC-SCN-TRM model.

Conductivity increased significantly by 61% in segment 7 below Ft Peck Dam, relative to segment 5 above the reservoir. It then decreased significantly by 29% between segments 8 and 10 with influx of Yellowstone River water above Lake Sakakawea. Both these differences contributed $\geq 2\%$ of BEND-SCC-SCN-TRM model variance. Below Lake Sakakawea conductivity increased significantly by 15% in segment 12, but this rise did not account for $\geq 2\%$ of model variance (Figure 9).

Turbidity was not significantly different above (segment 5) and below Ft. Peck Lake (segment 7), but increased 115% between segments 8 and 10 with influx of Yellowstone River water (Figure 8). Passage of water through Lake Sakakawea reduced mean turbidity from 119 NTUs to 10 NTUs in segment 12. This reduction in turbidity accounted for more variability in above-below reservoir contrasts than any other comparison. There was no significant change in turbidity between segments 12 and 14 (755 km distance), although we did not measure physical variables between lakes Oahe, Sharpe, and Francis Case. Turbidity significantly increased from 7.3 NTUs in segment 14 above Lewis & Clark Lake to 26.7 NTUs in segment 15 below the reservoir.

Water depth, current velocity, turbidity, water temperature, and % silt all increased between unchannelized inter-reservoir segment 15, below Lewis and Clark Lake, and the first channelized river segment (17), whereas conductivity and % sand decreased. However, none of these differences were statistically significant, nor did any contribute $> 0.71\%$ of the variability recorded among planned contrasts.

Five-zone (Table 11). This analysis divided the three zones previously described in five zones (Table 5, J) to segregate and highlight two somewhat unique segments: 9 and 15. Least-altered lower Yellowstone River segment 9 was partitioned from least-altered Missouri River segments 3 and 5, and the only “inter-reservoir” segment without a reservoir down river (15) was separated from the five segments between reservoirs (7, 8, 10, 12, and 14).

These contrasts showed that least-altered Missouri River segments 3 and 5 contained the highest percent gravel and the lowest conductivity, whereas least-altered lower Yellowstone River segment 9 was a large source of turbidity to the upper Missouri River. Segment 9 also contained a large percentage of gravel relative to down-river inter-reservoir segments with the exception of segment 15. Segments 9 and 15 were not significantly different in any physical variable, except for conductivity.

Table 12. Statistically significant ($P \leq 0.0024$) pairwise contrasts for the BEND-SCC-SCN-TRM model for selected Missouri (MOR) and lower Yellowstone (YSR) river segment groups whose Type III partial sums of squares accounted for $\geq 2.0\%$ of the overall contrasts in the ANOVA. Percent of total variance explained for each pairwise contrast is within parentheses. See Table 5 for description of contrasts.

Segment group	Least-altered YSR 9	Inter-reservoir below Ft. Peck Lake to YSR 7, 8	Inter-reservoir w/o segment 15, below Lewis & Clark 7, 8, 10, 12, 14	Segment below Lewis & Clark Lake 15	Channelized 17, 19, 22, 23, 25, 27
Least-altered MOR 3, 5	turbidity (2.1) conductivity (3.3)	temperature (6.2) conductivity (11.3) % gravel (11.4) geometric mean (3.6)	temperature (2.1) conductivity (11.8) % gravel (14.3)	conductivity (18.3) % gravel (7.5)	depth (4.9) temperature (3.9) turbidity (4.3) conductivity (10.8) % gravel (12.7)
Least-altered YSR 9		temperature (6.5) % gravel (2.5)	temperature (2.6) turbidity (3.3) % gravel (3.2)		temperature (2.2) % gravel (2.6)
Inter-reservoir w/o segment 15, below Lewis & Clark 7, 8, 10, 12, 14				velocity (2.3) temperature (5.4) conductivity (4.0)	temperature (28.4) turbidity (11.3)
Segment below Lewis & Clark Lake 15					turbidity (4.3) conductivity (4.4)

Table 13. Physical variable means (from transformed data) for BEND-SCC-SCN-TRM model contrasts among least-altered (LA) Missouri and lower Yellowstone river, Missouri River inter-reservoir (IR), and channelized (CH) zone segment groups and percent of overall ANOVA variance each pairwise contrast accounted for. Similar suffix letters denote pairwise zone contrasts in rows that were not significantly different at $P \leq 0.0024$. Significantly different contrasts where the percent variance was $\geq 2.0\%$ are in **bold**.

Physical variable	Zone/segment			Percent variance		
	Least-altered 3, 5, 9	Inter-reservoir 7, 8, 10, 12, 14, 15	Channelized 17, 19, 22, 23, 25, 27	LA vs IR	LA vs CH	IR vs CH
Depth (m)	1.2	1.7	2.2	2.14	5.62	1.67
Velocity (m/s)	0.42	0.33	0.43	0.29	0.34	2.15
Turbidity (NTU)	36.7	25.3	79.2	1.25	2.48	12.52
Temperature (°C)	21.5	19.7	25.1	2.27	5.07	24.25
Conductivity ($\mu\text{S}/\text{cm}$)	476	705	662	12.49	7.92	0.55
Gravel (%)	24.8	1.5a	2.0a	14.71	12.28	0.07
Sand (%)	29.6	54.0	39.8	1.94	0.76	0.41
Silt (%)	31.7a	38.0a	53.2	0.12	0.65	0.41
Geometric mean (mm)	1.92	0.47	0.66	0.12	0.65	0.41

Table 14. Physical variable means (from transformed data) for the BEND-SCC-SCN-TRM model for reservoir related pairwise Missouri River contrasts and percent of overall ANOVA variance each pairwise contrast accounted for. Similar suffix letters denote pairwise contrasts in rows that were not significantly different at $P \leq 0.0024$. Significantly different contrasts where the percent variance was $\geq 2.0\%$ are shown in **bold**. YSR: Yellowstone River, %v: percent variance.

Physical variable	Location/segment														
	Above Lake		Below Ft. Peck Lake to above YSR		Below YSR, to above Lake Sakakawea		Below YSR to above Lake Sakakawea		Above Lewis & Clark Lake		Below Lewis & Clark Lake		Below First channelized Lake segment		
	5	7	%v	7, 8	10	%v	10	12	%v	14	15	%v	15	17	%v
Depth (m)	1.28a	1.47a	0.12	1.66a	1.81a	0.03	1.81a	1.48a	0.16	1.93a	1.76a	<0.01	1.76	2.90	0.64
Velocity (m/s)	0.41a	0.32a	0.05	0.32a	0.37a	0.13	0.37	0.28	0.33	0.32a	0.40a	0.21	0.40	0.51	0.36
Turbidity	24.4a	19.8a	0.16	55.4	119.3	1.51	119.3	10.0	9.61	7.3	26.7	2.34	26.7	45.4	0.42
Temperature (°C)	20.9	14.4	6.03	18.5	20.8	1.00	20.8	16.4	1.88	23.4a	23.8a	0.01	23.8a	24.2a	0.19
Conductivity ($\mu\text{S}/\text{cm}$)	406	655	4.41	707	502	3.82	502	577	0.75	894a	872a	0.04	872	740	0.71
Gravel (%)	16.5	3.4	1.33	0.3a	1.0a	0.04	1.0a	1.5a	<0.01	1.2a	2.5a	0.08	2.5a	1.2a	0.02
Sand (%)	28.7a	45.8a	0.25	52.0	60.6	0.17	60.6a	54.6a	0.14	49.6a	63.1a	0.26	63.1a	49.6a	0.02
Silt (%)	43.2a	41.3a	<0.01	44.9a	35.0a	0.15	35.0a	36.9a	0.06	41.4a	27.3a	0.26	27.3a	44.0a	0.43
Geometric mean (mm)	1.15a	0.41a	<0.01	0.29a	0.43a	0.10	0.43a	0.46a	0.06	0.65a	0.69a	0.26	0.69a	0.87a	0.43

Dividing inter-reservoir segments into two zones revealed that segment **15**, below Lewis and Clark Lake, exhibited higher current velocity, water temperature, and conductivity than the combined inter-reservoir segments above Lewis and Clark Lake (i.e., **7, 8, 10, 12,** and **14**). Mean water temperature of inter-reservoir segments above Lewis and Clark Lake ranged from 2.5 to 6.4 °C lower than observed in other segment groups in these comparisons. Temperature differences between the zone composed of segments **7, 8, 10, 12,** and **14** and the channelized river zone (segments **17, 19, 22, 23, 25,** and **27**) also accounted for a large amount of the variability (28.4%) observed among the five segment groups in this contrast (Table 12). Conductivity in segment **15** was higher than in any segment group in this contrast and contributed 18.3 % to variability among the five segment groups.

Channelized river (Table 15). Potential differences in physical variables within the 1,191 km channelized zone were examined by dividing it into two groups of segments: (1) the ca. 600 km of channelized Missouri River above the Kansas River (segments **17, 19,** and **22**, including the Kansas River as a TRM in segment **22**), and (2) the ca. 591 km of channelized Missouri River from below the Kansas River to the Missouri-Mississippi river confluence (segments **23, 25,** and **27**).

Water depth, water temperature, and all measures of substrate particle size distribution were statistically similar between the two channelized Missouri River segment groups. Mean turbidity was 34% higher and mean velocity and conductivity were about 20 and 10% lower, respectively, below Kansas River than in channelized segments above it. Means for these three physical variables were significantly different between the two channelized segment groups, but had relatively small importance compared with other segment comparisons, contributing less than 2% to total variability in the BEND-SCC-SCN-TRM model.

Segment Comparisons: CHXO-ISB-OSB model

Differences in physical variables among segments in the CHXO-ISB-OSB model emphasize continuous macrohabitats within main-channel river BENDs. Although, measures of physical variables collected in discrete SCC, SCN, and TRM macrohabitats adjacent to the main channel are absent in the CHXO-ISB-OSB model, their impact on BENDs is reflected (e.g., dilution of BEND conductivity by TRM discharge of low conductivity water).

Upper Missouri and lower Yellowstone Rivers (Tables 16 and 17). Fewer physical variables differed between least-altered Missouri River and least-altered Yellowstone River segment groups when only CHXO,

ISB, and OSB macrohabitats within BENDs were included than for the BEND-SCC-SCN-TRM model. Water depth, turbidity, and conductivity were significantly higher in lower Yellowstone River BENDs than in least-altered Missouri River BENDs. However, only turbidity accounted for $\geq 2.0\%$ of overall CHXO-ISB-OSB model variance. No other physical variables were significantly different between least-altered segments of the two rivers above their confluence.

Three-zone: least-altered, inter-reservoir, and channelized (Table 18). Patterns in physical variables among the three zones were generally similar in the CHXO-ISB-OSB model to those observed in the BEND-SCC-SCN-TRM model with a few exceptions. Current velocities were not significantly different between least-altered and inter-reservoir zones. Measures of substrate particle size were not significantly different between inter-reservoir and channelized zones.

Reservoir related (Table 19). Percent of total variance for the above and below Lake Sakakawea contrast (segment **10** vs **12**) increased from $< 2.00\%$ for the BEND-SCC-SCN-TRM model to 4.75% for the CHXO-ISB-OSB model. A higher percentage of sand substrate in both segments and no significant difference in % gravel below Ft. Peck Lake than above it were the most noticeable differences among inter-reservoir comparisons for the CHXO-ISB-OSB model than the BEND-SCC-SCN-TRM model. Also, water temperature depression below Lake Sakakawea was more pronounced (6.0 °C) when only continuous CHXO, ISB, and OSB macrohabitats were included in the model than for the BEND-SCC-SCN-TRM model.

Five-zone (Tables 16 and 17). Significant differences between the two ANOVA models for contrasts that contributed $\geq 2\%$ of overall variance were most apparent between inter-reservoir segment **15**, below Lewis and Clark Lake, and the channelized river segment group. Mean water depth was 1.5 m or 48% deeper and mean turbidity was 74.6 NTUs or 294% higher in the channelized-segment group than in segment **15**. Conductivity differences between the two segment groups were less distinct when macrohabitats adjacent to the main channel were excluded. Average conductivity decreased in segment **15**, but increased in channelized segments. Geometric mean particle size was over twice as high in channelized segments than in segment **15**, even though the silt size fraction was proportionally greater in channelized segments.

Channelized river (Table 20). Mean water temperature in segments below Kansas River was significantly higher than in segments above it when only macrohabitats

Table 15. Physical variable means (from transformed data) and percent of overall ANOVA variance the contrast accounted for in the BEND-SCC-SCN-TRM model for channelized Missouri River segments above and below Kansas River. Similar suffix letters denote pairwise contrasts within rows that were not significantly different at $P \leq 0.0024$. There were no significantly different contrasts where the percent variance was $\geq 2.0\%$.

Physical variable	Segments		Percent variance
	Above Kansas River	Below Kansas River	
Depth (m)	17, 19, 22 2.7a	23, 25, 27 2.0a	0.11
Velocity (m/s)	0.49	0.39	0.31
Turbidity (NTU)	62.9	91.7	0.57
Temperature ($^{\circ}\text{C}$)	24.7a	25.3a	0.06
Conductivity ($\mu\text{S}/\text{cm}$)	705	633	1.14
Gravel (%)	2.1a	2.0a	<0.01
Sand (%)	34.3a	43.4a	<0.01
Silt (%)	58.5a	49.8a	<0.01
Geometric mean (mm)	0.67a	0.66a	<0.01

within BENDs were included in the ANOVA model. Additionally, conductivity was significantly lower in segments below Kansas River than in channelized segments above it. Both these differences were now $>2.0\%$ of total variability (compare with Table 15).

BEND and Macrohabitat Comparisons

Previous physical variable ANOVA results were for the main effect of segment and 21 segment group comparisons. BENDs and discrete macrohabitats were averaged in a BEND-SCC-SCN-TRM model and continuous macrohabitats within BENDs were averaged in a CHXO-ISB-OSB model. Here we report physical variable results for the main effect of BEND/macrohabitat where all segments were averaged within each of these models.

BEND-SCC-SCN-TRM model (Table 21). Differences in physical variables among BENDs and discrete macrohabitats accounted for more variability than among segments for depth, velocity, % sand, % silt, and geometric mean particle size in the BEND-SCC-SCN-TRM model (Table 9). Average water depth in BENDs (3.4 m) was significantly greater than in SCC (1.0 m), SCN (1.0 m), and TRM (1.8 m) macrohabitats. Tributary mouths were significantly deeper than either SCCs or SCNs, whereas mean depths of SCCs and SCN were not significantly different from each other.

Mean water velocity was very low in SCNs and TRMs, (<0.1 m/s) and not significantly different between these two discrete macrohabitats. Velocity was significantly higher in SCCs than SCNs or TRMs (mean: 0.40 m/s), but lower than in BENDs. Mean

water velocity in BENDs (0.87 m/s) was over twice as fast as in SCCs.

Gravel and sand composed over 70% of bottom substrates in BENDs and SCCs, whereas silt was over 85% of bottom material in SCNs and TRMs. The order of BEND and macrohabitats from most to least % gravel was BEND $>$ SCC $>$ SCN = TRM, for % sand it was BEND $>$ SCC $>$ SCN $>$ TRM, and for % silt it was TRM $>$ SCN $>$ SCC $>$ BEND, where $>$ indicates statistical significance. Geometric mean particle size was largest in BENDs, followed by SCCs, but did not significantly differ between SCNs and TRMs.

CHXO-ISB-OSB model (Table 22). Water depth, current velocity, % silt, and geometric mean particle size were physical variables whose differences were higher among macrohabitats than segments when only continuous macrohabitats within BENDs were evaluated (Table 10). Mean water depths were not statistically different between CHXOs and OSBs (4.0 m and 3.9 m, respectively), but were significantly deeper than in ISBs (2.1 m). Water velocity was highest in CHXOs, followed by OSBs, and lowest within ISB macrohabitats. Lowest % silt was recorded in CHXOs and highest % silt was in ISBs. Geometric mean particle size was highest in OSB macrohabitats, ISBs were intermediate, and CHXOs had the lowest values. All the above differences were significant among the three macrohabitats, except where noted.

Macrohabitat summary. Patterns in physical variables among macrohabitats were as follows: CHXOs and OSBs were deep, fast and contained the highest

Table 17. Statistically significant ($P \leq 0.0024$) contrasts for row \times column pairs of Missouri (MOR) and lower Yellowstone (YSR) river segment groups whose Type III partial sums of squares accounted for $\geq 2.0\%$ of the overall contrasts in the CHXO-ISB-OSB ANOVA model. Percent of total variance explained for each pairwise contrast is within parentheses.

Segment group	Least-altered YSR	Inter-reservoir below Ft. Peck Lake to YSR	Inter-reservoir w/o segment 15, below Lewis & Clark	Segment below Lewis & Clark Lake	Channelized
	9	7, 8	7, 8, 10, 12, 14	15	17, 19, 22, 23, 25, 27
Least-altered MOR 3, 5	turbidity (2.8)	depth (3.5) temperature (11.4) conductivity (9.5) % gravel (12.5) % sand (12.6) geometric mean (7.7)	depth (8.3) temperature (5.6) conductivity (13.2) % gravel (17.7) % sand (14.9) geometric mean (11.1)	depth (5.0) conductivity (26.9) % gravel (6.3) % sand (5.2) geometric mean (3.5)	depth (33.4) velocity (5.4) temperature (10.3) turbidity (11.2) conductivity (37.8) % gravel (18.9) % sand (10.9)
Least-altered YSR 9		temperature (10.8) % gravel (5.8) % sand (5.8) geometric mean (2.5)	temperature (5.8) turbidity (4.1) % gravel (7.3) % sand (5.8) geometric mean (3.2)	conductivity (11.3) % gravel (3.2) % sand (2.5)	depth (9.0) velocity (3.8) temperature (3.3) conductivity (10.0) % gravel (7.6) % sand (3.8)
Inter-reservoir w/o segment 15, below Lewis & Clark 7, 8, 10, 12, 14				temperature (10.3) conductivity (9.0)	depth (14.0) velocity (9.8) temperature (56.7) turbidity (21.8) conductivity (10.3) geometric mean (12.3)
Segment below Lewis & Clark Lake 15					depth (3.3) turbidity (5.6) geometric mean (2.3)

Table 18. BEND physical variable means (from transformed data) for least-altered (LA) Missouri and lower Yellowstone rivers, Missouri River inter-reservoir (IR) and channelized (CH) zone contrasts and percent of overall ANOVA variance each pairwise contrast accounted for. Similar suffix letters denote pairwise contrasts within rows that were not significantly different at $P \leq 0.0024$. Significantly different contrasts where percent variance was $\geq 2.0\%$ are shown in **bold**. Macrohabitats CHXO, ISB, and OSB compose the BEND model.

Physical variable	Zone/segment			Channelized 17, 19, 22, 23, 25, 27	Percent variance	
	Least-altered 3, 5, 9	Inter-reservoir 7, 8, 10, 12, 14, 15	Inter-reservoir 2, 9		LA vs IR	LA vs CH
Depth (m)	1.8	2.9	4.6	7.80	35.69	14.80
Velocity (m/s)	0.72a	0.75a	1.03	0.06	7.75	9.39
Turbidity (NTU)	35.8	23.6	100.0	1.31	8.34	23.45
Temperature (°C)	21.9	19.1	25.8	5.18	11.54	47.71
Conductivity ($\mu\text{S}/\text{cm}$)	445	638	734	18.70	40.15	5.94
Gravel (%)	37.1	5.3a	5.0a	21.25	22.56	0.02
Sand (%)	48.1	86.0a	80.6a	17.55	12.45	0.70
Silt (%)	4.7ab	3.6a	7.2b	0.10	0.46	1.42
Geometric mean (mm)	6.64a	1.55	5.33a	11.79	0.28	12.61

percentage of gravel substrate. Average water depth in ISBs was greater than in SCCs. Current velocity was similar between ISBs and SCCs and intermediate between fast CHXOs and OSBs and nearly quiescent SCNs and TRMs. Sand was the predominant substrate in ISBs and SCCs. Inside bends and TRMs had similar and intermediate water depths. Tributary mouths and SCNs exhibited very low current velocities and a substrate dominated by silt. Differences in turbidity, water temperature, and conductivity were present and sometimes significant among macrohabitats, but they accounted for a small percent of model variance relative to segments. Mean water temperature during the sampling period and over 3 years varied only between 21.7 °C and 22.6 °C among the six macrohabitats. Turbidity was lowest in SCNs and SCCs, whereas conductivity was highest in TRMs.

Interactions Between Segments and Macrohabitats

Conductivity was the only physical variable in the BEND-SCC-SCN-TRM model where a major interaction between segment and macrohabitat was observed (Table 9). Macrohabitat comparisons indicate tributaries were the primary source of patterns in dissolved salts among segments. Conductivity in BENDs showed an irregular longitudinal increase from upper river least-altered segments to the most downriver inter-reservoir segment (15) and then decreased gradually throughout the channelized zone (Figure 9). Tributary inflow showed high, albeit variable conductivity, in segments 3-15, except segment 10, where conductivity influenced by Yellowstone River discharge was relatively low and constant. Main channel conductivity was generally diluted by TRM discharge in the channelized zone.

Large segment and macrohabitat interactions in the CHXO-ISB-OSB model were observed for current velocity, % sand, % silt, and geometric mean particle size (Table 10). These interactions are best explained by generally higher current velocities recorded in CHXO and OSB macrohabitats in segments below than above reservoirs (except for Lake Sakakawea) and higher current velocities in channelized segments relative to inter-reservoir or least-altered segments (Tables 18, 19, and 22).

Interactions between segments and substrate were complex in continuous macrohabitats. Although sand was the predominant substrate

Table 19. BEND physical variable means (from transformed data) for pairwise Missouri River inter-reservoir contrasts and percent of overall ANOVA variance each pairwise contrast accounted for. Similar suffix letters denote pairwise contrasts within rows that were not significantly different at $P \leq 0.0024$. Significantly different contrasts where percent variance was $\geq 2.0\%$ are shown in **bold**. Macrohabitats CHXO, ISB, and OSB compose the BEND model.

