ASSEMBLAGE STRUCTURE AND SHALLOW-WATER HABITAT USE BY SMALL-BODIED FISHES AT LOWER MISSOURI RIVER SANDBARS

A thesis presented to the Faculty of the Graduate School
University of Missouri-Columbia

In partial Fulfillment of the Requirements for the Degree

Master of Science

by

CLAYTON RIDENOUR

Dr. David Galat, Thesis Supervisor

AUGUST 2007

The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

ASSEMBLAGE STRUCTURE AND SHALLOW-WATER HABITAT USE BY SMALL-BODIED FISHES AT LOWER MISSOURI RIVER SANDBARS

presented by C	layton Ridenour,
a candidate for	the degree of Master of Science,
and hereby cert	tify that, in their opinion, it is worthy of acceptance.
	Dr. David L. Galat
	Dr. Charles Rabeni
	Dr. Mark Ellersieck
	Dr. Vince Travnichek

ACKNOWLEDGEMENTS

The Missouri Department of Conservation provided funding and much of the equipment to support this project, including a large boat, motor and trailer. In addition, the University of Missouri Cooperative Fish and Wildlife Research Unit, the U.S.G.S. Columbia Environmental Research Center, and the U.S. Fish and Wildlife Service Fisheries Resource Office Region 3 offered equipment and expertise as needed. The J. Louis Crum Cooperation in Columbia, Missouri, and Russ DeVenney, Jr., deserves special acknowledgement for donating several hundred dollars of copper pipe; Russ's networking skills were invaluable for locating additional pipe at a discount price.

I would like to thank my major advisor, Dr. David L. Galat, for his encouragement, support, and criticism during this research and my education. David's expertise and eye for detail have fine tuned my scientific and creative thinking skills and improved my technical writing skills. My academic committee Drs. Charlie Rabeni, Mark Ellersieck, and Vince Travnichek provided much need professional expertise to improve this research and final product.

Several field and lab technicians devoted much hard work to assure successful completion of field and lab work for this project. Andrew Avis and Benedict Nagy, Brent (Parker) Fadler, and Tim and Scott Altnether proved to be skilled electrofishers and field biologists. A special thanks to Kerry Reeves, Kevin O'Donnell, Matt Mullins and Aaron Atkins for helping to collect data when they could. Heather Calkins and Dustin Martin were invaluably proficient processing fish in the lab.

Finally, I am grateful to numerous friends, family, and fellow students for their support and encouragement throughout my graduate education and work on this project.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	ii
LIST OF TABLES	v
LIST OF FIGURES	ix
ABSTRACT	xiii
CHAPTER I Native Fish Ecology and the Effects of Large-river Ecosystem Degrad	
Introduction	1
Small-bodied fishes	2
Fluvial fishes	
Missouri River	
Thesis objectives	13
Literature Cited	15
CHAPTER II Patterns of Distribution and Abundance by Small-bodied Fishes at Lo River Sandbars: The Importance of Body Length	wer Missouri 26
Introduction	20
Study Area	31
Methods	32
Sample Design	
Fish collection and handling	
Habitat data collection	
Data processing	
Analyses	48
Results	
Distribution, abundance, and environment	54
Small-bodied fish assemblage structure	54
	54 95
Small-bodied fish assemblage structure	
Small-bodied fish assemblage structure Discussion Use of sandbar ATTZ by small-bodied fishes Diel patterns of fishes at sandbar ATTZ	
Small-bodied fish assemblage structure Discussion Use of sandbar ATTZ by small-bodied fishes	

Literature Cited	115
CHAPTER III	127
Effect of Spatiotemporal and Environmental Factors on Small-bodied Fish	
Assemblage Composition at Sandbar ATTZ on Lower Missouri River	
Introduction	127
Study Area	131
Methods	132
Dataset Selection	133
Data Processing	134
Analyses	135
Interpreting multivariate analysis bi-plots	137
Results	138
Species	139
Body length	
Discussion	148
Body size and habitat use	152
Conclusion	155
Literature Cited	157
Summary, Conclusions and Implications	166
Appendix A	169
Small and submerged sandbar sample design	169
Appendix B	170
SAS codes used for data analyses	170
Metadata for SAS code input classes:	
Appendix C	172
September substrates	
Literature Cited	
Appendix D	173