Physical variable	Location/segment														
	5	7	%v	10	10	%v	10	12	%v	14	15	%v	15	17	%v
	Above Ft. Peck Lake	Below Ft. Peck Lake		Below YSR, to above Lake Sakakawea	Below YSR, to above Lake Sakakawea		Below YSR, to above Lake Sakakawea	Below YSR, to above Lake Sakakawea		Above Lewis & Clark Lake	Below Lewis & Clark Lake		Below Lewis & Clark Lake	First channelized segment	
Depth (m)	1.74	2.43	0.74	2.67	3.58	0.83	3.58	2.45	1.28	3.50a	3.12a	0.14	3.12	4.29	1.21
Velocity (m/s)	0.66a	0.74a	0.18	0.72a	0.78a	0.08	0.78a	0.77a	0.01	0.66	0.84	0.81	0.84	1.07	0.90
Turbidity	24.9	16.1	0.38	65.6	171.5	1.98	171.5	7.0	18.22	4.9	25.4	4.61	25.4	43.5	0.53
Temperature (°C)	21.6	13.1	10.11	17.5	20.8	1.64	20.8	14.8	4.75	23.0a	24.1a	0.21	24.1	25.3	0.30
Conductivity (μS/cm)	402	598	5.45	603	468	2.27	468a	494a	0.09	864a	834a	0.08	834a	827a	<0.01
Gravel (%)	29.2	10.8	1.72	1.4a	2.7 a	0.07	2.7a	9.2a	0.55	4.2a	7.1a	0.15	7.1a	3.8a	0.20
Sand (%)	58.8	84.2	2.13	93.1a	89.2a	0.14	89.2a	84.5a	0.14	80.4a	82.4a	0.02	82.4a	91.3a	0.45
Silt (%)	5.1a	1.6a	0.41	2.9a	4.8a	0.11	4.8a	1.9 a	0.18	9.5	2.9	0.91	2.9a	1.7a	0.05
Geometric mean (mm)	4.55	1.97	1.01	1.19a	1.06a	0.02	1.06	2.28	0.83	1.27a	1.96a	0.23	1.96	4.88	1.14

Table 20. BEND physical variable means (from transformed data) and percent of overall ANOVA variance the contrast accounted for in channelized Missouri River segments above and below Kansas City, Missouri. Similar suffix letters denote pairwise contrasts within rows that were not significantly different at $P \leq 0.0024$. Significantly different contrasts where percent variance was $\geq 2.0\%$ are shown in **bold**. Macrohabitats CHXO, ISB, and OSB compose the BEND model.

Physical variable	Zone/segment		Percent variance
	Above Kansas City	Below Kansas City	
	17, 19, 22	23, 25, 27	
Depth (m)	4.6a	4.7a	0.03
Velocity (m/s)	1.10	0.96	0.84
Turbidity (NTU)	67.4	147.9	0.30
Temperature (°C)	25.5	26.2	3.52
Conductivity ($\mu\text{S}/\text{cm}$)	788	680	3.09
Gravel (%)	6.2a	3.9a	0.26
Sand (%)	81.9a	79.3a	0.08
Silt (%)	4.8	10.0	1.19
Geometric mean (mm)	5.71a	4.98a	0.08

throughout all lower Yellowstone and Missouri river segments (range: 45.3-93.1%) and CHXO, ISB, and OSB macrohabitats (range: 70.3- 88.1%), mean % gravel was highest in least-altered segments (37.1%) and OSBs (17.5%). Percentage of silt was highest in the channelized zone (7.2%) and lowest in the inter-reservoir zone (3.6 %). Inside bends were the continuous macrohabitat where mean % silt was highest (17.6%). Geometric mean particle size was low in the inter-reservoir zone relative to the least-altered and channelized zones and OSBs were the continuous macrohabitat with the highest average particle size.

Principal Components Analysis

Results of PCA corroborated ANOVA and provided a visual perspective of how physical variables collectively defined relationships among zones and segments. Additionally, patterns among BENDs and SCC, SCN, and TRM macrohabitats and CHXO, ISB, and OSB macrohabitats within BENDs over all segments and years were displayed.

BENDs and SCC, SCN, and TRM macrohabitats

The first three principal components accounted for 79% of variability in the data for this analysis (Table 23). Principal component 1 accounted for nearly one-half of this total and was positively correlated with all six physical variables, except conductivity. Correlation coefficients were ≥ 0.50 for depth, velocity and geometric mean particle size. Principal component 2 was significantly and positively correlated with water temperature and turbidity at ≥ 0.50 , and also significantly with

conductivity, but at <0.50 . Negative correlations of <0.50 were present for PC2 for water velocity and geometric mean of substrate particle sizes. Principal component 3 was positively correlated with water depth and conductivity and negatively correlated with turbidity. Turbidity and conductivity exhibited correlation coefficients ≥ 0.50 .

Points plotted within each bivariate graph represent individual BENDs and SCC, SCN, and TRM macrohabitats for each segment averaged over the three study years. The next three figures all display the same data or a subset of them, but each highlights a different spatial aspect: zones, BENDs and discrete macrohabitats, or individual segments. Comparing the graphs enables discerning the interplay among physical variables at these spatial scales. Bivariate plots of PC1 vs PC2 and PC1 vs PC3 illustrate an increase in depth, velocity, and geometric mean particle size moving right from zero along the X axis (PC1), increasing temperature and increasing turbidity moving up from zero on the Y axis for PC2, and decreasing turbidity and increasing conductivity moving up from zero along the Y axis for PC3 (e.g., Figure 15).

Least-altered, inter-reservoir, and channelized zones.

There was substantial overlap among BENDs and discrete macrohabitats for the three zones highlighted in Figure 15. However, 76% for PC2 and 89% for PC3 of BENDs and discrete macrohabitats in least-altered segments plotted below zero. The least-altered zone was characterized by relatively cool, low conductivity water. Sixty-six percent of locations within the

Table 21. Physical variable means (from transformed data) among 15 segments in Missouri and lower Yellowstone rivers for BENDs and secondary channel connected (SCC), secondary channel non connected (SCN), and tributary mouth (TRM) discrete macrohabitats. * Indicates physical variables where BEND or macrohabitat accounted for $\geq 10\%$ of total variance. Similar suffix letters denote BEND or macrohabitat means within rows that were not significantly different using a Bonferroni corrected probability level of $P \leq 0.0083$. Significantly different contrasts where percent variance was $\geq 2\%$ are shown in **bold**.

Physical variable	Macrohabitat						Percent variance					
	BEND	SCC	SCN	TRM	BEND vs SCC	BEND vs SCN	BEND vs TRM	SCC vs SCN	SCC vs TRM	SCN vs TRM		
	*Depth (m)	3.4	1.0a	1.0a	1.8	45.75	26.78	13.27	0.00	5.31	3.57	
*Velocity (m/s)	0.87	0.40	0.03a	0.07a	17.71	39.69	48.96	9.33	9.80	0.12		
Turbidity (NTU)	47.8a	37.6b	36.8b	44.8a	0.84	1.01	0.04	0.10	0.92	1.12		
Temperature ($^{\circ}$ C)	22.3a	21.7a	21.7a	22.4a	0.06	0.06	0.06	0.00	0.00	0.00		
Conductivity (μ S/cm)	633a	613a	664a	700	0.00	0.33	3.64	0.35	3.35	0.90		
*Gravel (%)	11.5	5.9	0.2a	0.1a	3.32	13.46	20.43	4.82	7.50	0.02		
*Sand (%)	75.1	65.9	11.1	3.2	1.07	20.55	39.25	12.98	25.62	0.50		
*Silt (%)	9.1	18.9	86.9	95.9	1.67	26.08	47.40	15.73	29.49	0.45		
*Geometric mean (mm)	5.61	1.08	0.10a	0.06a	10.46	32.40	51.96	9.65	16.70	0.15		

inter-reservoir zone plotted below zero on PC2 and 71% above zero on PC3, indicating water temperature and turbidity were lower and conductivity was higher relative to least-altered and channelized zones. The channelized zone showed the highest temperature and turbidity of the three zones (96% of locations above zero for PC2). A cluster of points within the channelized zone plotted to the far right of PC1; these channelized sites exhibited the deepest water, highest current velocity, and largest geometric mean particle size of any locations along the Missouri and lower Yellowstone rivers.

BENDs and discrete macrohabitats, all segments.

Figure 16 highlights BENDs and SCC, SCN, and TRM macrohabitats over all segments combined. Principal component 1 showed BENDs (containing CHXO, ISB, and OSB macrohabitats averaged) had the deepest water, fastest current velocity, and largest geometric mean particle size relative to SCC, SCN, and TRM macrohabitats (>95% of locations were >0.0 for PC1, Figure 16). These BENDs formed the tight cluster on the right side of PC1 in the channelized zone referred to previously (Figure 15). Tributary mouths grouped in the upper left quadrant for PC1 (95% of locations <0.0) vs. PC2 (81% of locations >0.0), indicating many were relatively warm, turbid, shallow, low velocity macrohabitats with fine substrates (Figure 16). Figure 15 indicates that the majority of these TRMs were in the channelized zone. Non-connected secondary channels were also relatively shallow, low velocity macrohabitats with fine substrates (100% of locations were <0.0 for PC1), and were warm and turbid (71% of locations >0.0 for PC2). Connected secondary channels showed no clear distribution among PCs as they were fairly evenly distributed among the four quadrants and clustered near zero.

BENDs and discrete macrohabitats, segments 10 and 12.

Differences in physical variables among BENDs and discrete macrohabitats between segments can be clearly observed when principal component values for only a pair of the 15 segments are retained in PCA plots. This is illustrated for inter-reservoir segment 10, above Lake Sakakawea, and segment 12, below Lake Sakakawea (Figure 17). BENDs cluster together and stand out as the deepest, highest velocity habitat units with the largest geometric mean particle size in both segments, although more so in segment 10 (PC1). Principal component 2 shows that all macrohabitats, except TRMs, had lower

Table 22. Physical variable means (from transformed data) among 15 segments in Missouri and lower Yellowstone Rivers for macrohabitats within BEND: channel cross-over (CHXO), inside bend (ISB), and outside bend (OSB). * Indicates physical variables where macrohabitat accounted for $\geq 10\%$ of total variance. Similar suffix letters denote macrohabitat means within rows that were not significantly different using a Bonferonni corrected probability level $P \leq 0.0167$. Significantly different contrasts where percent variance was $\geq 2\%$ are shown in **bold**.

Physical variable	Macrohabitat			Percent variance		
	CHXO	ISB	OSB	CHXO vs ISB	CHXO vs OSB	ISB vs OSB
	*Depth (m)	4.0a	2.1	3.9a	20.17	0.04
*Velocity (m/s)	1.13	0.54	0.96	36.82	2.76	19.49
Turbidity (NTU)	43.2a	48.2a	48.0a	0.04	0.01	0.01
Temperature (°C)	22.4a	22.6a	22.5a	0.02	0.00	0.03
Conductivity ($\mu\text{S}/\text{cm}$)	620a	640b	637ab	0.17	0.09	0.01
Gravel (%)	8.6	4.7	17.5	1.01	2.48	6.65
Sand (%)	88.1	70.3a	71.1a	6.40	5.67	0.02
*Silt (%)	0.3	17.6	3.4	28.18	4.15	10.52
*Geometric mean (mm)	1.89	2.62	8.27	0.71	14.84	9.12

temperature and turbidity in segment **12** than in segment **10**, although only one TRM (Yellowstone River) was sampled in segment **10** versus four in segment **12**. Conductivity was higher in segment **12** than in segment **10** and TRMs appeared to be the origin of this conductivity as they plotted highest on the PC3 axis.

CHXO, ISB, and OSB Macrohabitats Within BEND

The first three PCs accounted for 74% of the variability in the data. Principal component 1 contributed about one-half of this total, was significantly and positively correlated with all six physical variables, and all but geometric mean particle size were correlated at ≥ 0.50 (Table 23). Principal component 2 was positively correlated with water temperature, turbidity, and geometric mean particle size and negatively correlated with water depth, velocity, and conductivity. Turbidity, conductivity, and geometric mean particle size were correlated with PC2 at ≥ 0.50 . Principal component 3 was positively correlated with water temperature, turbidity, and conductivity and negatively correlated with water depth, velocity, and geometric mean of substrate sizes. However, only velocity was correlated with PC3 at ≥ 0.50 .

Bivariate plots of PC1 vs PC2 illustrate an increase in depth, velocity, temperature, turbidity, and conductivity moving right from zero along the X axis of PC1 and increasing turbidity, increasing geometric mean particle size, but decreasing conductivity moving up the Y axis from zero for PC2. Velocity is the major contributor to PC3 and decreases moving up the Y axis from zero for

PC3 relative to PC1.

Least-altered, inter-reservoir, and channelized zones.

Continuous macrohabitats in the channelized zone were deeper, faster, warmer, and more turbid than their counterparts in the least-altered and inter-reservoir zones (94% of channelized locations >0 for PC1, Figure 18). Channel cross-overs, ISBs, and OSBs in the inter-reservoir zone were more frequently clearer, had higher conductivity, and finer substrates (79% of locations <0 for PC2) than in the least-altered zone (2.2% of locations <0 for PC2). Two clusters of habitat units in the channelized zone were apparent in the PC1 vs PC3 bivariate plot. One group (referred to hereafter as group A, mostly in lower right quadrant) was deeper, faster, warmer, more turbid, and more conductive than the other more diffuse group (B).

BEND macrohabitats, all segments. There was substantial overlap in distribution along the physical variable gradients among CHXO, ISB, and OSB macrohabitats (Figure 19). However, 84% of ISB sites were in the upper one-half (>0) of the PC1 vs PC3 bivariate plot indicating this was the slowest water macrohabitat of the three within BENDs. Conversely, 84% of OSB and 68% of CHXO points were in the lower one-half (<0) of the PC1 vs PC3 plot indicating these were higher current velocity macrohabitats. Group A sites in the channelized zone of PC1 vs PC3 were all CHXO and OSB macrohabitats (compare Figures 18 and 19), whereas group B was a mix of the

three continuous macrohabitats. Inside bends were generally slower velocity macrohabitats (84% of locations >0 for PC3) than CHXOs and OSBs (32% and 16% of locations >0 for PC3, respectively). No obvious patterns in water clarity, conductivity, or geometric mean particle size were revealed among CHXO, ISB, and OSB macrohabitats in the PC1 vs PC2 bivariate plot.

BEND macrohabitats, segments 10 and 12. The interplay of continuous macrohabitats and segments is illustrated for inter-reservoir segments **10** and **12** in figure 20. Continuous macrohabitats within BENDS clustered more tightly than BEND and SCC, SCN and TRM macrohabitats in Figure 17, illustrating the greater similarity among CHXO, ISB, and OSB macrohabitats within BENDs than among BENDs and the discrete macrohabitats. Continuous macrohabitats showed the same physical differences between segments **10** and **12** as described previously for BENDs (Figures 17 and 20).

DISCUSSION

Our analysis provides the most standardized, comprehensive, and robust spatial synthesis of aquatic physical habitat assembled for a North American great river. Comparable analyses of physical habitat, but over a longer time period (~12 years) exist for a portion of the Mississippi River through the upper Mississippi River

Long-term Resource Monitoring Program (LTRMP, U. S. Geological Survey 1999). However, the LTRMP covers only about one-half the total length of the Mississippi River (versus about 83% of the Missouri in this study) and does not have a comparable spatially-nested sampling hierarchy. Biophysical assessments of European great rivers have historically lacked spatial breadth in due to the absence of interjurisdictional standardization among countries. This is changing under the European Union's Water Framework Directive (see papers in Jungwirth et al. 2000).

River Discharge

Missouri River flow during our sampling season and over the 3 study years was generally above its long-time average and has implications for applicability of our results to other seasons, years, and flow conditions. Number and juxtaposition of macrohabitats are affected by river discharge. High flows increase river stage, reducing the relative number and area of sandbars (BAR mesohabitat within ISBs) and their adjacent SCC macrohabitats. In contrast, high discharge also connects some SCN macrohabitats, reducing their number and increasing the proportion of secondary channels composed of SCC macrohabitats. The cumulative effect of high river discharge on the total number of SCC

Table 23. Eigenvalues (top) and Pearson correlation coefficients (bottom) for the first three principle components for each of six physical variables and all Missouri and lower Yellowstone river segments and 1996-1998 combined. BENDs and macrohabitats were combined into two groups: BEND, SCC, SCN, and TRM, and CHXO, ISB, and OSB. * = Significant at $P \leq 0.0001$; significant correlation coefficients ≥ 0.50 are in **bold**.

Variable	BEND, SCC, SCN, and TRM (N = 717)			CHXO, ISB, and OSB within BENDs (N = 636)		
	PC 1 (38.3%)	PC 2 (22.1%)	PC 3 (18.4%)	PC 1 (38.3%)	PC 2 (18.9%)	PC 3 (16.6%)
Depth	0.4975 0.75*	0.0010 <0.01	0.2673 0.28*	0.5407 0.82*	-0.2663 -0.28*	-0.2458 -0.25*
Velocity	0.5980 0.91*	-0.2520 -0.29*	0.0030 <0.01	0.4455 0.68*	-0.1285 -0.14	-0.6296 -0.63*
Temperature	0.2538 0.38*	0.6557 0.75*	-0.0439 -0.05	0.4796 0.73*	0.2292 0.24*	0.4894 0.49*
Turbidity	0.2459 0.37*	0.5471 0.62*	-0.4844 -0.51*	0.3419 0.52*	0.5742 0.61*	0.1910 0.19*
Conductivity	0.0231 0.04	0.3376 0.39*	0.8306 0.87*	0.3573 0.54*	-0.5452 -0.58*	0.4499 0.45*
Geometric mean particle size	0.5192 0.79*	-0.3054 -0.35*	-0.0456 -0.05	0.1860 0.28*	0.4827 0.51*	-0.2546 -0.25*

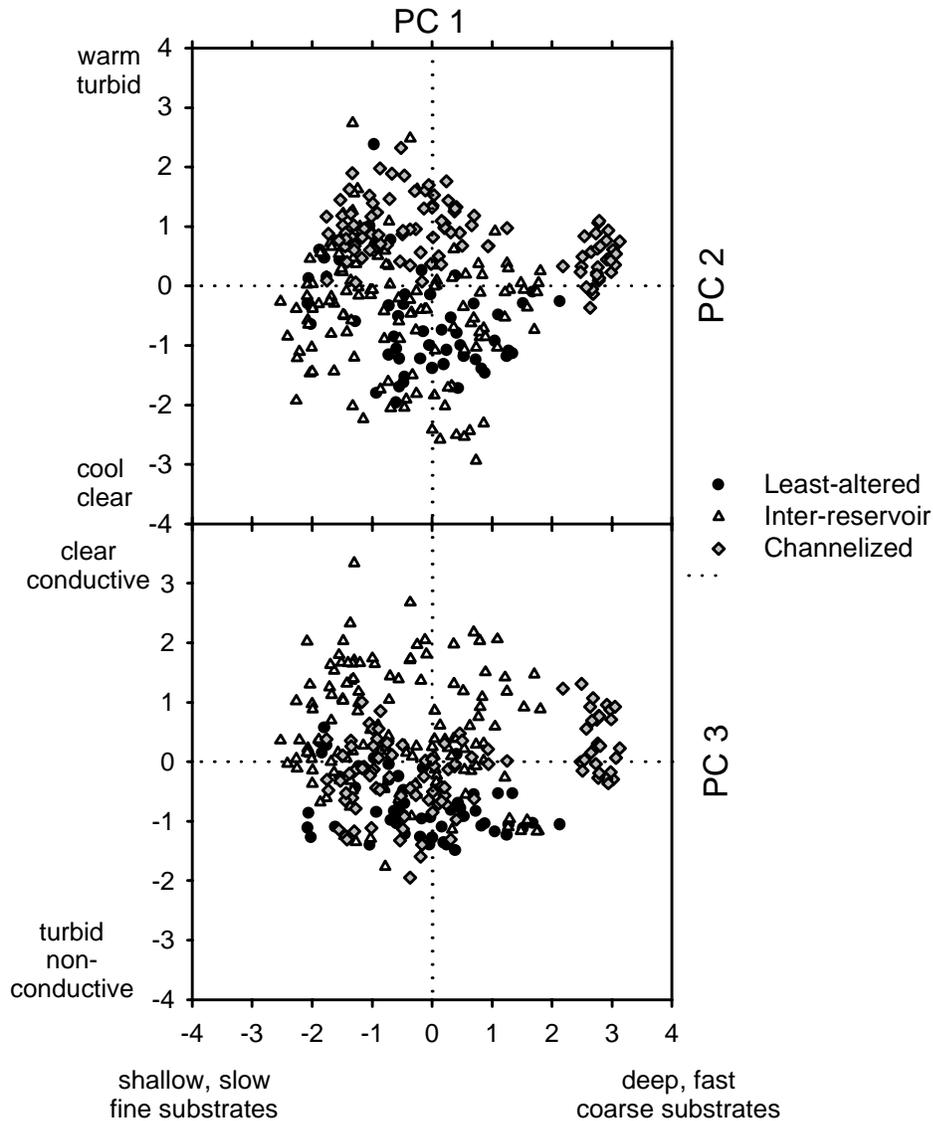


Figure 15. Physical variable principal component bivariate plots for BENDS and SCC, SCN, and TRM macrohabitats within least-altered, inter-reservoir, and channelized zones of Missouri and lower Yellowstone rivers, 1996-1998 combined.

macrohabitats is therefore equivocal.

High river discharge is generally associated with increases in main-channel turbidity, water depth, and velocity, and may also have increased the proportion of larger substrate particle sizes relative to normal flow years. Water depth in TRMs is often increased from high flows, whereas velocity is decreased, because high mainstem river stage acts as a water dam to tributaries. This effect can be particularly strong when the ratio of mainstem discharge to tributary discharge is high.

Flow variability within and among seasons, years, and locations along the Missouri River is high (Galat and Lipkin 2000) and argues for including a long-term temporal component in future Missouri River biophysical assessment programs. We have no way of estimating if, or how great an effect, high flows may have had on our results, but urge caution in applying them to normal or low flow years until a long-term, spatially-nested assessment program like the Missouri River Environmental Assessment Program (MOREAP,

Missouri River Natural Resources Committee, no date) is established.

Factors Affecting Patterns of Physical Variables

Environmental and anthropogenic factors interacted to produce the patterns we observed in physical variables at zone, segment, and macrohabitat scales. Establishing a nested spatial hierarchy for the Missouri and lower Yellowstone rivers better enabled us to partition sources of variability in physical variables.

Environmental Determinants

Temperature, turbidity, and conductivity differences were greatest at zone and segment scales. Latitude,

catchment physiography, and regional climate and runoff are generally the primary environmental determinants of regional and longitudinal gradients in rivers (Hynes 1975; Minshall et al. 1985). Variability in depth, velocity, % sand, % silt, and geometric mean substrate size was greater among macrohabitats within segments than among segments. Hydrology, channel geomorphology, and sedimentation are the dominant local environmental influences associated with these variables in rivers (Stalnaker et al. 1989; Gordon et al. 1992). Percent of gravel in the substrate varied significantly at both segment and macrohabitat scales and conductivity showed a significant segment-macrohabitat

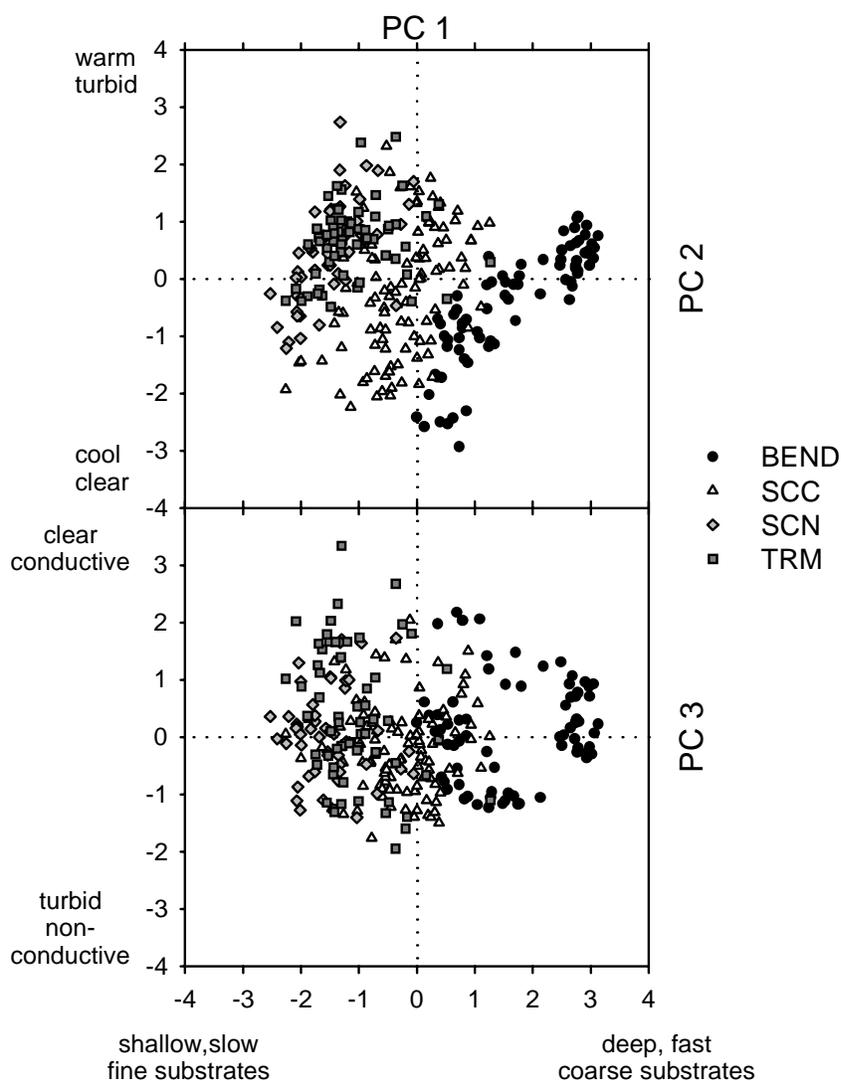


Figure 16. Physical variable principal component bivariate plots for Missouri and lower Yellowstone river BENDS and SCC, SCN, and TRM macrohabitats, including all segments and 1996-1998 combined.

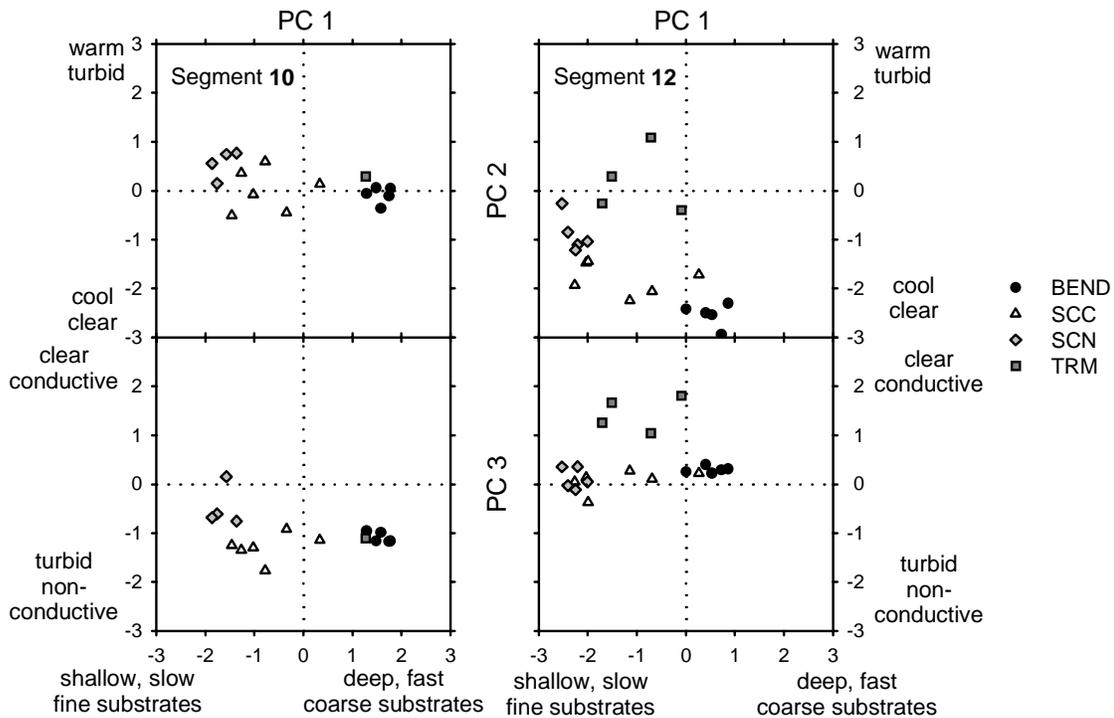


Figure 17. Physical variable principal component bivariate plots for Missouri and lower Yellowstone river BENDs and SCC, SCN, and TRM macrohabitats for inter-reservoir segments **10** and **12**, 1996-1998 combined.

interaction implying that all the above factors were important and operated across spatial scales.

Temperature was the only physical variable demonstrating a longitudinal increase (neglecting effects of impoundment) as predicted by the River Continuum Concept (Vannote et al. 1980; Sedell et al. 1989). The $\sim 9.3^\circ$ decrease in latitude between segments **8** and **27** (most northerly and southerly segments) was largely responsible for this trend. Longitudinal patterns of turbidity and conductivity, again excluding reservoir effects, were more complex than temperature among segments. They were greatly influenced by size and location of tributaries and thus the geology and soils within tributary catchments. Most inter-reservoir tributaries were less turbid than the Yellowstone River (the only large tributary in the least-altered zone), but varied in their contribution to mainstem conductivity. Turbidity in channelized segments increased gradually until discharge of north-flowing, clear-water rivers draining the limestone dominated Ozark highlands increased water clarity in the most downriver segment (**27**). Tributaries throughout the channelized zone

reduced conductivity of the mainstem Missouri River relative to upstream tributaries, except as noted for the Yellowstone River.

Anthropogenic Determinants

Impoundment. Impacts of mainstem regulation on downstream biophysical properties are well documented (Ward and Stanford 1979, 1982; Lillehammer and Saltveit 1984; Petts 1984; Davies and Walker 1986; Dodge 1989; National Research Council 1992; Ligon et al. 1995; Vörösmarty et al. 1997; Graf 1999; Rosenberg et al. 2000). Segments below most Missouri River mainstem dams exhibited the decrease in turbidity typically associated with sedimentation in reservoirs and lowered water temperature from reservoir storage and hypolimnetic water releases (Ligon et al. 1995). Segment **15** below Gavins Point Dam was the exception to this generality. Reductions in temperature or turbidity were not observed in segment **15** as in other inter-reservoir segments because Lewis and Clark Lake is a flow-through reservoir (i.e., run-of-the-river) with a short (5-7 day) residence time (Walburg 1971).

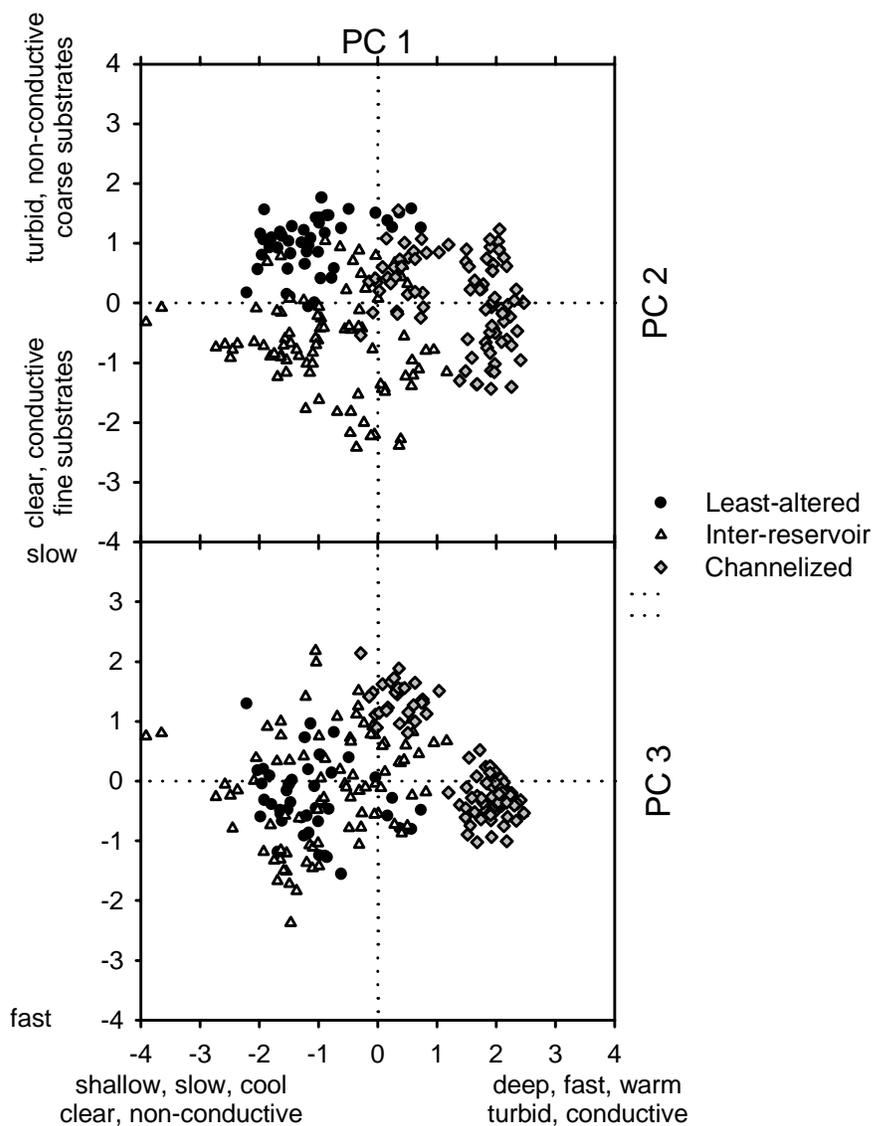


Figure 18. Physical variable principal component bivariate plots for CHXO, ISB, and OSB macrohabitats within BENDs for least-altered, inter-reservoir, and channelized zones of Missouri and lower Yellowstone rivers, 1996-1998 combined.

Proportion of coarser substrate size classes generally increased in segments immediately below dams due to downstream export of small, mobile size fractions and lack of sediment renewal from upstream. The six main-stem reservoirs contributed to increased conductivity through evaporation of about 3.6 km³/yr between 1996 and 1998 (U. S. Army Corps of Engineers, Reservoir Control Center, Omaha, Nebraska, personal communication), although this effect is considered small relative

to tributary sources of dissolved salts. Whereas Missouri River reservoirs influenced water depth and velocity in segments immediately downriver from tailwaters, these effects were less than observed for temperature and turbidity and were generally not greater than variability recorded among macrohabitats within segments.

Turbidity. Reductions in suspended sediment and

turbidity are one of the best documented effects of impoundment on the lower Missouri River (Morris et al. 1968; Whitley and Campbell 1974; Ford 1982; Slizeski et al. 1982; Schmulbach et al. 1992). Ford (1982 in Galat et al. 1996) calculated a reduction in average annual sediment load after 1955 below Gavins Point Dam of -99% at Yankton, South Dakota (km 1305), to -69% at Hermann, Missouri (km 161), compared with before 1953. Pflieger and Grace (1987) reported that

mean annual turbidity near the mouth of the Missouri River decreased four-fold from the 1930's to the 1950s.

Post-impoundment reductions in suspended sediment load and turbidity in the lower Missouri River were somewhat ameliorated by longitudinal increases. Ford (1982) reported a 6,930% increase in suspended sediment load between km 1305 and km 161 for the post-1955 interval, but only a 27% increase at km 161 compared with the nearest upriver site (Kansas City, km

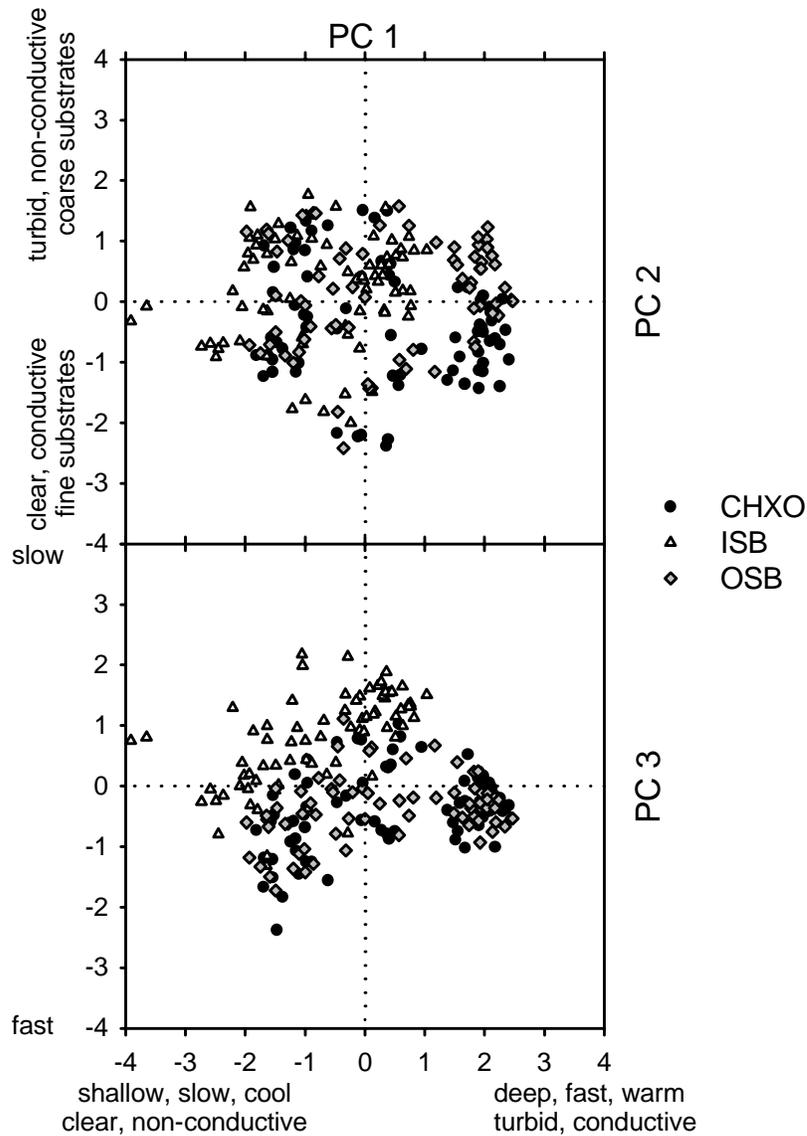


Figure 19. Physical variable principal component bivariate plots for Missouri and lower Yellowstone river macrohabitats within BENDs, including all segments and 1996-1998 combined.

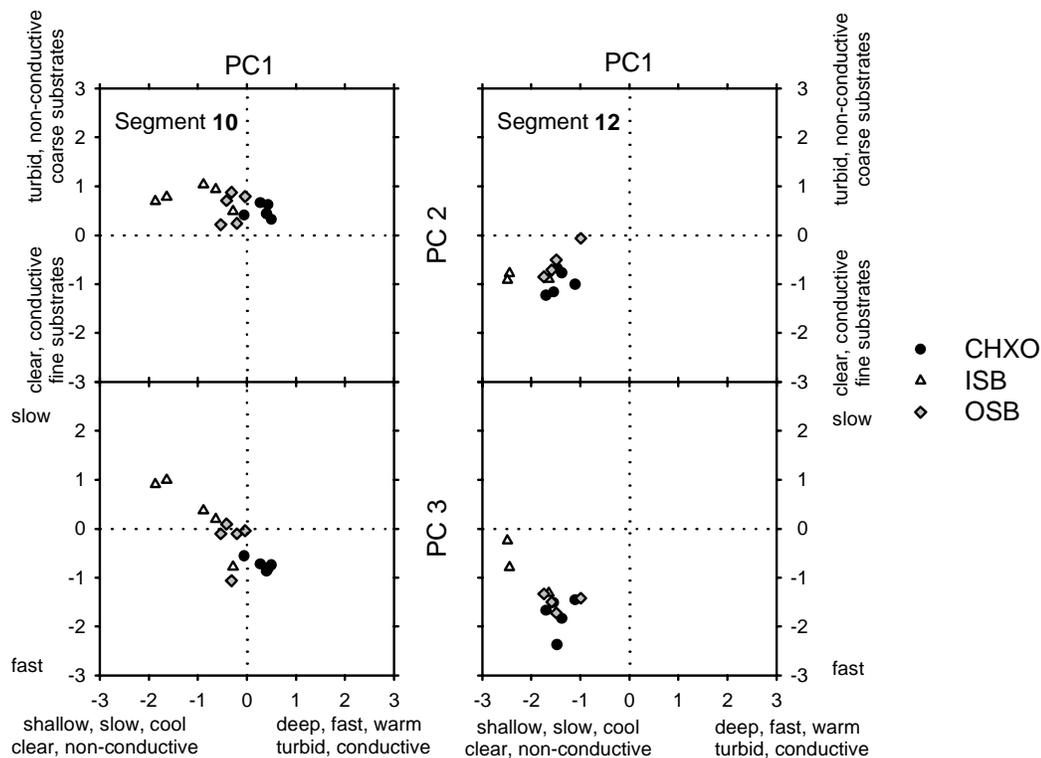


Figure 20. Physical variable principal component bivariate plots for Missouri and lower Yellowstone river CHXO, ISB, and OSB macrohabitats within BENDs for inter-reservoir segments **10** and **12**, 1996-1998 combined.

579). Longitudinal increases in turbidity may be less than suspended sediment load as we observed a 3,800% increase in turbidity between km 1303 and km 81 during 1996-1998.

Temperature. Water temperature depression from reservoir hypolimnetic water releases was the most significant physical change observed at the segment scale. The Serial Discontinuity Concept (SDC) was proposed by Ward and Stanford (1983) to generalize how dams affect upstream-downstream shifts in abiotic and biotic patterns and processes. They defined *Discontinuity distance* (DD) as the longitudinal shift of a given parameter by river regulation; it may be positive (downstream shift), negative (upstream shift), or near zero (no major shift). *Parameter intensity* (PI) is the difference in absolute parameter units between the natural and the regulated system and can be elevated (positive), depressed (negative), or unchanged (near zero) in comparison with the natural river system. We calculated DD and PI for temperature in Missouri River segments below dams. Although, turbidity also showed significant changes in segments below reservoirs, it was

not possible to estimate DD and PI because we could not isolate high turbidity influx from the Yellowstone River from turbidity reductions due to Ft. Peck Lake (Figure 8).

Discontinuity distance and PI were estimated for water temperature by predicting what “normal” temperature would be in inter-reservoir segments. This was accomplished by regressing mean BEND temperature ($x^{1.5}$ transformed) over the sampling period for the 3-year study on kilometer of segment midpoint (Table 1) for the three least-altered (3, 5, and 9) and six channelized (17-27) river segments (Figure 21). Discontinuity distance was calculated as the difference between the midpoint of each inter-reservoir segment and its midpoint kilometer location predicted from the regression. Similarly, PI was calculated as the difference between mean BEND temperature predicted from the regression and observed mean BEND temperature for each inter-reservoir segment. Predicted and observed BEND temperatures were back transformed before subtracting to calculate PI.

Ninety-six percent of the variability in water temperature for least-altered and channelized river segments

was explained by longitudinal position of segments, i.e. kilometer (Figure 21). Parameter intensity for water temperature ranged from -0.6 to -9.2 °C for inter-reservoir segments and largest temperature depressions occurred in segments immediately below the tailwaters of Ft. Peck Lake (7) and Lake Sakakawea (12) (Table 24). Temperature depression below these reservoirs was so great as to yield upstream discontinuity distances outside the range of prediction for the regression (>417.5 km).

To refine our estimate of DD we examined historical water temperature data for the colder water Missouri River about 477 km above the study area at Toston, Montana, (km 3694.4). Toston is the uppermost Missouri River USGS gage, located about 74 km below the origin of the Missouri River at Three Forks, Montana (Figure 1), and about 3 km below Toston dam. Toston is a run-of-the river dam, so has little effect on Missouri River temperature, and temperature at Toston is also little influenced by tributary reservoirs above Three Forks (Hauer et al. 1991). Also, Toston dam is above Canyon Ferry reservoir (km 3688), which depresses Missouri River temperature (Hauer et al. 1991). Mean (\pm 1SD) daily water temperature at Toston between 15 July and 15 October from 1977 to 1986 was 16.5 °C (\pm 4.3 °C), or on average about 3.5 °C warmer

than we recorded for the same season about 910 km downstream in BENDS of segment 7.

Temperature reduction by hypolimnetic releases from large storage reservoirs has a well chronicled history of negative impacts on composition, life-history patterns, population dynamics, and production of native aquatic invertebrates and fishes in rivers below dams (see Ward and Stanford 1982; Petts 1984; National Research Council 1992; Stanford and Ward in press; and references therein). Programs to normalize temperatures and biotic responses below impoundments are meeting with mixed success (O’Keefe et al. 1990; Palmer and O’Keefe 1990; Vinson 2001).

Channelization. The most pervasive association between channelization and bank stabilization was increased water depths and velocities in macrohabitats within channelized segments relative to up-river inter-reservoir and least altered-segments. Water velocity generally tends to increase in the downstream direction (Gordon et al. 1992). However, differences we observed in velocity cannot be attributed entirely to the naturally higher discharge in the lower Missouri River as Latka et al. (1993) reported a higher frequency of shallow, low velocity water in the pre-regulation river channel than following channelization and bank

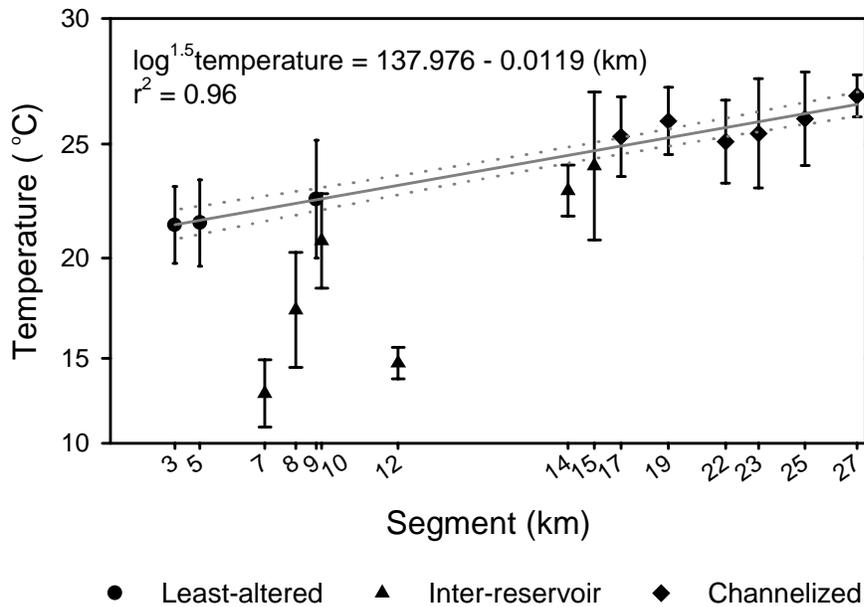


Figure 21. Mean (\pm 1SD) water temperature of BEND macrohabitats (CHXO, ISB, and OSB combined) for all 15 segments and regression \pm 95% confidence intervals for least-altered (3, 5, and 9) and channelized (17-27) segments of Missouri and lower Yellowstone rivers, approximately mid July to early October 1996-1998. Temperature data are $x^{1.5}$ transformed.