LIST OF TABLES

Tabl	Page
2.1.	Fish species collected at sandbar ATTZ with family and species name, common name, four letter species code, number (#) of individuals in all samples and number of samples species present in, collected on lower Missouri River (LMOR). Heritage status to LMOR and membership to a habitat use guild defined by Galat et al. (2005)
2.2.	Spit-split split plot ANOVA table for fish catch-per-unit-effort (CPUE #/m3), fish body length (mm TL), and environmental factors for spatial and temporal scales and their interactions. Shoreline sinuosity has fewer degrees of freedom for effects involving region because head and tail regions were not tested. Effect codes: SB=sandbar, RG=region, SC=sample unit category, MN=month
2.3.	Means of catch-per-unit-effort (CPUE #/m3) and body length (mm TL) ± standard error (pooled variance) of fishes (≥9 sample units, ≤105-mm TL) pooled across all spatial scales and months, and by sandbar, region, and sample unit category among months. Fisher's least significant difference (LSD) is listed under each spatial scale to determine significance between means*, **. Codes for sandbar and region: PB = point sandbar, WD = wing-dike sandbar, HR = head region, UP = upstream primary region, US = upstream secondary region, DP = downstream primary region, DS = downstream secondary region, TR = tail region
2.4.	Spit-split plot ANOVA table for fish catch-per-unit-effort (CPUE #/m³), fish body length, water depth, water velocity, and water temperature for effects diel period (DL), region (RG), sample unit category (SC), and their interactions
2.5.	Means \pm standard error (SE, pooled variance) of fish (\geq 9 sample units, \leq 105-mm TL) catch-per-unit-effort (CPUE #/m³), fish body length (mm TL), water depth (m), water velocity (m/s), and water temperature (C°) between light and dark diel period among region and sample unit scale in water adjacent to Petite Saline sandbar in lower Missouri River. Factors were tested with split-split plot ANOVA and Fisher's least significant difference post hoc comparison ($P \leq 0.05$); water depth and water velocity were tested under square-root transformation, <i>italic</i> values below square

	root transformed mean ± SE are back-transformed means. Asterisk indicates significance between means
2.6.	Descriptive statistics for the distribution of small-bodied fishes body lengths (mm TL) collected in near-shore, moderate, and offshore sample units between light and dark diel periods for fishes collected in ≥ 9 sample units and ≤ 105 -mm TL. Statistic 'n' is the number of fish collected ≤ 105 -mm TL, median, mode, and percentile (P_i) are relative to total length of fishes rounded to the nearest millimeter. Percentiles indicate the body length that i percent of fishes collected were shorter than
2.7.	Mean catch-per-unit-effort (CPUE #/m³) ± standard error of small-bodied fishes (i.e., ≤105 mm TL) by length class that were collected in near-shore, moderate, and offshore samples in light and dark periods during diel sampling. Length classes are 5-mm are labeled by the shortest length within each class (e.g., '10' is 10-14 mm TL)
2.8.	Mean catch-per-unit-effort (CPUE #/m³) and body length (mm TL) ± standard error (SE, pooled variance) of species (≥9 sample units, ≤105-mm TL) collected in sandbar ATTZ on lower Missouri River by month. An asterisk preceding mean or SE value indicates the value is greater than 0.0 and less than 0.05. —————————————————————————————————
2.9.	Summary of available reports for length-at-age-0 and age-1 for 14 Missouri River species. See Literature Cited for full citation to each report79
2.10	Body length, depth, and velocity profiles (mean ± standard error, SE; pooled variance) of species (≥9 sample units, <105-mm TL) of small-bodied fishes collected at sandbar ATTZ on lower Missouri River. Select species labeled in italics are those currently monitored by U.S Fish and Wildlife Service programs. Depth and velocity were square-root transformed for ANOVA test and are reported here as such; italic values below square root transformed mean ± SE are back-transformed means
2.11	Means ± standard error (SE, pooled variance) of environmental factors measured in sandbar ATTZ among months, between point and wing-dike sandbars among months, and among regions within and between point and wing-dike sandbars among months. Means for successively higher levels of organization are estimable by averaging up from the lower level. Depth, velocity, turbidity and slope were square-root transformed (sqrt) for ANOVA and are reported here as such; <i>italic</i> values below square root transformed means ± SEs are back-transformed means. Sinuosity ranges from approaching zero (straight) to approaching 100 (sinuous). Low substrate (Gs) values correspond to substrates dominated by small diameter particles (e.g., silt and sand), high values indicate large particles are dominant (e.g., gravel and cobble); see Appendix Table D1 to