Table 24. BEND mean water temperature (from $\log^{1.5}$ transformed data) from approximately mid July to early October 1996-1998 and Missouri River inter-reservoir segment midpoint distances above the Missouri River mouth. Predicted segment midpoint and predicted mean temperature are from the regression in Figure 21. Parameter intensity and discontinuity distance were calculated as observed minus predicted temperature and kilometer, respectively.

Segment	Segment midpoint (km)	Observed mean temperature (°C)	Predicted segment midpoint (km)	Predicted mean temperature (°C)	Discontinuity distance (km)	Parameter intensity (°C)
Ft. Peck Lake						
7	2784.4	13.1	7644.8	22.2	-4860.4	-9.1
8	2641.2	17.5	5449.7	22.5	-2808.5	-5.0
10	2521.3	20.8	3633.0	22.7	-1111.7	-1.9
Lake Sakakawea						
12	2166.5	14.8	6846.4	23.3	-4679.9	-8.5
Lakes Oahe Sharp, and Francis Case						
14	1379.7	23.0	2309.6	24.5	-929.9	-1.5
Lewis and Clark Lake						
15	1257.4	24.1	1661.7	24.7	-404.3	-0.6

stabilization.

Conclusions and Management Recommendations

1. Spatial scale was an important feature explaining physical variability in the Missouri and lower Yellowstone rivers. Temperature, turbidity and conductivity were primarily large spatial-scale variables (zone: $\geq 1,000$ km; segment: ~ 30 - ~ 200 km), although turbidity and conductivity were affected by tributaries at a smaller spatial scale. Differences in depth and velocity were more important at smaller spatial scales (≤ 10 km) and substrate particle size varied at both large and small spatial scales. These results may not be the same for shorter rivers, rivers in non-temperate climates, or rivers that encompass less latitudinal gradient than the Missouri River (i.e., predominately east-west flowing rivers).

These conclusions imply that management actions to normalize water temperature and turbidity along the Missouri River will be more successful if regionally applied at the zone and segment scales through re-regulating flow and

sediment releases from impoundments.

Normalizing depth and velocity can be more effectively accomplished at a local scale by enhancing natural channel geomorphology within river bends (e.g., increasing discrete SCC and SCN macrohabitats).

2. Tributaries ameliorated effects of impoundment and hypolimnetic water releases on depression of temperature and turbidity in the Missouri River. Galat and Lipkin (2000) similarly concluded that tributary discharge was the most important factor offsetting reservoir flow modifications. Management actions to restore some semblance of pre-regulation flow, temperature, and turbidity regimes of the Missouri River need to recognize the role of maintaining or restoring free-flowing tributaries, i.e. incorporate a catchment perspective in river management.

3. Segments with numerous discrete macrohabitats (SCC, SCN, and TRM) exhibited a wider range of most physical variables than segments with reduced macrohabitat

diversity (e.g., low variability in upper channelized segments). Number of tributaries per segment is fixed, but connected and non-connected secondary channels can be increased in the channelized zone where they were historically abundant (Funk and Robinson 1974; Hallberg et al. 1979) by restoring a more natural braided channel geomorphology. This can be accomplished through passive (e.g., abandonment of dikes, revetments, and levees) and intensive (e.g., dike and levee notching and lowering, reconnecting cut-off secondary channels to the main channel, excavating sedimented secondary channels) rehabilitation techniques. Normalization of the Missouri River hydrograph to increase intra- and inter-annual flow and stage variability (Hesse and Mestl 1992; Galat and Lipkin 2000) can improve seasonal connectivity between main and secondary channels, increasing the number of SCCs, their associated sandbars and use by biota. Increasing flow variability will also improve substrate diversity by encouraging channel aggradation and degradation.

4. Parameter intensity provided initial guidelines to re-establish more normal water temperatures in river segments below Ft. Peck Lake and Lake Sakakawea (e.g., +9.2 C for segment 7) between approximately mid July and early October. Resource managers along the Missouri River are proposing to ameliorate temperature depressions below Ft. Peck Dam by controlled surface-water dam releases during the spawning season of the endangered pallid sturgeon (*Scaphirhynchus albus*) (U. S. Fish and Wildlife Service 2000; Patrick Braaten, U. S. Geological Survey, personal communication). Timing of pallid sturgeon reproduction (March-July; Bramblett 1996) largely precedes the period when we evaluated temperature, so our findings cannot contribute directly to this program. However, our sampling interval encompassed much of the growth period for age-0 pallid sturgeon and other warm-water fishes in the inter-reservoir Missouri River. If pallid sturgeon recruitment below Ft. Peck Lake is stimulated by the proposed warm-water releases, it may become beneficial to enhance food resources and sturgeon growth rates by implementing longer duration warm-water releases. The river kilometer-temperature regression approach applied here could aid this effort if refined to shorter time intervals and additional water temperature data are incorpo-

rated. It could further aid in defining a more normalized upper Missouri River water temperature continuum below Ft. Peck and Garrison dams during the growing season for other imperiled and recreational warm-water fishes.

5. Spatial patterns in physical variables reflect natural environmental (i.e., latitude, regional climate, active channel geomorphology, etc.) and anthropogenic (i.e., impoundment, flow regulation, channelization, etc.) determinants. Management actions to improve physical habitat need to distinguish between these two sources of variation, rely on the capacity for self-repair inherent in large rivers, and implement rehabilitation actions at the appropriate spatial scale(s).

6. Patterns of physical variables among zones, segments, and macrohabitats provide a template to assess differences in distribution and abundance of benthic fishes (Volume 3) and their growth, mortality, recruitment, condition, and size structure (Volume 4). A few questions relating spatial scale and physical variables to fishes that will be considered in subsequent volumes of the benthic fishes study include: Are sight-feeding, predatory fishes more common in low turbidity segments below impoundments than higher turbidity segments above impoundments? What benthic fishes frequent high velocity CHXO and OSB macrohabitats versus low velocity TRMS and SCNs? Are some benthic fishes captured at similar velocities (although these might occur in CHXOs in the least-altered zone, but in ISBs in the channelized zone) indicating that velocity rather than macrohabitat is determining habitat use? Are growth and condition of warm-water benthic fishes lower in thermally depressed segments?

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Appendix Tables A1-A9

Macrohabitats not present in a segment were either absent from that segment or not sampled because they did not meet design criteria. Segments 6, 18 and 21 were sampled only in 1996.

Table A1. Mean (untransformed), mean-t (square-root transformed), standard deviation (SD-t, square-root transformed), and sample size (N) for water depth (m) from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Depth 1996				Depth 1997				Depth 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	1.417	1.190	0.114	5	1.289	1.135	0.143	5	1.274	1.129	0.058	5
3	CHXO	1.627	1.276	0.301	5	1.567	1.252	0.203	5	1.668	1.292	0.081	5
3	ISB	1.030	1.015	0.190	5	0.988	0.994	0.110	5	0.855	0.925	0.167	5
3	OSB	1.493	1.222	0.193	5	1.275	1.129	0.229	5	1.268	1.126	0.121	5
3	SCC	0.346	0.588	0.117	5	0.627	0.792	0.278	6	0.334	0.578	0.115	5
3	SCN	0.461	0.679	.	1
5	BEND	1.899	1.378	0.130	5	1.697	1.303	0.289	5	1.754	1.324	0.144	5
5	CHXO	2.418	1.555	0.230	5	2.093	1.447	0.354	5	2.167	1.472	0.231	5
5	ISB	1.164	1.079	0.101	5	1.221	1.105	0.239	5	1.287	1.134	0.112	5
5	OSB	2.046	1.430	0.270	5	1.752	1.324	0.317	5	1.761	1.327	0.234	5
5	SCC	1.791	1.338	0.590	5	1.265	1.125	0.438	10	0.827	0.909	0.417	9
5	SCN	0.739	0.859	0.120	2	0.485	0.697	0.122	3	0.811	0.901	.	1
9	BEND	2.696	1.642	0.200	5	2.504	1.582	0.180	5	2.094	1.447	0.082	5
9	CHXO	2.840	1.685	0.249	5	1.886	1.373	0.197	5	2.295	1.515	0.105	5
9	ISB	1.622	1.274	0.515	5	1.576	1.255	0.107	5	1.246	1.116	0.062	5
9	OSB	3.220	1.795	0.547	5	3.997	1.999	0.335	5	2.705	1.645	0.224	5
9	SCC	0.549	0.741	0.337	5	0.973	0.987	0.351	10	0.961	0.981	0.333	9
9	SCN	1.039	1.019	0.133	5	1.009	1.005	0.133	6	1.188	1.090	0.097	5
9	TRM	1.200	1.095	.	1	1.186	1.089	0.357	2
Inter-reservoir zone													
6	BEND	1.175	1.084	.	1
6	CHXO	1.600	1.265	.	1
6	ISB	0.750	0.866	.	1
6	SCC	0.523	0.723	0.131	5
6	SCN	3.089	1.758	0.168	5
6	TRM	3.214	1.793	0.072	2
7	BEND	2.742	1.656	0.091	5	2.885	1.698	0.238	5	1.940	1.393	0.096	5
7	CHXO	2.695	1.642	0.208	5	3.114	1.765	0.240	5	2.101	1.450	0.190	5
7	ISB	1.815	1.347	0.183	5	1.726	1.314	0.360	5	1.142	1.068	0.103	5
7	OSB	3.610	1.900	0.284	5	3.748	1.936	0.255	5	2.542	1.594	0.161	5
7	SCC	0.820	0.906	0.205	3	1.558	1.248	0.331	7	0.818	0.905	0.249	10
7	SCN	0.708	0.842	0.000	2	1.091	1.045	0.075	5	1.089	1.044	0.141	5
7	TRM	1.123	1.060	0.120	4	1.981	1.407	0.352	5	1.712	1.309	0.007	2
8	BEND	3.113	1.764	0.171	5	3.044	1.745	0.084	5	2.277	1.509	0.111	5
8	CHXO	3.651	1.911	0.259	5	2.764	1.662	0.143	5	2.527	1.590	0.352	5
8	ISB	1.398	1.182	0.092	5	1.779	1.334	0.219	5	1.418	1.191	0.049	5
8	OSB	4.186	2.046	0.378	5	4.514	2.125	0.211	5	2.772	1.665	0.232	5
8	SCC	1.452	1.205	0.456	5	1.286	1.134	0.402	10	1.006	1.003	0.245	10
8	SCN	1.097	1.048	0.125	5	1.535	1.239	0.316	5	1.262	1.124	0.164	6

Table A1, water depth, continued.

Segment	Macrohabitat	Depth 1996				Depth 1997				Depth 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
8	TRM	1.915	1.384	0.107	3	2.246	1.499	0.342	5	1.808	1.344	0.366	4
10	BEND	4.442	2.108	0.127	5	3.622	1.903	0.164	5	3.528	1.878	0.106	5
10	CHXO	6.764	2.601	0.413	5	4.649	2.156	0.297	5	4.324	2.079	0.240	5
10	ISB	1.460	1.208	0.794	5	2.039	1.428	0.596	5	2.946	1.716	0.552	5
10	OSB	4.483	2.117	0.150	5	3.877	1.969	0.366	4	3.019	1.738	0.193	4
10	SCC	0.845	0.919	0.640	5	0.675	0.821	0.514	6	0.611	0.782	0.445	4
10	SCN	1.129	1.063	0.357	4	1.273	1.128	0.182	4	0.840	0.917	0.141	2
10	TRM	3.939	1.985	.	1	3.344	1.829	.	1
12	BEND	3.211	1.792	0.343	5	3.203	1.790	0.114	5	2.083	1.443	0.165	5
12	CHXO	4.096	2.024	0.234	5	3.697	1.923	0.127	5	2.403	1.550	0.220	5
12	ISB	0.421	0.649	0.071	4	1.656	1.287	0.584	5	1.294	1.138	0.561	5
12	OSB	3.947	1.987	0.175	4	4.091	2.023	0.228	4	2.243	1.498	0.073	4
12	SCC	1.818	1.348	0.902	5	0.351	0.593	0.210	5	0.528	0.727	0.462	6
12	SCN	0.575	0.758	0.237	5	0.795	0.892	0.179	5	1.588	1.260	0.109	2
12	TRM	2.260	1.503	0.060	4	2.728	1.652	0.055	2	1.804	1.343	0.088	2
14	BEND	4.082	2.020	0.111	5	3.905	1.976	0.115	5	2.893	1.701	0.192	5
14	CHXO	4.850	2.202	0.336	5	4.500	2.121	0.171	5	3.294	1.815	0.314	5
14	ISB	3.665	1.915	0.395	5	2.511	1.585	0.117	5	1.677	1.295	0.128	5
14	OSB	3.250	1.803	0.263	4	4.681	2.164	0.158	5	3.675	1.917	0.184	5
14	SCC	1.577	1.256	0.239	4	2.153	1.467	0.400	6	0.993	0.997	0.276	10
14	SCN	1.074	1.036	0.186	4	1.467	1.211	.	1	0.750	0.866	0.259	2
14	TRM	1.803	1.343	0.067	4	2.142	1.463	0.145	5	1.010	1.005	0.177	3
15	BEND	3.319	1.822	0.261	5	3.810	1.952	0.090	5	2.784	1.669	0.179	5
15	CHXO	3.736	1.933	0.271	5	3.552	1.885	0.242	5	2.602	1.613	0.313	5
15	ISB	1.678	1.295	0.757	5	2.143	1.464	0.163	5	1.777	1.333	0.213	5
15	OSB	4.144	2.036	0.237	5	5.663	2.380	0.174	5	3.821	1.955	0.379	5
15	SCC	1.086	1.042	0.352	5	1.165	1.080	0.503	10	1.009	1.004	0.332	10
15	SCN	1.010	1.005	0.149	4	0.540	0.735	0.108	2	1.338	1.157	0.153	2
15	TRM	2.092	1.447	0.503	5	2.464	1.570	0.655	5	2.450	1.565	0.348	3
Channelized zone													
17	BEND	5.026	2.242	0.069	5	4.855	2.203	0.066	5	3.577	1.891	0.038	5
17	CHXO	5.728	2.393	0.094	5	6.355	2.521	0.159	5	4.529	2.128	0.115	5
17	ISB	3.046	1.745	0.236	5	2.162	1.471	0.139	5	1.795	1.340	0.141	5
17	OSB	6.238	2.498	0.181	5	6.010	2.452	0.122	5	4.357	2.087	0.176	5
17	SCC	0.750	0.866	.	1
17	TRM	1.930	1.389	0.479	6	1.909	1.382	0.150	6	1.975	1.405	0.332	5
18	BEND	5.065	2.251	0.097	5
18	CHXO	6.040	2.458	0.138	5
18	ISB	3.498	1.870	0.124	5
18	OSB	5.631	2.373	0.167	5
18	SCC	2.900	1.703	.	1
18	TRM	1.803	1.343	0.237	6
19	BEND	5.359	2.315	0.024	5	5.211	2.283	0.085	5	4.007	2.002	0.085	5
19	CHXO	6.187	2.487	0.066	5	6.091	2.468	0.107	5	4.682	2.164	0.102	5
19	ISB	3.934	1.983	0.182	5	3.603	1.898	0.348	5	2.673	1.635	0.168	5

Table A1, water depth, continued.

Segment	Macrohabitat	Depth 1996				Depth 1997				Depth 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
19	OSB	5.909	2.431	0.156	5	5.842	2.417	0.105	5	4.647	2.156	0.087	5
19	SCC	0.805	0.897	0.463	2	1.325	1.151	0.015	2	2.206	1.485	0.551	2
19	TRM	1.825	1.351	0.458	6	2.035	1.426	0.303	6	2.073	1.440	0.131	4
21	BEND	4.888	2.211	0.112	5
21	CHXO	5.710	2.390	0.177	5
21	ISB	3.358	1.832	0.155	5
21	OSB	5.570	2.360	0.117	5
21	SCC	2.700	1.643	.	1
21	TRM	1.497	1.224	0.481	5
22	BEND	4.747	2.179	0.127	5	5.515	2.348	0.169	5	3.988	1.997	0.034	5
22	CHXO	6.225	2.495	0.209	5	7.159	2.676	0.148	4	5.197	2.280	0.126	5
22	ISB	2.806	1.675	0.070	5	4.588	2.142	0.257	5	2.259	1.503	0.280	5
22	OSB	5.199	2.280	0.124	5	5.347	2.312	0.074	5	4.414	2.101	0.155	5
22	SCC	0.933	0.966	.	1	0.467	0.683	.	1
22	SCN	1.817	1.348	.	1	0.790	0.889	0.048	3
22	TRM	1.435	1.198	0.341	5	1.468	1.211	0.412	7	1.295	1.138	0.319	7
23	BEND	5.295	2.301	0.048	5	4.829	2.197	0.061	5	4.692	2.166	0.076	5
23	CHXO	6.581	2.565	0.156	5	6.282	2.506	0.102	5	5.802	2.409	0.099	5
23	ISB	3.452	1.858	0.164	5	3.203	1.790	0.271	5	3.327	1.824	0.151	5
23	OSB	5.799	2.408	0.143	5	4.936	2.222	0.089	5	4.894	2.212	0.228	5
23	SCC	2.329	1.526	0.223	5	2.267	1.506	0.152	5	1.593	1.262	0.288	5
23	SCN	0.667	0.817	.	1
23	TRM	2.085	1.444	0.399	5	2.039	1.428	0.500	6	1.654	1.286	0.440	6
25	BEND	4.989	2.234	0.110	5	4.626	2.151	0.068	5	4.637	2.153	0.137	5
25	CHXO	6.235	2.497	0.135	5	5.403	2.325	0.182	5	5.685	2.384	0.176	5
25	ISB	3.200	1.789	0.361	5	3.375	1.837	0.170	5	3.276	1.810	0.091	5
25	OSB	5.433	2.331	0.103	5	5.052	2.248	0.113	5	4.936	2.222	0.185	5
25	SCC	1.838	1.356	0.703	5	0.717	0.847	0.478	10	0.734	0.856	0.460	10
25	SCN	2.858	1.691	.	1
25	TRM	1.999	1.414	0.164	5	1.684	1.298	0.296	7	2.081	1.442	0.413	7
27	BEND	4.744	2.178	0.116	5	4.594	2.143	0.077	5	4.705	2.169	0.066	5
27	CHXO	5.877	2.424	0.126	5	5.202	2.281	0.148	5	6.121	2.474	0.108	5
27	ISB	3.045	1.745	0.235	5	3.533	1.880	0.218	5	2.529	1.590	0.178	5
27	OSB	5.281	2.298	0.083	5	4.986	2.233	0.160	5	5.437	2.332	0.081	5
27	SCC	1.141	1.068	0.551	5	0.899	0.948	0.410	10	0.779	0.883	0.422	10
27	SCN	0.802	0.895	0.395	5	1.358	1.165	0.307	5	1.052	1.026	0.291	5
27	TRM	1.114	1.055	0.204	3	0.721	0.849	0.202	4	0.802	0.895	0.132	4

Table A2. Mean (untransformed), mean-t [$\log_{10}(x+1)$ transformed], standard deviation [SD-t, $\log_{10}(x+1)$ transformed], and sample size (N) for current velocity (m/s) from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Velocity 1996				Velocity 1997				Velocity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	0.730	0.238	0.054	5	0.958	0.292	0.042	5	0.815	0.259	0.034	5
3	CHXO	0.958	0.292	0.104	5	1.236	0.350	0.038	5	0.976	0.296	0.032	5
3	ISB	0.549	0.190	0.026	5	0.771	0.248	0.031	5	0.643	0.216	0.034	5
3	OSB	0.661	0.220	0.033	5	0.852	0.268	0.082	5	0.820	0.260	0.055	5
3	SCC	0.576	0.198	0.033	5	0.555	0.192	0.037	6	0.399	0.146	0.064	5
3	SCN	0.017	0.007	.	1
5	BEND	0.595	0.203	0.042	5	0.643	0.216	0.055	5	0.744	0.241	0.031	5
5	CHXO	0.583	0.199	0.060	5	0.716	0.235	0.077	5	0.828	0.262	0.028	5
5	ISB	0.559	0.193	0.020	5	0.550	0.190	0.033	5	0.625	0.211	0.054	5
5	OSB	0.632	0.213	0.067	5	0.656	0.219	0.063	5	0.771	0.248	0.036	5
5	SCC	0.404	0.147	0.040	5	0.359	0.133	0.045	10	0.430	0.155	0.067	9
5	SCN	0.000	0.000	0.000	2	0.000	0.000	0.000	3	0.000	0.000	.	1
9	BEND	0.607	0.206	0.045	5	0.652	0.218	0.093	5	0.884	0.275	0.053	5
9	CHXO	0.718	0.235	0.090	4	0.825	0.261	0.130	5	1.017	0.305	0.065	5
9	ISB	0.390	0.143	0.078	5	0.412	0.150	0.046	5	0.618	0.209	0.052	5
9	OSB	0.684	0.226	0.033	4	0.701	0.231	0.102	5	1.014	0.304	0.051	5
9	SCC	0.183	0.073	0.027	5	0.340	0.127	0.068	10	0.524	0.183	0.075	9
9	SCN	0.010	0.004	0.009	5	0.018	0.008	0.019	6	0.029	0.012	0.022	5
9	TRM	0.000	0.000	.	1	0.000	0.000	0.000	2
Inter-reservoir zone													
6	BEND	0.733	0.239	.	1
6	CHXO	0.850	0.267	.	1
6	ISB	0.617	0.209	.	1
6	SCC	0.201	0.080	0.046	5
6	SCN	0.000	0.000	0.000	5
6	TRM	0.277	0.106	0.092	2
7	BEND	0.850	0.267	0.022	5	0.756	0.245	0.039	5	0.639	0.215	0.028	5
7	CHXO	0.913	0.282	0.020	5	0.866	0.271	0.047	5	0.734	0.239	0.026	5
7	ISB	0.704	0.231	0.044	5	0.543	0.188	0.058	5	0.546	0.189	0.050	5
7	OSB	0.923	0.284	0.042	5	0.853	0.268	0.029	5	0.632	0.213	0.018	5
7	SCC	0.491	0.173	0.045	3	0.541	0.188	0.064	7	0.401	0.146	0.063	10
7	SCN	0.045	0.019	0.027	2	0.000	0.000	0.000	5	0.001	0.001	0.001	5
7	TRM	0.000	0.000	0.000	4	0.000	0.000	0.000	5	0.000	0.000	0.000	2
8	BEND	0.659	0.220	0.025	5	0.817	0.259	0.028	5	0.716	0.234	0.019	5
8	CHXO	0.759	0.245	0.056	5	0.859	0.269	0.035	5	0.784	0.251	0.018	5
8	ISB	0.452	0.162	0.019	5	0.664	0.221	0.046	5	0.547	0.189	0.016	5
8	OSB	0.745	0.242	0.065	5	0.914	0.282	0.047	5	0.814	0.259	0.032	5
8	SCC	0.528	0.184	0.079	5	0.419	0.152	0.052	10	0.507	0.178	0.062	10
8	SCN	0.076	0.032	0.035	5	0.000	0.000	0.000	5	0.005	0.002	0.005	6

Table A2, current velocity, continued.

Segment	Macrohabitat	Velocity 1996				Velocity 1997				Velocity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
8	TRM	0.044	0.019	0.021	3	0.000	0.000	0.000	5	0.113	0.046	0.093	4
10	BEND	0.638	0.214	0.056	5	0.830	0.262	0.029	5	0.977	0.296	0.023	5
10	CHXO	0.820	0.260	0.052	5	1.017	0.305	0.027	5	1.216	0.346	0.032	5
10	ISB	0.406	0.148	0.116	5	0.624	0.211	0.129	5	0.949	0.290	0.106	5
10	OSB	0.668	0.222	0.019	5	0.752	0.244	0.033	4	0.700	0.230	0.021	4
10	SCC	0.261	0.101	0.073	5	0.262	0.101	0.077	6	0.222	0.087	0.091	4
10	SCN	0.000	0.000	0.000	4	0.000	0.000	0.000	4	0.025	0.011	0.015	2
10	TRM	0.606	0.206	.	1	0.681	0.225	.	1
12	BEND	0.773	0.249	0.054	5	0.959	0.292	0.063	5	0.747	0.242	0.033	5
12	CHXO	1.123	0.327	0.050	5	1.093	0.321	0.054	5	0.985	0.298	0.043	5
12	ISB	0.142	0.058	0.040	4	0.733	0.239	0.140	5	0.515	0.181	0.112	5
12	OSB	0.814	0.259	0.040	4	1.002	0.302	0.053	4	0.658	0.220	0.017	4
12	SCC	0.458	0.164	0.160	5	0.074	0.031	0.020	5	0.197	0.078	0.084	6
12	SCN	0.000	0.000	0.000	5	0.014	0.006	0.009	5	0.000	0.000	0.000	2
12	TRM	0.009	0.004	0.005	4	0.060	0.025	0.016	2	0.029	0.012	0.017	2
14	BEND	0.785	0.252	0.014	5	0.679	0.225	0.013	5	0.432	0.156	0.091	5
14	CHXO	0.910	0.281	0.023	5	0.697	0.230	0.017	5	0.586	0.200	0.072	3
14	ISB	0.754	0.244	0.018	5	0.597	0.203	0.019	5	0.377	0.139	0.104	4
14	OSB	0.655	0.219	0.006	4	0.741	0.241	0.026	5	0.592	0.202	0.027	4
14	SCC	0.311	0.118	0.043	4	0.501	0.176	0.078	6	0.269	0.104	0.068	8
14	SCN	0.048	0.020	0.025	4	0.017	0.007	.	1	0.000	0.000	.	1
14	TRM	0.027	0.012	0.023	4	0.000	0.000	0.000	3	0.000	0.000	.	1
15	BEND	0.879	0.274	0.052	5	0.785	0.252	0.020	5	0.953	0.291	0.053	5
15	CHXO	1.078	0.318	0.032	5	0.815	0.259	0.042	4	1.040	0.310	0.017	4
15	ISB	0.594	0.202	0.118	5	0.513	0.180	0.025	5	0.722	0.236	0.103	5
15	OSB	0.933	0.286	0.058	5	1.022	0.306	0.037	5	1.015	0.304	0.036	5
15	SCC	0.502	0.177	0.069	5	0.432	0.156	0.075	10	0.463	0.165	0.068	8
15	SCN	0.032	0.014	0.027	4	0.061	0.026	0.036	2	0.175	0.070	.	1
15	TRM	0.015	0.006	0.011	5	0.024	0.010	0.021	4	0.142	0.057	0.038	3
Channelized zone													
17	BEND	1.151	0.333	0.037	5	1.241	0.350	0.018	5	0.978	0.296	0.009	5
17	CHXO	1.490	0.396	0.044	5	1.704	0.432	0.015	5	1.325	0.366	0.010	5
17	ISB	0.656	0.219	0.042	5	0.533	0.186	0.034	5	0.471	0.168	0.028	5
17	OSB	1.302	0.362	0.036	5	1.482	0.395	0.028	5	1.130	0.328	0.034	5
17	SCC	0.200	0.079	.	1
17	TRM	0.214	0.084	0.034	6	0.050	0.021	0.014	6	0.154	0.062	0.060	5
18	BEND	1.284	0.359	0.015	5
18	CHXO	1.612	0.417	0.022	5
18	ISB	0.817	0.259	0.015	5
18	OSB	1.418	0.383	0.023	5
18	SCC	0.950	0.290	.	1
18	TRM	0.143	0.058	0.092	6
19	BEND	1.276	0.357	0.040	5	1.416	0.383	0.008	5	1.075	0.317	0.012	5
19	CHXO	1.718	0.434	0.036	4	2.054	0.485	0.014	5	1.542	0.405	0.024	5
19	ISB	0.802	0.256	0.048	5	0.418	0.152	0.037	5	0.413	0.150	0.039	5

Table A2, current velocity, continued.

Segment	Macrohabitat	Velocity 1996				Velocity 1997				Velocity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
19	OSB	1.471	0.393	0.013	5	1.768	0.442	0.022	5	1.262	0.354	0.018	5
19	SCC	0.433	0.156	0.048	2	0.582	0.199	0.003	2	0.566	0.195	0.023	2
19	TRM	0.113	0.047	0.038	6	0.071	0.030	0.022	6	0.235	0.092	0.053	4
21	BEND	1.162	0.335	0.017	5
21	CHXO	1.627	0.419	0.009	5
21	ISB	0.555	0.192	0.054	5
21	OSB	1.297	0.361	0.023	5
21	SCC	1.013	0.304	.	1
21	TRM	0.052	0.022	0.017	5
22	BEND	1.106	0.324	0.019	5	1.145	0.331	0.042	5	1.023	0.306	0.011	5
22	CHXO	1.510	0.400	0.052	5	1.741	0.438	0.024	4	1.599	0.415	0.034	5
22	ISB	0.442	0.159	0.029	5	0.570	0.196	0.041	5	0.351	0.131	0.031	5
22	OSB	1.353	0.372	0.014	5	1.318	0.365	0.027	5	1.111	0.325	0.018	5
22	SCC	0.350	0.130	.	1	0.333	0.125	.	1
22	SCN	0.183	0.073	.	1	0.078	0.033	0.032	3
22	TRM	0.022	0.009	0.014	5	0.013	0.006	0.010	7	0.155	0.063	0.105	7
23	BEND	1.138	0.330	0.007	5	1.082	0.318	0.005	5	1.084	0.319	0.032	5
23	CHXO	1.616	0.418	0.017	5	1.619	0.418	0.016	5	1.621	0.418	0.041	5
23	ISB	0.532	0.185	0.040	5	0.485	0.172	0.023	5	0.457	0.164	0.028	5
23	OSB	1.257	0.353	0.024	5	1.138	0.330	0.010	5	1.170	0.336	0.033	5
23	SCC	0.817	0.259	0.038	5	0.640	0.215	0.031	5	0.471	0.168	0.041	5
23	SCN	0.417	0.151	.	1
23	TRM	0.053	0.022	0.044	5	0.066	0.028	0.027	6	0.151	0.061	0.070	6
25	BEND	0.923	0.284	0.105	5	0.926	0.285	0.012	5	0.985	0.298	0.031	5
25	CHXO	1.653	0.424	0.066	4	1.197	0.342	0.023	5	1.342	0.370	0.047	5
25	ISB	0.468	0.167	0.038	5	0.501	0.176	0.039	5	0.452	0.162	0.014	5
25	OSB	0.966	0.294	0.128	5	1.071	0.316	0.028	5	1.155	0.333	0.041	5
25	SCC	0.384	0.141	0.131	4	0.380	0.140	0.089	10	0.287	0.110	0.071	10
25	SCN	0.000	0.000	.	1
25	TRM	0.012	0.005	0.008	5	0.025	0.011	0.017	7	0.173	0.069	0.077	7
27	BEND	0.816	0.259	0.120	5	1.012	0.304	0.028	5	0.973	0.295	0.008	5
27	CHXO	1.721	0.435	0.030	3	1.441	0.388	0.052	5	1.394	0.379	0.012	5
27	ISB	0.424	0.154	0.050	5	0.470	0.167	0.041	5	0.311	0.118	0.035	5
27	OSB	0.929	0.285	0.134	5	1.111	0.325	0.024	5	1.208	0.344	0.026	5
27	SCC	0.409	0.149	0.114	5	0.310	0.117	0.101	10	0.372	0.137	0.068	10
27	SCN	0.074	0.031	0.042	5	0.083	0.035	0.050	5	0.050	0.021	0.026	5
27	TRM	0.008	0.004	0.006	3	0.000	0.000	0.000	4	0.029	0.012	0.004	4

Table A3. Mean (untransformed), mean-t ($x^{1.5}$ transformed), standard deviation (SD-t, $x^{1.5}$ transformed), and sample size (N) for water temperature ($^{\circ}\text{C}$) from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Temperature 1996				Temperature 1997				Temperature 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	21.51	99.77	8.18	5	20.91	95.63	5.82	5	22.12	104.06	18.96	5
3	CHXO	21.67	100.87	12.19	5	20.65	93.86	5.85	5	21.74	101.40	23.00	5
3	ISB	21.51	99.77	7.54	5	21.22	97.75	5.63	5	22.70	108.12	16.45	5
3	OSB	21.36	98.71	5.90	5	20.87	95.32	7.17	5	21.94	102.80	18.36	5
3	SCC	21.20	97.63	3.65	5	23.72	115.54	5.95	6	20.68	94.06	3.22	5
3	SCN	20.10	90.11	.	1
5	BEND	21.62	100.50	6.94	5	22.41	106.08	13.38	5	20.78	94.75	18.15	5
5	CHXO	22.08	103.72	5.41	5	22.33	105.50	13.90	5	20.70	94.15	17.58	5
5	ISB	20.42	92.29	10.90	5	23.02	110.48	14.50	5	20.97	96.03	19.26	5
5	OSB	22.37	105.78	8.74	5	21.88	102.38	13.21	5	20.68	94.07	17.66	5
5	SCC	22.12	104.01	11.46	5	19.20	84.12	31.65	10	19.51	86.16	31.14	9
5	SCN	23.97	117.32	25.91	2	20.16	90.49	16.98	3	26.85	139.13	.	1
9	BEND	22.57	107.24	7.92	5	21.71	101.18	30.90	5	23.65	115.03	6.98	5
9	CHXO	22.38	105.90	11.35	5	21.88	102.38	30.35	5	23.60	114.68	6.63	5
9	ISB	22.67	107.96	2.58	5	21.76	101.48	30.59	5	23.79	116.02	7.16	5
9	OSB	22.67	107.95	10.87	5	21.50	99.72	32.11	5	23.57	114.40	7.29	5
9	SCC	23.08	110.89	10.25	5	18.98	82.67	22.70	10	22.19	104.50	25.02	9
9	SCN	22.70	108.19	12.00	5	20.16	90.52	25.83	6	23.92	116.99	17.87	5
9	TRM	23.70	115.38	.	1	22.80	108.84	13.92	2
Inter-reservoir zone													
6	BEND	13.48	49.46	.	1
6	CHXO	10.00	31.62	.	1
6	ISB	16.95	69.78	.	1
6	SCC	12.12	42.21	2.01	5
6	SCN	16.91	69.54	21.80	5
6	TRM	18.70	80.87	0.00	2
7	BEND	11.52	39.12	8.34	5	13.52	49.69	3.53	5	14.05	52.68	13.42	5
7	CHXO	11.65	39.76	9.09	5	13.41	49.11	3.64	5	13.67	50.57	12.98	5
7	ISB	11.75	40.26	9.70	5	13.66	50.50	4.10	5	14.31	54.14	14.52	5
7	OSB	11.20	37.47	8.46	5	13.48	49.49	3.46	5	14.18	53.38	13.05	5
7	SCC	12.01	41.65	12.21	3	14.67	56.21	5.82	7	14.81	57.00	13.26	0
7	SCN	8.28	23.81	5.79	2	16.35	66.10	7.36	5	19.41	85.50	15.66	5
7	TRM	8.21	23.50	6.85	4	14.90	57.50	7.80	4	21.75	101.44	14.83	2
8	BEND	14.88	57.37	17.40	5	17.20	71.31	3.37	5	20.24	91.03	9.88	5
8	CHXO	15.13	58.86	18.31	5	17.17	71.14	4.13	5	20.29	91.42	10.22	5

Table A3, water temperature continued.

Segment	Macrohabitat	Temperature 1996				Temperature 1997				Temperature 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
18	CHXO	25.00	125.00	0.84	5
18	ISB	24.99	124.94	2.99	5
18	OSB	25.05	125.40	1.61	5
18	SCC	25.20	126.50	.	1
18	TRM	23.97	117.36	13.70	6
19	BEND	25.40	128.02	2.95	5	26.08	133.15	15.93	5	26.40	135.67	9.09	5
19	CHXO	25.51	128.86	3.67	5	26.25	134.48	16.78	5	26.54	136.72	8.90	5
19	ISB	25.26	126.99	2.27	5	25.81	131.12	15.70	5	26.40	135.66	9.50	5
19	OSB	25.43	128.22	3.23	5	26.17	133.90	16.32	5	26.27	134.64	8.91	5
19	SCC	25.95	132.19	1.62	2	23.07	110.80	3.74	2	28.15	149.33	8.53	2
19	TRM	23.44	113.50	13.14	6	23.43	113.43	18.37	6	24.96	124.67	22.07	4
21	BEND	25.42	128.19	4.40	5
21	CHXO	24.93	124.45	6.97	5
21	ISB	25.65	129.92	2.52	5
21	OSB	25.69	130.24	4.77	5
21	SCC	25.75	130.67	.	1
21	TRM	24.86	123.98	6.84	5
22	BEND	24.44	120.86	17.89	5	24.39	120.47	6.09	5	26.45	136.07	6.03	5
22	CHXO	23.35	112.87	28.56	5	24.30	119.81	4.80	5	26.42	135.80	12.48	5
22	ISB	25.00	124.97	15.48	5	24.43	120.77	7.87	5	26.49	136.36	5.02	5
22	OSB	25.06	125.45	17.00	5	24.44	120.82	6.09	5	26.46	136.13	4.20	5
22	SCC	26.50	136.42	.	1	25.55	129.15	.	1
22	SCN	26.35	135.26	.	1	23.86	116.55	6.04	3
22	TRM	24.28	119.63	12.45	5	24.95	124.62	8.20	7	23.88	116.71	18.17	7
23	BEND	24.72	122.91	21.52	5	24.66	122.46	15.72	5	26.93	139.75	8.31	5
23	CHXO	24.59	121.96	19.54	5	24.07	118.10	14.24	5	26.91	139.62	5.33	5
23	ISB	24.82	123.62	23.55	5	25.03	125.21	17.87	5	27.52	144.41	21.53	5
23	OSB	24.76	123.17	21.71	5	24.89	124.16	16.06	5	26.38	135.51	4.30	5
23	SCC	22.22	104.71	30.79	5	25.35	127.61	17.34	5	26.20	134.08	5.39	5
23	SCN	27.05	140.69	.	1
23	TRM	21.86	102.23	19.75	5	23.25	112.10	11.63	6	23.22	111.92	24.26	6
25	BEND	25.88	131.69	1.95	5	26.19	134.00	19.03	5	26.09	133.25	19.51	5
25	CHXO	25.98	132.39	2.32	5	26.34	135.18	19.68	5	25.81	131.14	18.54	5
25	ISB	25.84	131.32	2.49	5	26.11	133.41	18.66	5	26.44	135.97	21.29	5
25	OSB	25.84	131.36	1.72	5	26.11	133.42	18.82	5	26.01	132.65	18.83	5
25	SCC	24.53	121.49	18.03	5	23.91	116.89	25.39	10	26.64	137.50	15.42	0
25	SCN	23.50	113.92	.	1
25	TRM	24.06	118.04	16.61	5	22.36	105.74	20.36	7	24.53	121.52	23.94	7
27	BEND	27.08	140.91	4.25	5	26.64	137.51	4.36	5	27.23	142.08	9.84	5
27	CHXO	27.20	141.89	6.03	5	26.50	136.43	3.85	5	27.11	141.19	8.52	5
27	ISB	27.07	140.85	2.95	5	26.83	138.99	5.45	5	27.46	143.92	11.52	5

Table A3, water temperature continued.

Segment	Macrohabitat	Temperature 1996				Temperature 1997				Temperature 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
27	OSB	26.96	139.98	3.84	5	26.59	137.10	4.23	5	27.11	141.16	9.59	5
27	SCC	28.20	149.75	.	1	25.23	126.72	19.87	10	27.66	145.50	13.75	0
27	SCN	27.58	144.85	8.24	3	25.90	131.78	19.77	5	28.48	151.96	16.64	5
27	TRM	26.25	134.50	2.72	2	24.10	118.32	16.75	4	24.50	121.27	13.47	4

Table A4. Mean (untransformed), mean-t (\log_{10} transformed), standard deviation (SD-t, \log_{10} transformed), and sample size (N) for turbidity (NTU) from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Turbidity 1996				Turbidity 1997				Turbidity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	31.3	1.496	0.537	5	23.3	1.368	0.264	5	34.8	1.542	0.327	5
3	CHXO	19.6	1.292	0.387	5	16.1	1.208	0.054	5	30.2	1.480	0.336	5
3	ISB	42.0	1.623	0.717	5	20.4	1.310	0.187	5	39.4	1.595	0.403	5
3	OSB	17.5	1.242	0.232	5	26.9	1.430	0.426	5	32.1	1.506	0.280	5
3	SCC	19.8	1.297	0.347	5	69.6	1.843	0.185	6	10.8	1.035	0.026	5
3	SCN	20.0	1.301	.	1
5	BEND	18.4	1.266	0.155	5	51.6	1.712	0.279	5	21.9	1.340	0.196	5
5	CHXO	13.1	1.117	0.063	5	31.6	1.500	0.283	5	18.6	1.269	0.141	5
5	ISB	26.2	1.419	0.315	5	51.3	1.711	0.346	5	23.7	1.375	0.235	5
5	OSB	11.9	1.074	0.103	5	56.4	1.752	0.407	5	22.5	1.352	0.218	5
5	SCC	16.0	1.205	0.135	5	21.4	1.331	0.126	10	21.4	1.331	0.196	9
5	SCN	52.4	1.719	0.185	2	27.0	1.431	0.097	3	65.8	1.818	.	1
9	BEND	26.5	1.423	0.149	5	114.1	2.057	0.664	5	126.3	2.101	0.534	5
9	CHXO	25.1	1.400	0.194	5	114.5	2.059	0.679	5	131.8	2.120	0.559	5
9	ISB	29.0	1.462	0.090	5	115.8	2.064	0.636	5	125.7	2.099	0.518	5
9	OSB	24.6	1.390	0.188	5	109.7	2.040	0.687	5	120.1	2.080	0.523	5
9	SCC	25.2	1.401	0.169	5	49.1	1.691	0.442	10	81.8	1.913	0.431	8
9	SCN	24.9	1.396	0.218	5	88.8	1.948	0.504	6	59.5	1.775	0.262	5
9	TRM	648.0	2.812	.	1	73.5	1.866	0.506	2
Inter-reservoir zone													
6	BEND	9.7	0.986	.	1
6	CHXO	9.5	0.977	.	1
6	ISB	9.9	0.996	.	1
6	SCC	3.1	0.495	0.117	5
6	SCN	2.7	0.432	0.063	5
6	TRM	15.2	1.183	0.152	2
7	BEND	12.0	1.079	0.106	5	16.5	1.219	0.270	5	24.8	1.394	0.611	5
7	CHXO	10.9	1.039	0.282	5	16.5	1.218	0.317	5	24.7	1.393	0.731	5
7	ISB	10.5	1.022	0.165	5	17.4	1.241	0.192	5	18.0	1.255	0.404	5
7	OSB	12.0	1.078	0.214	5	15.1	1.180	0.324	5	27.3	1.437	0.635	5
7	SCC	11.0	1.043	0.260	3	18.6	1.271	0.242	7	17.2	1.237	0.156	10
7	SCN	15.0	1.176	0.052	2	18.5	1.268	0.080	5	38.9	1.590	0.322	5
7	TRM	16.7	1.222	0.115	3	17.1	1.233	0.303	5	182.0	2.260	0.473	2
8	BEND	43.3	1.637	0.215	5	59.5	1.775	0.131	5	111.8	2.049	0.425	5
8	CHXO	40.8	1.611	0.277	5	60.2	1.779	0.116	5	110.5	2.043	0.438	5
8	ISB	43.9	1.643	0.122	5	57.6	1.760	0.153	5	115.6	2.063	0.422	5
8	OSB	43.2	1.635	0.273	5	60.7	1.783	0.126	5	108.4	2.035	0.421	5
8	SCC	53.0	1.724	0.104	5	54.8	1.739	0.216	10	81.3	1.910	0.278	10

Table A4, turbidity continued.