	reference index values for proportions of silt, sand, gravel, and cobble. Region codes: HR = head; UP = upstream primary; US = upstream secondary; DP = downstream primary; DS = downstream secondary; TR = tail.	84
2.12. Me	eans ± standard error (SE, pooled variance) of environmental factors measured in sandbar ATTZ among sample units within and among regions by month. Means for successively higher levels of organization are estimable by averaging up from the lower level. Depth, velocity, turbidity and slope were square-root transformed (sqrt) for ANOVA and are reported here as such; <i>italic</i> values below square root transformed means ± SEs are back-transformed means. Sinuosity ranges from approaching zero (straight) to approaching 100 (sinuous). Low substrate (Gs) values correspond to substrates dominated by small diameter particles (e.g., silt and sand), high values indicate large particles are dominant (e.g., gravel and cobble); see Appendix Table D1 to reference index values for proportions of silt, sand, gravel, and cobble. Region codes: HR = head; UP = upstream primary; US = upstream secondary; DP = downstream primary; DS = downstream secondary; TR = tail.	89
2.13. Co	ounts of fishes used in detrended correspondence analysis (DCA) analyses to test assemblage structure relative to species, body length class (5-mm class width), and macrohabitat use guild. Length classes are 5-mm and labeled by the shortest length within each class (e.g., '10' is 10-14 mm TL). Matrix to determine number of individuals is interpretable by species, length class, macrohabitat use guild, species by length class, or macrohabitat use guild by length class. Length class sums (bold by column) apply to species (above) and macrohabitat use guild (below). See Table 2.1 for species code definitions. Macrohabitat use guild codes: FS = fluvial specialist, FD = fluvial dependent, MG = macrohabitat generalist. Length class '5' occurred in less than 1% of samples; therefore, those individuals were excluded from DCA analyses.	96
2.14. Re	sults of detrended correspondence analysis (DCA) ordinations by species, length class, and macrohabitat use guild. Guild assemblage group was not included in comparison of total inertia (lower is better) among groups to determine which best explained small-bodied fish assemblage structure due to low <i>n</i> .	98
3.1. Bea	aufort scale used to visually estimate wind speed	165
3.2. Car	nonical correspondence analysis (CCA) correlation coefficients of spatiotemporal and environmental factors with the first two canonical axes of small-bodied fish assemblages organized by species and body length	.142

D1.	Chart to convert substrate particle size index values to four particle size classes on the modified Wentworth scale. Index values representing equal proportions of adjacent particle size classes were extracted directly from the raw data.	173
D2.	Mean catch-per-unit-effort (CPUE m³) and body length (mm TL) ± standard error (SE) between light and dark diel periods for species collected in shallow waters adjacent to sandbars on lower Missouri River. An asterisk preceding mean or SE value indicates the value is greater than 0.0 and less	.173
	than 0.5	.174

LIST OF FIGURES

Figu	ire	Page
1.1.	Missouri River basin (shaded area) showing major tributaries to Missouri River and location of six main-stem dams with associated reservoirs upstream of Sioux City, IA. Dams are represented by thick white lines at the downstream end of each reservoir. Dams and associated reservoirs (in parentheses) from upstream to downstream are: Fort Peck Dam (Fort Peck Lake), Garrison Dam (Lake Sakakawea), Oahe Dam (Lake Oahe), Big Bend Dam (Lake Sharpe), Fort Randall Dam (Lake Francis Case), Gavins Point Dam (Lewis and Clark Lake). The reach of Missouri River from Gavins Point Dam to its confluence with Mississippi River is defined as lower Missouri River.	8
2.1.	Map of study reach along Missouri River in central Missouri showing sandbars studied and major tributaries	33
2.2.	Flow chart illustrating nested spatial scale design for sampling lower Missouri River (LMOR) sandbars. Sandbars are the largest spatial scale and contain regions; sample units are the smallest scale and compose regions.	
2.3.	Idealized lower Missouri River sandbar showing spatial delineation design used to collect small-bodied fishes. "X" represent reference crosses used to sight (dashed lines) position of transects (solid dark lines) to place sample units (white boxes) within regions (shaded area between transects).	36
2.4.	Diagram of Missouri River prepositioned areal electrofishing device (PAED) depicting DWV-copper and aircraft cable linkages of electrodes, PVC, stabilizing eyebolt, and 12-guage power cord. PAEDs were staked through eye bolt for stability and to indicate location of downstream terminal end.	41
2.5.	Length frequency distribution for all fishes collected from all sample units at sandbar ATTZ in lower Missouri River. Frequencies of individuals were counted within 5-mm length classes labeled by the smallest value within each class (e.g., 5 to 9-mm is '5'). Fish lengths ranged from 8 to 830-mm total length (TL). Fishes shorter than or equal to105-mm TL (solid vertical line) composed 99.4% of all fishes collected and were included in further analyses.	60