Segment	Macrohabitat	Turbidity 1996				Turbidity 1997				Turbidity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
8	SCN	52.2	1.718	0.232	5	33.2	1.522	0.149	5	76.8	1.886	0.307	6
8	TRM	29.8	1.475	0.360	3	31.4	1.497	0.293	5	47.7	1.679	0.430	4
10	BEND	78.3	1.894	0.144	5	189.8	2.278	0.160	5	548.4	2.739	0.079	5
10	CHXO	79.9	1.903	0.215	5	176.7	2.247	0.189	5	865.7	2.937	0.073	4
10	ISB	84.4	1.926	0.181	5	161.9	2.209	0.059	5	505.7	2.704	0.435	4
10	OSB	65.9	1.819	0.025	5	261.9	2.418	0.188	4	162.1	2.210	0.128	4
10	SCC	84.7	1.928	0.267	5	148.8	2.173	0.176	6	81.6	1.912	0.202	4
10	SCN	48.6	1.687	0.220	4	51.4	1.711	0.173	4	108.7	2.036	0.089	2
10	TRM	235.3	2.372	.	1	197.1	2.295	.	1
12	BEND	10.3	1.011	0.170	5	5.5	0.742	0.057	5	8.4	0.922	0.149	5
12	CHXO	6.8	0.832	0.301	5	4.8	0.684	0.100	5	7.8	0.890	0.252	5
12	ISB	11.5	1.061	0.113	3	5.1	0.705	0.105	5	6.5	0.815	0.069	5
12	OSB	9.5	0.976	0.090	4	6.6	0.822	0.106	4	8.8	0.945	0.236	4
12	SCC	8.1	0.907	0.282	5	5.1	0.705	0.074	5	12.4	1.093	0.150	6
12	SCN	6.9	0.841	0.348	5	11.4	1.058	0.563	5	10.3	1.013	0.050	2
12	TRM	10.2	1.008	0.142	4	42.1	1.624	0.797	2	121.6	2.085	0.447	2
14	BEND	3.5	0.550	0.128	5	4.7	0.675	0.122	5	7.3	0.862	0.136	5
14	CHXO	3.0	0.474	0.077	5	3.6	0.562	0.071	5	5.8	0.765	0.166	5
14	ISB	3.4	0.532	0.167	4	4.5	0.654	0.106	5	8.4	0.924	0.279	5
14	OSB	5.9	0.774	0.044	3	5.8	0.766	0.194	5	6.4	0.808	0.106	4
14	SCC	6.4	0.806	0.138	3	6.2	0.793	0.124	5	6.7	0.824	0.232	10
14	SCN	5.8	0.762	.	1	34.0	1.532	.	1	20.2	1.306	0.107	2
14	TRM	7.4	0.872	0.149	3	9.6	0.983	0.088	5	19.9	1.298	0.182	3
15	BEND	30.5	1.485	0.099	5	25.8	1.411	0.049	5	23.9	1.378	0.108	5
15	CHXO	27.0	1.432	0.071	3	25.6	1.408	0.041	5	21.1	1.323	0.178	5
15	ISB	32.1	1.507	0.111	5	26.7	1.426	0.060	5	22.4	1.350	0.023	4
15	OSB	26.5	1.424	0.125	4	25.0	1.398	0.067	5	23.8	1.376	0.178	4
15	SCC	22.4	1.350	0.230	4	29.1	1.464	0.069	9	22.1	1.345	0.122	10
15	SCN	22.4	1.351	0.161	3	16.2	1.210	0.173	2	21.3	1.329	0.040	2
15	TRM	29.8	1.474	0.147	5	37.2	1.570	0.289	5	44.8	1.652	0.339	3
Channelized zone													
17	BEND	71.5	1.854	0.541	5	31.5	1.498	0.050	5	37.5	1.574	0.095	5
17	CHXO	69.7	1.844	0.595	5	31.7	1.501	0.067	5	36.6	1.564	0.075	5
17	ISB	68.7	1.837	0.453	5	31.4	1.497	0.049	5	39.9	1.601	0.159	5
17	OSB	72.8	1.862	0.562	5	31.1	1.493	0.062	5	35.0	1.545	0.060	5
17	SCC	32.5	1.512	.	1
17	TRM	77.3	1.888	0.452	6	22.9	1.361	0.230	6	64.7	1.811	0.232	5
18	BEND	35.5	1.550	0.077	5
18	CHXO	31.9	1.504	0.031	5
18	ISB	33.1	1.520	0.024	5
18	OSB	40.2	1.604	0.159	5
18	SCC	213.5	2.329	.	1
18	TRM	138.6	2.142	0.476	6
19	BEND	107.3	2.031	0.144	5	44.2	1.646	0.033	5	75.0	1.875	0.133	5

Table A4, turbidity continued.

Segment	Macrohabitat	Turbidity 1996				Turbidity 1997				Turbidity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
19	CHXO	104.4	2.019	0.156	5	44.3	1.646	0.049	5	73.3	1.865	0.136	5
19	ISB	98.3	1.992	0.127	5	43.0	1.633	0.037	5	72.2	1.859	0.172	5
19	OSB	117.3	2.069	0.172	5	45.2	1.655	0.037	5	77.8	1.891	0.133	5
19	SCC	83.8	1.923	0.077	2	45.0	1.654	0.008	2	57.5	1.760	0.201	2
19	TRM	87.3	1.941	0.232	6	40.5	1.607	0.183	6	162.6	2.211	0.307	4
21	BEND	85.3	1.931	0.128	5
21	CHXO	92.7	1.967	0.066	5
21	ISB	82.7	1.918	0.181	5
21	OSB	78.7	1.896	0.153	5
21	SCC	166.0	2.220	.	1
21	TRM	78.3	1.894	0.269	5
22	BEND	88.2	1.945	0.120	5	96.7	1.986	0.444	5	150.1	2.176	0.348	5
22	CHXO	87.9	1.944	0.144	5	106.8	2.029	0.476	5	135.7	2.133	0.557	3
22	ISB	84.3	1.926	0.117	5	87.7	1.943	0.458	5	163.6	2.214	0.421	5
22	OSB	91.6	1.962	0.107	5	94.6	1.976	0.390	5	99.0	1.995	0.294	5
22	SCC	120.0	2.079	.	1	47.0	1.672	.	1
22	SCN	56.9	1.755	.	1	43.9	1.642	0.132	3
22	TRM	61.1	1.786	0.282	5	61.9	1.791	0.371	7	53.9	1.731	0.586	7
23	BEND	190.3	2.279	0.264	5	83.0	1.919	0.148	5	134.2	2.128	0.225	5
23	CHXO	188.4	2.275	0.388	4	82.9	1.919	0.134	5	127.7	2.106	0.289	5
23	ISB	199.6	2.300	0.279	5	77.1	1.887	0.160	5	125.6	2.099	0.258	5
23	OSB	170.6	2.232	0.188	5	86.1	1.935	0.185	5	145.2	2.162	0.166	5
23	SCC	115.7	2.063	0.224	5	71.0	1.851	0.096	5	110.5	2.043	0.361	5
23	SCN	94.4	1.975	.	1
23	TRM	34.6	1.539	0.283	5	44.9	1.652	0.283	6	112.3	2.051	0.494	6
25	BEND	443.8	2.647	0.331	5	57.0	1.756	0.089	5	347.5	2.541	0.250	5
25	CHXO	502.4	2.701	0.377	5	58.1	1.765	0.101	5	394.2	2.596	0.200	5
25	ISB	390.6	2.592	0.273	5	57.2	1.758	0.088	5	293.6	2.468	0.326	5
25	OSB	428.3	2.632	0.343	5	55.6	1.745	0.079	5	345.4	2.538	0.253	5
25	SCC	250.0	2.398	0.630	5	55.2	1.742	0.243	9	134.3	2.128	0.483	10
25	SCN	13.1	1.117	.	1
25	TRM	49.8	1.698	0.340	5	30.3	1.481	0.202	7	70.8	1.850	0.360	7
27	BEND	165.2	2.218	0.200	5	64.1	1.807	0.371	5	197.4	2.295	0.141	5
27	CHXO	126.9	2.103	0.064	5	61.0	1.785	0.339	5	220.4	2.343	0.156	5
27	ISB	192.9	2.285	0.299	5	64.5	1.809	0.398	5	172.5	2.237	0.107	5
27	OSB	165.7	2.219	0.185	5	66.4	1.822	0.375	5	197.8	2.296	0.164	5
27	SCC	80.5	1.906	0.222	5	66.7	1.824	0.281	10	145.1	2.162	0.173	10
27	SCN	76.5	1.884	0.363	5	72.2	1.859	0.578	5	107.4	2.031	0.198	5
27	TRM	88.5	1.947	0.212	3	52.7	1.722	0.156	4	55.3	1.743	0.179	4

Table A5. Mean (untransformed), mean-t (square-root transformed), standard deviation (SD-t, square-root transformed), and sample size (N) for conductivity ($\mu\text{S}/\text{cm}$) from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Conductivity 1996				Conductivity 1997				Conductivity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	425	20.621	0.832	5	441	21.002	1.943	5	438	20.923	1.224	5
3	CHXO	399	19.961	0.067	5	370	19.232	0.676	5	397	19.936	0.360	5
3	ISB	478	21.858	2.260	5	508	22.536	6.117	5	510	22.592	3.368	5
3	OSB	397	19.924	0.232	5	419	20.480	2.468	5	400	19.994	0.403	5
3	SCC	400	19.989	0.376	5	426	20.637	1.491	6	384	19.583	0.091	5
3	SCN	364	19.081	.	1
5	BEND	412	20.303	0.356	5	398	19.957	0.313	5	396	19.905	0.297	5
5	CHXO	405	20.125	0.458	5	392	19.792	0.346	5	395	19.878	0.337	5
5	ISB	416	20.406	0.320	5	401	20.029	0.492	5	397	19.917	0.274	5
5	OSB	415	20.373	0.406	5	402	20.045	0.287	5	397	19.922	0.281	5
5	SCC	402	20.060	0.556	5	388	19.700	0.050	10	403	20.076	0.214	9
5	SCN	487	22.061	0.864	2	421	20.518	0.642	3	505	22.468	.	1
9	BEND	514	22.668	1.419	5	506	22.483	1.220	5	505	22.472	1.565	5
9	CHXO	501	22.387	1.468	5	503	22.426	1.339	5	505	22.465	1.573	5
9	ISB	535	23.138	1.291	5	510	22.578	1.131	5	504	22.453	1.596	5
9	OSB	486	22.039	1.344	4	504	22.444	1.210	5	506	22.498	1.529	5
9	SCC	523	22.864	1.493	5	553	23.504	0.872	10	577	24.021	2.146	9
9	SCN	617	24.831	3.182	5	599	24.481	2.427	6	605	24.586	1.559	5
9	TRM	1067	32.665	.	1	722	26.873	0.414	2
6	BEND	550	23.461	.	1
6	CHXO	506	22.502	.	1
6	ISB	595	24.382	.	1
6	SCC	598	24.448	0.059	5
6	SCN	605	24.594	0.113	5
6	TRM	715	26.739	3.173	2
Inter-reservoir zone													
7	BEND	612	24.728	0.154	5	595	24.391	0.212	5	589	24.271	0.367	5
7	CHXO	619	24.885	0.296	5	595	24.389	0.202	5	593	24.349	0.469	5
7	ISB	604	24.566	0.207	5	592	24.320	0.130	5	586	24.214	0.470	5
7	OSB	612	24.731	0.179	5	598	24.462	0.343	5	588	24.248	0.341	5
7	SCC	600	24.488	0.701	3	599	24.481	0.292	7	604	24.575	1.329	10
7	SCN	675	25.977	1.837	2	702	26.498	4.384	5	647	25.427	1.691	5
7	TRM	954	30.889	6.308	4	682	26.119	2.403	5	916	30.264	4.577	2
8	BEND	611	24.722	0.073	5	596	24.417	0.168	5	602	24.528	0.294	5
8	CHXO	612	24.728	0.095	5	599	24.480	0.083	5	601	24.524	0.293	5
8	ISB	611	24.712	0.043	5	591	24.305	0.364	5	602	24.533	0.328	5
8	OSB	611	24.726	0.107	5	599	24.465	0.077	5	602	24.528	0.283	5
8	SCC	610	24.699	0.059	5	602	24.534	0.341	10	588	24.254	0.411	10

Table A5, conductivity continued.

Segment	Macrohabitat	Conductivity 1996				Conductivity 1997				Conductivity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
8	SCN	629	25.075	1.419	5	638	25.258	1.143	5	879	29.654	8.561	6
8	TRM	1422	37.714	8.515	3	757	27.514	1.579	5	1374	37.061	9.199	4
10	BEND	481	21.920	0.195	5	480	21.919	0.181	5	447	21.143	0.403	5
10	CHXO	459	21.425	0.221	5	483	21.982	0.133	5	420	20.498	0.627	5
10	ISB	467	21.603	0.390	5	480	21.913	0.186	5	416	20.402	0.866	5
10	OSB	516	22.708	0.121	5	475	21.793	0.308	4	516	22.705	0.822	4
10	SCC	474	21.778	0.546	5	480	21.910	0.333	6	512	22.631	0.657	4
10	SCN	529	22.990	0.377	4	585	24.181	1.729	4	699	26.439	3.280	2
10	TRM	448	21.166	.	1	510	22.592	.	1
12	BEND	500	22.351	0.350	5	479	21.881	0.157	5	504	22.450	0.583	5
12	CHXO	491	22.157	0.468	5	480	21.908	0.097	5	483	21.979	1.424	5
12	ISB	522	22.856	0.577	4	485	22.025	0.148	5	483	21.975	0.314	5
12	OSB	500	22.352	0.305	4	469	21.655	0.290	4	545	23.350	0.983	4
12	SCC	502	22.409	0.775	5	484	21.998	0.460	5	588	24.239	0.331	6
12	SCN	538	23.193	1.355	5	542	23.272	0.915	5	606	24.607	0.400	2
12	TRM	831	28.830	3.419	4	944	30.722	6.482	2	1066	32.655	1.762	2
14	BEND	936	30.591	0.533	5	866	29.432	0.924	5	795	28.198	0.217	5
14	CHXO	957	30.938	0.652	5	851	29.164	0.589	5	801	28.296	0.079	5
14	ISB	921	30.355	0.929	5	874	29.558	1.277	5	794	28.184	0.233	5
14	OSB	941	30.668	0.182	4	874	29.563	1.086	5	790	28.110	0.475	5
14	SCC	958	30.944	0.698	4	826	28.743	1.160	6	801	28.293	0.209	10
14	SCN	1017	31.883	3.032	4	843	29.040	.	1	975	31.231	0.555	2
14	TRM	933	30.541	0.698	4	842	29.013	1.066	3	1250	35.361	7.160	3
15	BEND	893	29.883	2.061	5	833	28.853	1.124	5	779	27.901	0.512	5
15	CHXO	898	29.972	2.284	5	846	29.089	1.174	5	763	27.613	0.546	5
15	ISB	884	29.739	1.961	5	824	28.711	0.961	5	772	27.776	0.606	5
15	OSB	896	29.933	1.981	5	827	28.753	1.307	5	801	28.298	0.992	5
15	SCC	819	28.609	2.335	5	808	28.428	1.302	10	790	28.107	0.466	10
15	SCN	907	30.113	1.347	4	865	29.410	0.361	2	803	28.332	0.306	2
15	TRM	1130	33.608	3.305	5	957	30.930	3.033	5	1140	33.762	5.045	3
Channelized zone													
17	BEND	823	28.690	0.505	5	834	28.887	0.989	5	822	28.671	0.797	5
17	CHXO	819	28.609	0.545	5	832	28.836	1.007	5	825	28.726	0.792	5
17	ISB	832	28.838	0.482	5	840	28.983	1.014	5	815	28.541	0.762	5
17	OSB	819	28.622	0.547	5	832	28.840	0.948	5	826	28.744	0.854	5
17	SCC	835	28.896	.	1
17	TRM	590	24.291	6.656	6	698	26.416	2.637	6	709	26.621	1.230	5
18	BEND	793	28.167	0.128	5
18	CHXO	795	28.203	0.154	5
18	ISB	792	28.136	0.112	5
18	OSB	793	28.162	0.163	5
18	SCC	778	27.893	.	1
18	TRM	565	23.765	3.200	6
19	BEND	802	28.320	0.286	5	848	29.119	0.860	5	803	28.343	0.475	5

Table A5, conductivity continued.

Segment	Macrohabitat	Conductivity 1996				Conductivity 1997				Conductivity 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
19	CHXO	804	28.352	0.320	5	849	29.139	0.936	5	810	28.465	0.452	5
19	ISB	804	28.362	0.284	5	846	29.079	0.785	5	793	28.153	0.752	5
19	OSB	798	28.246	0.264	5	849	29.136	0.898	5	807	28.407	0.432	5
19	SCC	785	28.009	0.139	2	801	28.310	0.039	2	814	28.528	0.595	2
19	TRM	652	25.536	1.299	6	662	25.734	2.171	6	610	24.707	0.495	4
21	BEND	785	28.010	0.154	5
21	CHXO	787	28.055	0.232	5
21	ISB	779	27.907	0.222	5
21	OSB	788	28.068	0.200	5
21	SCC	768	27.713	.	1
21	TRM	460	21.454	1.720	5
22	BEND	791	28.116	0.452	5	765	27.665	1.161	5	635	25.189	2.308	5
22	CHXO	789	28.088	0.565	5	763	27.614	1.272	5	510	22.591	7.525	5
22	ISB	790	28.102	0.407	5	766	27.669	1.165	5	692	26.301	0.821	5
22	OSB	793	28.157	0.394	5	768	27.710	1.078	5	667	25.828	1.207	5
22	SCC	785	28.018	.	1	829	28.784	.	1
22	SCN	837	28.935	.	1	762	27.601	1.029	3
22	TRM	637	25.234	3.765	5	575	23.980	3.581	7	464	21.547	2.733	7
23	BEND	731	27.041	0.716	5	798	28.250	1.085	4	600	24.503	3.615	5
23	CHXO	712	26.676	1.099	5	787	28.046	0.961	3	510	22.577	8.225	5
23	ISB	739	27.175	0.866	5	796	28.204	1.174	4	675	25.983	0.815	5
23	OSB	743	27.250	0.843	5	797	28.229	1.147	4	581	24.096	3.935	5
23	SCC	789	28.088	0.630	5	790	28.106	0.895	5	667	25.823	1.292	5
23	SCN	814	28.526	.	1
23	TRM	572	23.910	3.439	5	598	24.447	3.241	5	345	18.585	5.002	6
25	BEND	638	25.248	1.346	5	797	28.229	0.516	5	603	24.547	2.193	5
25	CHXO	645	25.387	1.581	5	795	28.198	0.459	5	587	24.237	2.034	5
25	ISB	631	25.124	1.115	5	797	28.224	0.550	5	614	24.786	2.370	5
25	OSB	637	25.228	1.378	5	799	28.265	0.551	5	606	24.612	2.196	5
25	SCC	644	25.378	1.210	5	777	27.867	0.904	10	621	24.922	2.639	10
25	SCN	706	26.571	.	1
25	TRM	411	20.269	5.269	4	581	24.101	4.039	7	440	20.965	5.784	7
27	BEND	712	26.688	0.802	5	768	27.704	0.943	5	551	23.467	1.755	5
27	CHXO	735	27.104	0.435	5	774	27.822	0.850	5	540	23.244	1.885	5
27	ISB	687	26.215	1.309	5	764	27.639	0.991	5	559	23.639	1.604	5
27	OSB	715	26.730	0.754	5	764	27.648	1.002	5	553	23.513	1.787	5
27	SCC	756	27.496	.	1	738	27.160	0.854	10	573	23.945	1.510	10
27	SCN	646	25.406	2.644	3	732	27.057	0.894	5	571	23.887	2.911	5
27	TRM	677	26.024	0.747	2	715	26.740	1.542	4	392	19.786	4.605	4

Table A6. Mean (untransformed), mean-t (arcsin square-root transformed), standard deviation (SD-t, arcsin square-root transformed), and sample size (N) for percent gravel from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Gravel 1996				Gravel 1997				Gravel 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	0.513	0.798	0.203	5	0.627	0.914	0.115	5	0.393	0.677	0.165	5
3	CHXO	0.479	0.764	0.615	5	0.841	1.160	0.328	5	0.366	0.649	0.308	5
3	ISB	0.491	0.776	0.189	5	0.589	0.874	0.210	5	0.406	0.691	0.355	5
3	OSB	0.495	0.780	0.275	5	0.465	0.751	0.128	5	0.348	0.631	0.153	5
3	SCC	0.628	0.915	0.294	5	0.761	1.060	0.199	6	0.783	1.086	0.155	5
3	SCN	0.000	0.000	.	1
5	BEND	0.263	0.538	0.130	5	0.476	0.761	0.300	5	0.198	0.461	0.163	5
5	CHXO	0.201	0.465	0.340	5	0.405	0.689	0.396	5	0.162	0.415	0.184	5
5	ISB	0.223	0.492	0.114	5	0.369	0.653	0.264	5	0.148	0.394	0.254	5
5	OSB	0.305	0.585	0.239	5	0.633	0.920	0.426	5	0.254	0.529	0.186	5
5	SCC	0.164	0.417	0.295	5	0.082	0.290	0.207	10	0.181	0.440	0.325	9
5	SCN	0.000	0.000	0.000	2	0.060	0.248	0.286	3	0.100	0.322	.	1
9	BEND	0.299	0.578	0.432	5	0.389	0.673	0.406	5	0.404	0.688	0.386	5
9	CHXO	0.387	0.671	0.543	5	0.450	0.735	0.617	5	0.388	0.673	0.524	5
9	ISB	0.143	0.387	0.396	5	0.272	0.548	0.432	5	0.302	0.582	0.462	5
9	OSB	0.350	0.633	0.530	5	0.201	0.465	0.439	5	0.471	0.756	0.357	5
9	SCC	0.198	0.461	0.334	5	0.147	0.394	0.403	10	0.287	0.566	0.439	9
9	SCN	0.009	0.095	0.157	5	0.032	0.179	0.202	6	0.018	0.134	0.239	5
9	TRM	0.000	0.000	.	1	0.000	0.000	0.000	2
Inter-reservoir zone													
6	BEND	0.469	0.754	.	1
6	CHXO	0.638	0.925	.	1
6	ISB	0.300	0.580	.	1
6	SCC	0.153	0.402	0.426	5
6	SCN	0.002	0.039	0.087	5
6	TRM	0.388	0.673	0.951	2
7	BEND	0.139	0.381	0.117	5	0.108	0.335	0.262	5	0.150	0.398	0.313	5
7	CHXO	0.073	0.274	0.101	5	0.115	0.346	0.357	5	0.070	0.268	0.296	5
7	ISB	0.021	0.145	0.155	5	0.018	0.135	0.141	5	0.099	0.320	0.340	5
7	OSB	0.270	0.546	0.328	5	0.184	0.444	0.318	5	0.260	0.535	0.385	5
7	SCC	0.126	0.364	0.386	3	0.078	0.283	0.303	7	0.026	0.162	0.282	10
7	SCN	0.000	0.000	0.000	2	0.000	0.000	0.000	5	0.000	0.000	0.000	5
7	TRM	0.006	0.080	0.161	4	0.000	0.000	0.000	5	0.013	0.113	0.160	2
8	BEND	0.052	0.231	0.154	5	0.008	0.092	0.102	5	0.020	0.143	0.162	5
8	CHXO	0.059	0.246	0.283	5	0.001	0.023	0.052	5	0.003	0.059	0.131	5
8	ISB	0.007	0.085	0.071	5	0.001	0.026	0.058	5	0.000	0.012	0.026	5
8	OSB	0.049	0.223	0.238	5	0.021	0.147	0.173	5	0.060	0.247	0.278	5
8	SCC	0.003	0.058	0.080	5	0.003	0.056	0.107	10	0.000	0.006	0.018	10

Table A6, percent gravel, continued.

Segment	Macrohabitat	Gravel 1996				Gravel 1997				Gravel 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
8	SCN	0.000	0.000	0.000	5	0.000	0.000	0.000	5	0.007	0.081	0.198	6
8	TRM	0.000	0.000	0.000	3	0.000	0.000	0.000	5	0.002	0.040	0.079	4
10	BEND	0.036	0.192	0.143	5	0.043	0.210	0.154	5	0.037	0.194	0.101	5
10	CHXO	0.003	0.052	0.074	5	0.032	0.179	0.104	5	0.041	0.205	0.184	5
10	ISB	0.015	0.124	0.171	5	0.011	0.107	0.110	5	0.012	0.109	0.111	5
10	OSB	0.077	0.282	0.226	5	0.086	0.298	0.320	4	0.024	0.155	0.082	4
10	SCC	0.012	0.110	0.247	5	0.000	0.018	0.043	6	0.004	0.061	0.121	4
10	SCN	0.000	0.000	0.000	4	0.000	0.000	0.000	4	0.000	0.000	0.000	2
10	TRM	0.008	0.091	.	1	0.022	0.150	.	1
12	BEND	0.160	0.411	0.207	5	0.091	0.306	0.267	5	0.105	0.330	0.175	5
12	CHXO	0.227	0.497	0.364	5	0.098	0.319	0.457	5	0.145	0.391	0.528	5
12	ISB	0.008	0.090	0.181	4	0.038	0.195	0.226	5	0.031	0.178	0.116	5
12	OSB	0.273	0.550	0.338	4	0.082	0.290	0.390	4	0.061	0.249	0.245	4
12	SCC	0.013	0.115	0.181	5	0.000	0.000	0.000	5	0.002	0.044	0.053	6
12	SCN	0.000	0.000	0.000	5	0.000	0.000	0.000	5	0.000	0.000	0.000	2
12	TRM	0.000	0.000	0.000	4	0.003	0.056	0.079	2	0.000	0.000	0.000	2
14	BEND	0.034	0.185	0.145	5	0.085	0.296	0.184	5	0.045	0.213	0.141	5
14	CHXO	0.023	0.153	0.175	5	0.047	0.219	0.171	5	0.003	0.057	0.098	5
14	ISB	0.021	0.145	0.155	5	0.032	0.180	0.125	5	0.031	0.177	0.253	5
14	OSB	0.054	0.234	0.193	4	0.209	0.474	0.434	5	0.045	0.213	0.261	5
14	SCC	0.004	0.066	0.077	4	0.012	0.111	0.134	6	0.026	0.162	0.314	10
14	SCN	0.000	0.000	0.000	4	0.000	0.000	.	1	0.000	0.000	0.000	2
14	TRM	0.000	0.000	0.000	4	0.000	0.000	0.000	5	0.000	0.000	0.000	3
15	BEND	0.120	0.354	0.236	5	0.119	0.353	0.279	5	0.025	0.158	0.101	5
15	CHXO	0.073	0.274	0.217	5	0.185	0.444	0.299	3	0.028	0.167	0.215	5
15	ISB	0.064	0.255	0.285	5	0.039	0.200	0.200	5	0.004	0.066	0.068	5
15	OSB	0.185	0.444	0.436	5	0.232	0.502	0.413	5	0.021	0.145	0.102	5
15	SCC	0.060	0.248	0.209	5	0.010	0.098	0.165	9	0.050	0.225	0.204	10
15	SCN	0.000	0.000	0.000	4	0.000	0.000	0.000	2	0.006	0.079	0.112	2
15	TRM	0.009	0.095	0.213	5	0.000	0.000	0.000	4	0.000	0.000	0.000	3
Channelized zone													
17	BEND	0.029	0.172	0.070	5	0.069	0.266	0.128	5	0.083	0.292	0.155	5
17	CHXO	0.010	0.099	0.099	5	0.018	0.134	0.165	5	0.000	0.020	0.045	5
17	ISB	0.001	0.025	0.055	5	0.012	0.108	0.137	5	0.002	0.039	0.041	5
17	OSB	0.074	0.275	0.157	5	0.203	0.467	0.399	5	0.307	0.587	0.362	5
17	SCC	0.000	0.000	.	1
17	TRM	0.000	0.000	0.000	6	0.000	0.000	0.000	6	0.000	0.000	0.000	5
18	BEND	0.028	0.169	0.107	5
18	CHXO	0.006	0.078	0.080	5
18	ISB	0.005	0.071	0.073	5
18	OSB	0.072	0.271	0.266	5
18	SCC	0.000	0.000	.	1
18	TRM	0.000	0.000	0.000	6
19	BEND	0.187	0.448	0.181	5	0.169	0.423	0.163	5	0.187	0.447	0.077	5

Table A6, percent gravel, continued.

Segment	Macrohabitat	Gravel 1996				Gravel 1997				Gravel 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
19	CHXO	0.228	0.498	0.331	5	0.181	0.440	0.299	5	0.110	0.339	0.204	5
19	ISB	0.019	0.137	0.194	5	0.030	0.175	0.249	5	0.037	0.194	0.187	5
19	OSB	0.320	0.601	0.263	5	0.260	0.535	0.248	5	0.374	0.658	0.165	5
19	SCC	0.000	0.000	0.000	2	0.001	0.037	0.053	2	0.082	0.290	0.410	2
19	TRM	0.000	0.000	0.000	6	0.007	0.082	0.202	6	0.000	0.000	0.000	4
21	BEND	0.036	0.190	0.037	5
21	CHXO	0.004	0.064	0.087	5
21	ISB	0.012	0.109	0.068	5
21	OSB	0.084	0.294	0.054	5
21	SCC	0.030	0.174	.	1
21	TRM	0.000	0.000	0.000	5
22	BEND	0.035	0.189	0.024	5	0.047	0.218	0.054	5	0.033	0.182	0.080	5
22	CHXO	0.012	0.108	0.107	5	0.011	0.104	0.096	5	0.023	0.154	0.053	5
22	ISB	0.003	0.055	0.063	5	0.006	0.079	0.122	5	0.000	0.019	0.029	5
22	OSB	0.089	0.303	0.121	5	0.120	0.354	0.119	5	0.087	0.299	0.181	5
22	SCC	0.000	0.000	.	1	0.000	0.000	.	1
22	SCN	0.000	0.000	.	1	0.000	0.000	0.000	3
22	TRM	0.018	0.134	0.301	5	0.005	0.070	0.186	7	0.003	0.052	0.136	7
23	BEND	0.081	0.288	0.100	5	0.052	0.230	0.129	5	0.036	0.192	0.107	5
23	CHXO	0.066	0.259	0.124	5	0.025	0.159	0.132	5	0.005	0.073	0.046	5
23	ISB	0.014	0.118	0.098	5	0.003	0.056	0.021	5	0.005	0.073	0.057	5
23	OSB	0.168	0.423	0.239	5	0.141	0.385	0.288	5	0.122	0.357	0.230	5
23	SCC	0.061	0.250	0.095	5	0.044	0.212	0.093	5	0.016	0.129	0.101	5
23	SCN	0.000	0.000	.	1
23	TRM	0.000	0.000	0.000	5	0.000	0.000	0.000	6	0.000	0.000	0.000	6
25	BEND	0.024	0.155	0.084	5	0.041	0.205	0.175	5	0.053	0.232	0.089	5
25	CHXO	0.011	0.103	0.148	5	0.013	0.114	0.142	5	0.015	0.123	0.096	5
25	ISB	0.002	0.050	0.049	5	0.005	0.070	0.070	5	0.015	0.121	0.095	5
25	OSB	0.055	0.237	0.112	5	0.104	0.328	0.396	5	0.114	0.345	0.241	5
25	SCC	0.000	0.020	0.045	5	0.012	0.112	0.161	10	0.004	0.066	0.097	10
25	SCN	0.000	0.000	.	1
25	TRM	0.000	0.016	0.035	5	0.000	0.012	0.031	7	0.001	0.033	0.087	7
27	BEND	0.141	0.386	0.263	5	0.016	0.126	0.040	5	0.066	0.260	0.112	5
27	CHXO	0.006	0.079	0.093	5	0.001	0.034	0.048	5	0.057	0.242	0.216	5
27	ISB	0.049	0.222	0.280	5	0.010	0.100	0.083	5	0.047	0.218	0.104	5
27	OSB	0.377	0.661	0.587	5	0.032	0.180	0.088	5	0.059	0.245	0.169	5
27	SCC	0.057	0.242	0.267	5	0.037	0.194	0.232	10	0.142	0.386	0.271	10
27	SCN	0.025	0.159	0.356	5	0.006	0.080	0.178	5	0.002	0.044	0.071	5
27	TRM	0.000	0.000	0.000	3	0.000	0.000	0.000	4	0.011	0.104	0.208	4

Table A7. Mean (untransformed), mean-t (arcsin square-root transformed), standard deviation (SD-t, arcsin square-root transformed), and sample size (N) for percent sand from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Sand 1996				Sand 1997				Sand 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	0.359	0.642	0.259	5	0.212	0.479	0.096	5	0.488	0.773	0.086	5
3	CHXO	0.223	0.492	0.521	5	0.092	0.308	0.277	5	0.597	0.883	0.240	5
3	ISB	0.215	0.482	0.194	5	0.187	0.447	0.284	5	0.373	0.657	0.193	5
3	OSB	0.455	0.740	0.264	5	0.330	0.612	0.297	5	0.522	0.807	0.233	5
3	SCC	0.167	0.421	0.157	5	0.108	0.334	0.175	6	0.047	0.218	0.151	5
3	SCN	0.400	0.685	.	1
5	BEND	0.674	0.963	0.162	5	0.380	0.664	0.234	5	0.661	0.950	0.192	5
5	CHXO	0.791	1.096	0.352	5	0.595	0.881	0.396	5	0.818	1.130	0.172	5
5	ISB	0.687	0.977	0.140	5	0.392	0.677	0.356	5	0.546	0.832	0.312	5
5	OSB	0.589	0.875	0.222	5	0.224	0.493	0.186	5	0.614	0.901	0.235	5
5	SCC	0.334	0.616	0.311	5	0.333	0.615	0.354	10	0.106	0.331	0.310	9
5	SCN	0.000	0.000	0.000	2	0.011	0.107	0.186	3	0.000	0.000	.	1
9	BEND	0.550	0.836	0.307	5	0.489	0.774	0.345	5	0.550	0.836	0.363	5
9	CHXO	0.563	0.849	0.474	5	0.550	0.836	0.617	5	0.589	0.875	0.508	5
9	ISB	0.508	0.793	0.191	5	0.401	0.686	0.157	5	0.597	0.883	0.380	5
9	OSB	0.619	0.906	0.485	5	0.507	0.792	0.567	5	0.491	0.777	0.343	5
9	SCC	0.500	0.785	0.438	5	0.538	0.824	0.290	10	0.516	0.801	0.367	9
9	SCN	0.041	0.205	0.199	5	0.077	0.281	0.075	6	0.159	0.410	0.201	5
9	TRM	0.000	0.000	.	1	0.075	0.278	0.169	2
Inter-reservoir zone													
6	BEND	0.531	0.817	.	1
6	CHXO	0.363	0.646	.	1
6	ISB	0.700	0.991	.	1
6	SCC	0.692	0.982	0.285	5
6	SCN	0.858	1.185	0.325	5
6	TRM	0.013	0.113	0.160	2
7	BEND	0.835	1.152	0.120	5	0.796	1.102	0.215	5	0.816	1.128	0.315	5
7	CHXO	0.927	1.297	0.101	5	0.885	1.225	0.357	5	0.916	1.277	0.327	5
7	ISB	0.940	1.323	0.163	5	0.861	1.188	0.240	5	0.852	1.175	0.314	5
7	OSB	0.693	0.984	0.350	5	0.699	0.990	0.263	5	0.707	0.998	0.410	5
7	SCC	0.560	0.846	0.260	3	0.757	1.056	0.292	7	0.873	1.207	0.257	10
7	SCN	0.097	0.317	0.448	2	0.011	0.105	0.234	5	0.083	0.293	0.225	5
7	TRM	0.048	0.222	0.443	4	0.019	0.137	0.306	5	0.000	0.000	0.000	2
8	BEND	0.887	1.228	0.137	5	0.924	1.291	0.160	5	0.901	1.251	0.178	5
8	CHXO	0.941	1.324	0.283	5	0.985	1.447	0.136	5	0.997	1.512	0.131	5
8	ISB	0.920	1.284	0.135	5	0.914	1.273	0.294	5	0.938	1.318	0.236	5
8	OSB	0.874	1.208	0.291	5	0.927	1.297	0.250	5	0.783	1.086	0.315	5
8	SCC	0.948	1.341	0.431	5	0.670	0.959	0.221	10	0.867	1.198	0.304	10

Table A7, percent sand, continued.

Segment	Macrohabitat	Sand 1996				Sand 1997				Sand 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
8	SCN	0.406	0.691	0.469	5	0.009	0.093	0.207	5	0.033	0.181	0.246	6
8	TRM	0.011	0.107	0.186	3	0.043	0.209	0.289	5	0.094	0.312	0.625	4
10	BEND	0.771	1.072	0.114	5	0.878	1.215	0.135	5	0.902	1.253	0.084	5
10	CHXO	0.977	1.418	0.107	5	0.965	1.383	0.106	5	0.956	1.359	0.185	5
10	ISB	0.684	0.974	0.419	5	0.889	1.231	0.339	5	0.965	1.383	0.149	5
10	OSB	0.767	1.067	0.298	5	0.824	1.138	0.355	4	0.818	1.129	0.057	4
10	SCC	0.747	1.044	0.296	5	0.815	1.126	0.336	6	0.615	0.901	0.251	4
10	SCN	0.120	0.353	0.427	4	0.000	0.000	0.000	4	0.073	0.274	0.068	2
10	TRM	0.917	1.278	.	1	0.686	0.976	.	1
12	BEND	0.713	1.006	0.259	5	0.878	1.214	0.259	5	0.880	1.217	0.172	5
12	CHXO	0.773	1.074	0.364	5	0.902	1.252	0.457	5	0.855	1.180	0.528	5
12	ISB	0.608	0.895	0.114	4	0.958	1.365	0.223	5	0.963	1.377	0.119	5
12	OSB	0.608	0.895	0.350	4	0.808	1.117	0.379	4	0.896	1.243	0.270	4
12	SCC	0.767	1.067	0.304	5	0.558	0.844	0.578	5	0.945	1.334	0.201	6
12	SCN	0.267	0.544	0.600	5	0.039	0.200	0.280	5	0.168	0.423	0.143	2
12	TRM	0.252	0.526	0.446	4	0.074	0.276	0.390	2	0.053	0.232	0.328	2
14	BEND	0.878	1.214	0.184	5	0.851	1.174	0.144	5	0.604	0.890	0.271	5
14	CHXO	0.966	1.386	0.154	5	0.950	1.346	0.168	5	0.850	1.173	0.241	5
14	ISB	0.971	1.400	0.175	5	0.899	1.248	0.120	5	0.668	0.957	0.477	5
14	OSB	0.629	0.916	0.382	4	0.683	0.973	0.404	5	0.290	0.568	0.409	5
14	SCC	0.923	1.289	0.227	4	0.869	1.200	0.122	6	0.676	0.965	0.264	10
14	SCN	0.132	0.372	0.256	4	0.043	0.210	.	1	0.190	0.451	0.182	2
14	TRM	0.030	0.173	0.049	4	0.009	0.096	0.144	5	0.000	0.000	0.000	3
15	BEND	0.840	1.159	0.213	5	0.814	1.124	0.222	5	0.866	1.195	0.143	5
15	CHXO	0.889	1.231	0.236	5	0.815	1.127	0.299	3	0.876	1.212	0.104	5
15	ISB	0.928	1.299	0.307	5	0.838	1.157	0.171	5	0.878	1.214	0.161	5
15	OSB	0.766	1.066	0.411	5	0.468	0.753	0.518	5	0.852	1.175	0.215	5
15	SCC	0.843	1.163	0.236	5	0.923	1.289	0.168	9	0.832	1.148	0.147	10
15	SCN	0.317	0.598	0.152	4	0.705	0.997	0.156	2	0.387	0.672	0.018	2
15	TRM	0.096	0.315	0.266	5	0.020	0.144	0.107	4	0.000	0.000	0.000	3
Channelized zone													
17	BEND	0.890	1.232	0.182	5	0.906	1.260	0.147	5	0.900	1.249	0.141	5
17	CHXO	0.968	1.392	0.147	5	0.982	1.436	0.165	5	0.999	1.537	0.048	5
17	ISB	0.802	1.110	0.300	5	0.916	1.277	0.155	5	0.958	1.365	0.078	5
17	OSB	0.897	1.244	0.129	5	0.791	1.096	0.389	5	0.693	0.984	0.362	5
17	SCC	0.155	0.405	.	1
17	TRM	0.101	0.324	0.362	6	0.075	0.277	0.332	6	0.331	0.613	0.289	5
18	BEND	0.899	1.248	0.077	5
18	CHXO	0.994	1.493	0.080	5
18	ISB	0.799	1.106	0.106	5
18	OSB	0.924	1.292	0.274	5
18	SCC	0.700	0.991	.	1
18	TRM	0.040	0.202	0.494	6
19	BEND	0.643	0.930	0.127	5	0.707	0.999	0.157	5	0.693	0.983	0.070	5

Table A7, percent sand, continued.

Segment	Macrohabitat	Sand 1996				Sand 1997				Sand 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
19	CHXO	0.615	0.901	0.150	5	0.819	1.131	0.299	5	0.890	1.232	0.204	5
19	ISB	0.699	0.990	0.258	5	0.605	0.891	0.259	5	0.543	0.828	0.208	5
19	OSB	0.619	0.905	0.215	5	0.739	1.035	0.248	5	0.626	0.913	0.165	5
19	SCC	0.689	0.980	0.381	2	0.594	0.880	0.658	2	0.457	0.743	0.276	2
19	TRM	0.002	0.049	0.091	6	0.007	0.082	0.202	6	0.073	0.274	0.449	4
21	BEND	0.773	1.075	0.038	5
21	CHXO	0.864	1.193	0.672	5
21	ISB	0.527	0.812	0.130	5
21	OSB	0.849	1.171	0.102	5
21	SCC	0.965	1.383	.	1
21	TRM	0.012	0.108	0.197	5
22	BEND	0.748	1.044	0.085	5	0.794	1.100	0.052	5	0.796	1.103	0.018	5
22	CHXO	0.964	1.381	0.215	5	0.989	1.467	0.096	5	0.977	1.417	0.053	5
22	ISB	0.434	0.719	0.099	5	0.646	0.934	0.091	5	0.531	0.816	0.082	5
22	OSB	0.894	1.240	0.134	5	0.736	1.031	0.107	5	0.909	1.264	0.182	5
22	SCC	0.725	1.019	.	1	0.300	0.580	.	1
22	SCN	0.213	0.479	.	1	0.000	0.000	0.000	3
22	TRM	0.008	0.090	0.114	5	0.020	0.141	0.202	7	0.050	0.226	0.351	7
23	BEND	0.711	1.003	0.060	5	0.779	1.082	0.077	5	0.785	1.088	0.074	5
23	CHXO	0.934	1.312	0.124	5	0.975	1.412	0.132	5	0.995	1.498	0.046	5
23	ISB	0.470	0.755	0.137	5	0.546	0.832	0.126	5	0.542	0.827	0.178	5
23	OSB	0.700	0.991	0.122	5	0.842	1.162	0.281	5	0.821	1.134	0.209	5
23	SCC	0.855	1.181	0.237	5	0.707	0.999	0.125	5	0.633	0.920	0.124	5
23	SCN	0.000	0.000	.	1
23	TRM	0.002	0.039	0.087	5	0.000	0.021	0.050	6	0.010	0.098	0.240	6
25	BEND	0.845	1.167	0.125	5	0.726	1.020	0.109	5	0.715	1.007	0.075	5
25	CHXO	0.989	1.468	0.148	5	0.987	1.457	0.142	5	0.957	1.361	0.080	5
25	ISB	0.713	1.005	0.286	5	0.429	0.714	0.239	5	0.474	0.760	0.073	5
25	OSB	0.879	1.216	0.182	5	0.828	1.143	0.374	5	0.756	1.054	0.291	5
25	SCC	0.879	1.215	0.420	5	0.876	1.211	0.305	10	0.714	1.007	0.354	10
25	SCN	0.075	0.277	.	1
25	TRM	0.001	0.028	0.061	5	0.013	0.114	0.210	7	0.019	0.137	0.211	7
27	BEND	0.649	0.937	0.300	5	0.802	1.110	0.071	5	0.742	1.038	0.192	5
27	CHXO	0.738	1.033	0.654	5	0.999	1.537	0.048	5	0.914	1.273	0.203	5
27	ISB	0.559	0.845	0.225	5	0.531	0.817	0.128	5	0.444	0.730	0.282	5
27	OSB	0.595	0.881	0.595	5	0.868	1.200	0.109	5	0.895	1.241	0.254	5
27	SCC	0.765	1.064	0.625	5	0.550	0.835	0.482	10	0.585	0.871	0.224	10
27	SCN	0.305	0.585	0.651	5	0.264	0.539	0.502	5	0.217	0.484	0.381	5
27	TRM	0.001	0.037	0.065	3	0.000	0.000	0.000	4	0.018	0.136	0.204	4

Table A8. Mean (untransformed), mean-t (arcsin square-root transformed), standard deviation (SD-t, arcsin square-root transformed), and sample size (N) for percent silt from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Silt 1996				Silt 1997				Silt 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	0.110	0.338	0.076	5	0.145	0.391	0.149	5	0.099	0.321	0.147	5
3	CHXO	0.000	0.000	0.000	5	0.019	0.137	0.306	5	0.004	0.064	0.144	5
3	ISB	0.230	0.500	0.322	5	0.178	0.435	0.127	5	0.170	0.425	0.157	5
3	OSB	0.011	0.105	0.234	5	0.157	0.408	0.191	5	0.069	0.267	0.292	5
3	SCC	0.154	0.404	0.326	5	0.054	0.235	0.344	6	0.156	0.406	0.116	5
3	SCN	0.600	0.886	.	1
5	BEND	0.047	0.219	0.150	5	0.104	0.328	0.174	5	0.118	0.350	0.179	5
5	CHXO	0.002	0.045	0.101	5	0.000	0.000	0.000	5	0.007	0.082	0.113	5
5	ISB	0.048	0.221	0.250	5	0.168	0.423	0.296	5	0.243	0.515	0.240	5
5	OSB	0.056	0.238	0.239	5	0.057	0.241	0.378	5	0.080	0.287	0.271	5
5	SCC	0.405	0.690	0.357	5	0.512	0.798	0.302	10	0.622	0.908	0.275	9
5	SCN	1.000	1.571	0.000	2	0.906	1.259	0.286	3	0.900	1.249	.	1
9	BEND	0.078	0.283	0.182	5	0.080	0.287	0.105	5	0.023	0.152	0.109	5
9	CHXO	0.006	0.077	0.108	5	0.000	0.000	0.000	5	0.005	0.071	0.103	5
9	ISB	0.233	0.503	0.328	5	0.228	0.498	0.205	5	0.034	0.186	0.170	5
9	OSB	0.001	0.032	0.071	5	0.000	0.000	0.000	5	0.016	0.127	0.121	5
9	SCC	0.179	0.437	0.375	5	0.208	0.474	0.235	10	0.110	0.338	0.245	9
9	SCN	0.936	1.315	0.226	5	0.860	1.188	0.078	6	0.792	1.098	0.268	5
9	TRM	1.000	1.571	.	1	0.925	1.293	0.169	2
Inter-reservoir zone													
6	BEND	0.000	0.000	.	1
6	CHXO	0.000	0.000	.	1
6	ISB	0.000	0.000	.	1
6	SCC	0.050	0.227	0.221	5
6	SCN	0.137	0.379	0.312	5
6	TRM	0.500	0.785	1.111	2
7	BEND	0.009	0.093	0.154	5	0.071	0.271	0.067	5	0.023	0.151	0.112	5
7	CHXO	0.000	0.000	0.000	5	0.000	0.000	0.000	5	0.005	0.070	0.156	5
7	ISB	0.015	0.122	0.184	5	0.112	0.341	0.213	5	0.020	0.143	0.153	5
7	OSB	0.009	0.093	0.207	5	0.050	0.227	0.209	5	0.019	0.137	0.151	5
7	SCC	0.247	0.520	0.006	3	0.102	0.325	0.235	7	0.070	0.267	0.113	10
7	SCN	0.903	1.254	0.448	2	0.989	1.466	0.234	5	0.917	1.278	0.225	5
7	TRM	0.912	1.269	0.418	4	0.981	1.434	0.306	5	0.987	1.458	0.160	2
8	BEND	0.031	0.177	0.182	5	0.062	0.251	0.152	5	0.060	0.247	0.166	5
8	CHXO	0.000	0.000	0.000	5	0.010	0.101	0.147	5	0.000	0.000	0.000	5
8	ISB	0.048	0.221	0.213	5	0.084	0.294	0.289	5	0.057	0.241	0.249	5
8	OSB	0.036	0.192	0.263	5	0.022	0.149	0.267	5	0.112	0.342	0.236	5
8	SCC	0.037	0.195	0.435	5	0.311	0.591	0.246	10	0.132	0.372	0.304	10

Table A8, percent silt, continued.

Segment	Macrohabitat	Silt 1996				Silt 1997				Silt 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
8	SCN	0.594	0.880	0.469	5	0.991	1.478	0.207	5	0.953	1.353	0.325	6
8	TRM	0.989	1.464	0.186	3	0.957	1.362	0.289	5	0.881	1.219	0.603	4
10	BEND	0.170	0.424	0.162	5	0.051	0.229	0.174	5	0.057	0.241	0.034	5
10	CHXO	0.010	0.101	0.138	5	0.001	0.026	0.058	5	0.001	0.026	0.058	5
10	ISB	0.240	0.512	0.473	5	0.053	0.233	0.406	5	0.006	0.080	0.178	5
10	OSB	0.139	0.382	0.217	5	0.070	0.268	0.182	4	0.154	0.403	0.057	4
10	SCC	0.197	0.460	0.297	5	0.183	0.442	0.336	6	0.357	0.641	0.305	4
10	SCN	0.880	1.218	0.427	4	1.000	1.571	0.000	4	0.927	1.297	0.068	2
10	TRM	0.075	0.277	.	1	0.292	0.571	.	1
12	BEND	0.099	0.320	0.192	5	0.015	0.124	0.122	5	0.006	0.076	0.106	5
12	CHXO	0.000	0.000	0.000	5	0.000	0.000	0.000	5	0.000	0.000	0.000	5
12	ISB	0.354	0.638	0.178	4	0.001	0.026	0.058	5	0.001	0.036	0.081	5
12	OSB	0.070	0.269	0.184	4	0.070	0.267	0.208	4	0.024	0.155	0.179	4
12	SCC	0.144	0.389	0.414	5	0.442	0.727	0.578	5	0.052	0.231	0.195	6
12	SCN	0.733	1.027	0.600	5	0.961	1.371	0.280	5	0.832	1.148	0.143	2
12	TRM	0.748	1.045	0.446	4	0.922	1.288	0.400	2	0.947	1.339	0.328	2
14	BEND	0.078	0.283	0.149	5	0.041	0.203	0.142	5	0.327	0.609	0.288	5
14	CHXO	0.002	0.042	0.069	5	0.000	0.020	0.045	5	0.118	0.351	0.297	5
14	ISB	0.005	0.068	0.101	5	0.040	0.202	0.187	5	0.252	0.526	0.433	5
14	OSB	0.270	0.547	0.383	4	0.047	0.218	0.268	5	0.613	0.899	0.491	5
14	SCC	0.057	0.241	0.262	4	0.090	0.305	0.185	6	0.226	0.495	0.256	10
14	SCN	0.868	1.199	0.256	4	0.957	1.361	.	1	0.810	1.120	0.182	2
14	TRM	0.970	1.398	0.049	4	0.841	1.161	0.662	5	1.000	1.571	0.000	3
15	BEND	0.019	0.139	0.135	5	0.035	0.188	0.112	5	0.093	0.310	0.184	5
15	CHXO	0.009	0.096	0.214	5	0.000	0.000	0.000	3	0.049	0.223	0.169	5
15	ISB	0.006	0.077	0.108	5	0.081	0.289	0.204	5	0.112	0.342	0.171	5
15	OSB	0.010	0.100	0.190	5	0.000	0.015	0.033	5	0.104	0.329	0.263	5
15	SCC	0.043	0.209	0.294	5	0.051	0.229	0.134	9	0.079	0.286	0.169	10
15	SCN	0.683	0.973	0.152	4	0.295	0.574	0.156	2	0.600	0.886	0.000	2
15	TRM	0.877	1.213	0.332	5	0.980	1.427	0.107	4	1.000	1.571	0.000	3
Channelized zone													
17	BEND	0.078	0.282	0.171	5	0.023	0.151	0.078	5	0.013	0.113	0.037	5
17	CHXO	0.012	0.110	0.154	5	0.000	0.000	0.000	5	0.000	0.014	0.032	5
17	ISB	0.194	0.456	0.302	5	0.062	0.251	0.133	5	0.040	0.200	0.072	5
17	OSB	0.013	0.116	0.108	5	0.000	0.014	0.032	5	0.000	0.000	0.000	5
17	SCC	0.845	1.166	.	1
17	TRM	0.899	1.247	0.362	6	0.925	1.294	0.332	6	0.669	0.958	0.289	5
18	BEND	0.066	0.260	0.046	5
18	CHXO	0.000	0.000	0.000	5
18	ISB	0.193	0.454	0.100	5
18	OSB	0.001	0.037	0.082	5
18	SCC	0.300	0.580	.	1
18	TRM	0.960	1.369	0.494	6
19	BEND	0.140	0.383	0.171	5	0.090	0.305	0.217	5	0.108	0.334	0.132	5

Table A8, percent silt, continued.

Segment	Macrohabitat	Silt 1996				Silt 1997				Silt 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
19	CHXO	0.044	0.211	0.324	5	0.000	0.000	0.000	5	0.000	0.000	0.000	5
19	ISB	0.249	0.522	0.233	5	0.266	0.542	0.420	5	0.380	0.664	0.288	5
19	OSB	0.021	0.145	0.211	5	0.000	0.015	0.033	5	0.000	0.000	0.000	5
19	SCC	0.311	0.591	0.381	2	0.402	0.687	0.653	2	0.342	0.625	0.564	2
19	TRM	0.998	1.521	0.091	6	0.985	1.448	0.300	6	0.927	1.297	0.449	4
21	BEND	0.190	0.451	0.041	5
21	CHXO	0.000	0.000	0.000	5
21	ISB	0.457	0.742	0.136	5
21	OSB	0.043	0.209	0.197	5
21	SCC	0.005	0.071	.	1
21	TRM	0.988	1.463	0.197	5
22	BEND	0.216	0.484	0.086	5	0.157	0.407	0.059	5	0.165	0.419	0.036	5
22	CHXO	0.010	0.102	0.228	5	0.000	0.000	0.000	5	0.000	0.000	0.000	5
22	ISB	0.560	0.846	0.106	5	0.336	0.618	0.087	5	0.468	0.754	0.084	5
22	OSB	0.006	0.074	0.130	5	0.087	0.299	0.286	5	0.001	0.029	0.066	5
22	SCC	0.275	0.552	.	1	0.700	0.991	.	1
22	SCN	0.788	1.092	.	1	1.000	1.571	0.000	3
22	TRM	0.967	1.387	0.318	5	0.970	1.396	0.278	7	0.942	1.327	0.384	7
23	BEND	0.200	0.464	0.082	5	0.158	0.408	0.063	5	0.171	0.427	0.060	5
23	CHXO	0.000	0.000	0.000	5	0.000	0.000	0.000	5	0.000	0.000	0.000	5
23	ISB	0.508	0.794	0.130	5	0.450	0.735	0.125	5	0.450	0.736	0.176	5
23	OSB	0.067	0.263	0.246	5	0.003	0.054	0.121	5	0.011	0.105	0.234	5
23	SCC	0.047	0.218	0.301	5	0.232	0.503	0.184	5	0.342	0.624	0.135	5
23	SCN	1.000	1.571	.	1
23	TRM	0.998	1.532	0.087	5	1.000	1.550	0.050	6	0.990	1.473	0.240	6
25	BEND	0.114	0.344	0.180	5	0.212	0.479	0.083	5	0.228	0.497	0.056	5
25	CHXO	0.000	0.000	0.000	5	0.000	0.000	0.000	5	0.022	0.149	0.072	5
25	ISB	0.283	0.561	0.285	5	0.560	0.846	0.226	5	0.504	0.790	0.062	5
25	OSB	0.032	0.180	0.252	5	0.021	0.147	0.201	5	0.111	0.340	0.182	5
25	SCC	0.120	0.354	0.418	5	0.095	0.314	0.281	10	0.267	0.543	0.367	10
25	SCN	0.925	1.293	.	1
25	TRM	0.999	1.539	0.071	5	0.987	1.456	0.212	7	0.979	1.426	0.230	7
27	BEND	0.178	0.435	0.165	5	0.181	0.440	0.068	5	0.187	0.447	0.145	5
27	CHXO	0.024	0.157	0.351	5	0.000	0.000	0.000	5	0.020	0.142	0.062	5
27	ISB	0.333	0.615	0.217	5	0.453	0.738	0.130	5	0.498	0.783	0.296	5
27	OSB	0.006	0.078	0.173	5	0.077	0.280	0.186	5	0.041	0.203	0.181	5
27	SCC	0.069	0.265	0.454	5	0.336	0.618	0.537	10	0.208	0.474	0.260	10
27	SCN	0.541	0.827	0.791	5	0.704	0.996	0.545	5	0.778	1.080	0.382	5
27	TRM	0.999	1.534	0.065	3	1.000	1.571	0.000	4	0.954	1.355	0.249	4

Table A9. Mean (untransformed), mean-t (log₁₀ transformed), standard deviation (SD-t, log₁₀ transformed), and sample size (N) for geometric mean particle size from BENDs and 6 macrohabitats (3 within each BEND) within 18 segments and three zones of Missouri and lower Yellowstone rivers. Macrohabitat means include averages from mesohabitats within macrohabitats and replicate measures at multiple sites per mesohabitat or macrohabitat. See text for additional information on how means were calculated. BEND = river bend, CHXO = channel cross-over, ISB = inside bend, OSB = outside bend, SCC = secondary channel connected, SCN = secondary channel non-connected, TRM = tributary mouth.

Segment	Macrohabitat	Geometric mean 1996				Geometric mean 1997				Geometric mean 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
Least-altered zone													
3	BEND	14.93	1.174	0.334	5	30.14	1.479	0.258	5	9.42	0.974	0.446	5
3	CHXO	14.32	1.156	0.684	5	33.38	1.524	0.140	5	6.77	0.831	0.680	5
3	ISB	12.28	1.089	0.252	5	21.21	1.326	0.350	5	4.81	0.682	0.557	5
3	OSB	9.03	0.956	0.328	5	30.71	1.487	0.418	5	13.01	1.114	0.429	5
3	SCC	12.28	1.089	0.544	5	17.63	1.246	0.121	6	12.52	1.098	0.169	5
3	SCN	0.13	-0.898	.	1
5	BEND	6.69	0.825	0.400	5	9.45	0.976	0.452	5	3.22	0.507	0.326	5
5	CHXO	4.61	0.664	0.684	5	9.60	0.982	0.599	5	2.72	0.435	0.394	5
5	ISB	3.09	0.491	0.263	5	6.16	0.789	0.330	5	2.26	0.353	0.443	5
5	OSB	5.88	0.770	0.571	5	7.26	0.861	0.872	5	3.74	0.573	0.351	5
5	SCC	1.22	0.085	0.700	5	0.65	-0.190	0.616	10	1.04	0.018	0.771	9
5	SCN	0.03	-1.505	0.000	2	0.08	-1.111	0.477	3	0.07	-1.168	.	1
9	BEND	4.42	0.646	0.667	5	6.52	0.814	0.704	5	6.41	0.807	0.522	5
9	CHXO	5.09	0.707	0.666	5	5.81	0.764	0.694	5	5.33	0.726	0.654	5
9	ISB	1.61	0.207	0.759	5	3.26	0.514	0.816	5	4.56	0.659	0.652	5
9	OSB	5.44	0.735	0.662	5	7.93	0.899	0.748	5	7.91	0.898	0.449	5
9	SCC	2.01	0.304	0.627	5	1.68	0.226	0.631	10	3.26	0.514	0.673	9
9	SCN	0.05	-1.265	0.353	5	0.15	-0.816	0.534	6	0.13	-0.884	0.619	5
9	TRM	0.03	-1.505	.	1	0.04	-1.366	0.135	2
Inter-reservoir zone													
6	BEND	8.01	0.904	.	1
6	CHXO	12.93	1.112	.	1
6	ISB	3.09	0.490	.	1
6	SCC	2.13	0.329	0.583	5
6	SCN	0.72	-0.143	0.132	5
6	TRM	0.93	-0.031	2.085	2
7	BEND	2.09	0.320	0.209	5	1.87	0.273	0.423	5	2.92	0.465	0.424	5
7	CHXO	1.40	0.147	0.100	5	2.19	0.340	0.515	5	2.22	0.346	0.450	5
7	ISB	1.10	0.042	0.134	5	1.04	0.018	0.152	5	2.07	0.316	0.481	5
7	OSB	3.35	0.524	0.367	5	2.14	0.331	0.440	5	3.85	0.585	0.449	5
7	SCC	1.53	0.185	0.658	3	1.45	0.160	0.388	7	1.15	0.061	0.335	10
7	SCN	0.06	-1.207	0.421	2	0.04	-1.400	0.236	5	0.06	-1.220	0.281	5
7	TRM	0.06	-1.202	0.430	4	0.04	-1.384	0.272	5	0.04	-1.383	0.173	2
8	BEND	1.53	0.185	0.223	5	1.02	0.007	0.092	5	1.82	0.260	0.466	5
8	CHXO	1.70	0.231	0.367	5	0.96	-0.019	0.062	5	1.11	0.046	0.073	5
8	ISB	0.90	-0.044	0.096	5	0.81	-0.093	0.111	5	0.85	-0.072	0.093	5
8	OSB	1.44	0.158	0.276	5	1.19	0.075	0.207	5	2.58	0.412	0.681	5
8	SCC	0.78	-0.109	0.296	5	0.52	-0.287	0.240	10	0.65	-0.187	0.271	10

Table A9, geometric mean particle size, continued.

Segment	Macrohabitat	Geometric mean 1996				Geometric mean 1997				Geometric mean 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
8	SCN	0.21	-0.682	0.507	5	0.04	-1.425	0.180	5	0.07	-1.163	0.631	6
8	TRM	0.04	-1.455	0.088	3	0.04	-1.353	0.215	5	0.07	-1.128	0.692	4
10	BEND	1.64	0.215	0.511	5	1.30	0.113	0.258	5	1.32	0.120	0.201	5
10	CHXO	0.97	-0.012	0.063	5	1.19	0.074	0.043	5	1.49	0.172	0.309	5
10	ISB	0.37	-0.435	0.503	5	0.68	-0.167	0.455	5	1.00	0.000	0.126	5
10	OSB	2.55	0.406	0.668	5	1.67	0.222	0.470	4	0.98	-0.008	0.152	4
10	SCC	0.66	-0.180	0.441	5	0.56	-0.249	0.302	6	0.40	-0.403	0.392	4
10	SCN	0.07	-1.178	0.423	4	0.03	-1.505	0.000	4	0.04	-1.375	0.067	2
10	TRM	0.86	-0.066	.	1	0.80	-0.097	.	1
12	BEND	3.94	0.596	0.516	5	3.99	0.601	0.507	5	2.37	0.375	0.489	5
12	CHXO	2.58	0.411	0.492	5	2.06	0.314	0.562	5	2.26	0.353	0.597	5
12	ISB	0.38	-0.417	0.320	4	1.45	0.160	0.228	5	1.19	0.075	0.076	5
12	OSB	10.33	1.014	0.633	4	8.08	0.908	0.683	4	3.27	0.515	0.657	4
12	SCC	0.63	-0.203	0.472	5	0.27	-0.573	0.597	5	0.88	-0.056	0.055	6
12	SCN	0.11	-0.942	0.675	5	0.05	-1.334	0.251	5	0.06	-1.234	0.163	2
12	TRM	0.33	-0.477	1.337	4	0.06	-1.256	0.353	2	0.06	-1.219	0.405	2
14	BEND	2.54	0.405	0.496	5	3.82	0.583	0.549	5	0.80	-0.098	0.303	5
14	CHXO	1.34	0.128	0.243	5	1.32	0.120	0.132	5	0.61	-0.214	0.305	5
14	ISB	1.18	0.071	0.084	5	1.03	0.013	0.109	5	0.67	-0.175	0.541	5
14	OSB	5.11	0.708	0.752	4	6.84	0.835	0.786	5	0.36	-0.446	0.878	5
14	SCC	0.82	-0.086	0.186	4	0.94	-0.025	0.103	6	1.30	0.115	0.791	10
14	SCN	0.22	-0.656	1.382	4	0.04	-1.435	.	1	1.55	0.191	1.718	2
14	TRM	0.04	-1.451	0.033	4	0.61	-0.213	1.765	5	0.03	-1.505	0.000	3
15	BEND	7.28	0.862	0.401	5	4.92	0.692	0.665	5	0.85	-0.072	0.219	5
15	CHXO	1.58	0.200	0.395	5	2.19	0.339	0.371	3	1.01	0.005	0.237	5
15	ISB	1.73	0.238	0.290	5	1.20	0.080	0.234	5	0.71	-0.147	0.175	5
15	OSB	13.64	1.135	0.701	5	8.38	0.923	0.742	5	0.75	-0.124	0.316	5
15	SCC	1.14	0.056	0.391	5	1.34	0.126	0.397	9	1.58	0.199	0.525	10
15	SCN	0.15	-0.813	0.346	4	0.40	-0.402	0.272	2	0.20	-0.696	0.285	2
15	TRM	0.13	-0.892	0.901	5	0.03	-1.461	0.038	4	0.03	-1.505	0.000	3
Channelized zone													
17	BEND	7.73	0.888	0.533	5	12.29	1.090	0.247	5	16.97	1.230	0.113	5
17	CHXO	0.99	-0.004	0.053	5	1.21	0.082	0.121	5	1.04	0.015	0.008	5
17	ISB	4.24	0.627	0.863	5	2.83	0.452	0.636	5	13.49	1.130	0.642	5
17	OSB	9.06	0.957	0.846	5	30.83	1.489	0.229	5	27.88	1.445	0.207	5
17	SCC	0.06	-1.216	.	1
17	TRM	0.08	-1.119	0.460	6	0.08	-1.091	0.536	6	0.20	-0.705	0.459	5
18	BEND	17.63	1.246	0.103	5
18	CHXO	1.07	0.031	0.020	5
18	ISB	9.45	0.976	0.602	5
18	OSB	38.24	1.583	0.076	5
18	SCC	0.37	-0.436	.	1
18	TRM	0.05	-1.281	0.548	6
19	BEND	14.63	1.165	0.307	5	9.90	0.996	0.134	5	17.42	1.241	0.112	5

Table A9, geometric mean particle size, continued.

Segment	Macrohabitat	Geometric mean 1996				Geometric mean 1997				Geometric mean 1998			
		Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N	Mean	Mean-t	SD-t	N
19	CHXO	2.41	0.382	0.693	5	2.31	0.363	0.420	5	1.88	0.273	0.310	5
19	ISB	7.74	0.889	0.516	5	0.82	-0.084	0.513	5	24.73	1.393	0.060	5
19	OSB	14.46	1.160	0.819	5	20.36	1.309	0.393	5	24.85	1.395	0.167	5
19	SCC	0.48	-0.316	0.251	2	0.40	-0.400	0.486	2	0.99	-0.006	0.765	2
19	TRM	0.03	-1.490	0.033	6	0.06	-1.214	0.713	6	0.06	-1.188	0.609	4
21	BEND	13.67	1.136	0.069	5
21	CHXO	1.06	0.026	0.025	5
21	ISB	12.03	1.080	0.104	5
21	OSB	27.51	1.439	0.092	5
21	SCC	1.12	0.051	.	1
21	TRM	0.04	-1.432	0.158	5
22	BEND	15.49	1.190	0.015	5	10.90	1.038	0.257	5	14.14	1.150	0.043	5
22	CHXO	1.06	0.024	0.069	5	1.10	0.041	0.026	5	1.13	0.054	0.027	5
22	ISB	10.44	1.019	0.065	5	11.21	1.050	0.053	5	5.77	0.761	0.583	5
22	OSB	34.89	1.543	0.004	5	14.05	1.148	0.673	5	32.48	1.512	0.077	5
22	SCC	0.52	-0.282	.	1	0.09	-1.024	.	1
22	SCN	0.07	-1.134	.	1	0.03	-1.505	0.000	3
22	TRM	0.09	-1.045	1.016	5	0.06	-1.222	0.627	7	0.07	-1.135	0.645	7
23	BEND	15.95	1.203	0.116	5	15.14	1.180	0.059	5	13.88	1.142	0.128	5
23	CHXO	1.36	0.134	0.106	5	1.19	0.074	0.081	5	1.06	0.024	0.009	5
23	ISB	11.11	1.046	0.055	5	11.08	1.045	0.055	5	10.52	1.022	0.068	5
23	OSB	34.50	1.538	0.169	5	32.92	1.518	0.084	5	28.94	1.462	0.214	5
23	SCC	1.17	0.069	0.092	5	0.97	-0.014	0.164	5	0.68	-0.169	0.076	5
23	SCN	0.03	-1.505	.	1
23	TRM	0.03	-1.494	0.026	5	0.09	-1.045	1.115	6	0.04	-1.395	0.271	6
25	BEND	10.25	1.011	0.208	5	12.36	1.092	0.109	5	6.60	0.820	0.546	5
25	CHXO	1.14	0.055	0.066	5	1.14	0.056	0.075	5	1.02	0.009	0.062	5
25	ISB	1.63	0.213	0.698	5	1.55	0.192	0.697	5	0.81	-0.091	0.588	5
25	OSB	26.06	1.416	0.201	5	32.09	1.506	0.113	5	15.56	1.192	0.678	5
25	SCC	0.75	-0.127	0.179	5	0.87	-0.061	0.165	10	0.47	-0.331	0.451	10
25	SCN	0.05	-1.340	.	1
25	TRM	0.03	-1.495	0.022	5	0.04	-1.388	0.259	7	0.05	-1.327	0.420	7
27	BEND	16.39	1.215	0.064	5	6.80	0.833	0.231	5	13.46	1.129	0.112	5
27	CHXO	0.94	-0.026	0.135	5	1.04	0.018	0.007	5	1.43	0.156	0.274	5
27	ISB	10.76	1.032	0.124	5	3.57	0.553	0.690	5	7.30	0.863	0.394	5
27	OSB	37.28	1.571	0.052	5	6.09	0.785	0.766	5	28.68	1.458	0.184	5
27	SCC	1.11	0.047	0.303	5	0.52	-0.287	0.673	10	1.60	0.205	0.584	10
27	SCN	0.30	-0.522	1.162	5	0.76	-0.120	0.997	5	0.12	-0.928	0.525	5
27	TRM	0.03	-1.498	0.012	3	0.03	-1.505	0.000	4	0.09	-1.056	0.687	4