2.6.	Annual hydrograph showing mean daily discharge (m3/s) on lower Missouri River (LMOR) measured at Boonville, MO (rkm 316) near midpoint of study reach. Area inside verticle dotted lines represents the period fish were collected in shallow waters adjacent to LMOR sandbars. Data are from USGS-NWIS web interface available online at http://waterdata.usgs.gove/nwis
2.7.	Relationship between catch-per-unit-effort (CPUE #/m3, dark bars) and mean body length (mm TL, light bars) of small-bodied fishes collected in sandbar ATTZ on lower Missouri River from July through October. Data are means ± SE (pooled variance)
2.8.	Catch-per-unit-effort (CPUE #/m³, dark bars) and body length (mm TL, light bars) of small-bodied fishes around sandbar ATTZ by region in lower Missouri River. Data are means ± SE (pooled variance)
2.9.	Plots of (A) catch-per-unit-effort (CPUE #/m3) and (B) body length of small-bodied fishes by sample unit category distance from shore among months. Data are means ± SE (pooled variance)
2.10.	Plot of mean small-bodied fishes total length ± standard error (pooled variance) collected in near-shore, moderate, and offshore sample units at sandbar ATTZ between light and dark diel periods on lower Missouri River. Data were analyzed as split-split plot ANOVA
2.11.	Box plots displaying the size distribution of small-bodied fishes to the nearest millimeter (TL) collected in near-shore, moderate, and offshore sample units between light and dark diel periods. Whiskers represent the middle 90%, rectangles the middle 50%, and horizontal line within rectangles the median of size fishes collected. See Table 2.6 for additional descriptive statistics related to this plot.
2.12.	Mean body length, depth, and velocity used by 10 fish species collected in sandbar ATTZ on lower Missouri River. Select species labeled in <i>italics</i> are currently monitored by U.S Fish and Wildlife Service programs. Depth and velocity were square-root transformed for ANOVA test then back-transformed for display here. See Table 2.1 for species code definition and Table 2.10 for mean values of body length, depth, and velocity by species.
2.13.	Sandbar slope mean \pm standard error (SE, pooled variance) among regions between point (open circles) and wing-dike (closed squares) sandbars. Sandbar slopes were tested with split-split-split plot ANOVA and reported here with square-root transformed data; see table 2.10 for back-transformed means. Solid lines with slope (m) and r^2 statistics represent

regressions through regions by sandbar type. Region codes: HR = head, UP = upstream primary, US = upstream secondary, DP = downstream primary, DS = downstream secondary, TR = tail region	94
2.14. Detrended correspondence analysis scores plotted along the first three ordination axes with percent of total variation explained (%TVE) for fishes organized by (A) length class and (B) species. Dots represent DCA score for all fishes analyzed within their length class or species units	99
2.15. Standard distance among lower Missouri River small-bodied fishes collected at sandbar ATTZ and grouped into (A) 5-mm length classes and (B) species. Standard distance above 150 in window 'A' indicates that fishes within a length class have a distribution pattern not consistent with clustering in DCA ordination space; standard distance below 150 indicates they have a distribution pattern consistent with clustering in DCA ordination space. Length classes that occur close together in DCA ordination space (i.e., clustering) are interpreted to co-occur more frequently than length classes that are space further apart (i.e., dispersal). Dashed line with associated statistics is the regression through points where <i>r</i> ² is fit of the line, <i>m</i> is slope of the line, and <i>P</i> is probability that the slope is different from zero.)2
3.1. Explained variation in small-bodied fish assemblage composition partitioned by (A) species and (B) body length. Percentages listed are percent of total variation explained (%TVE) partitioned by spatiotemporal and environmental factor subgroups. Interaction TVEs were calculated by difference and are listed in <i>italics</i> . See text for explanation of negative interaction value.	43
3.2 Canonical correspondence analysis (CCA) biplot depicting relationships among (A) species, (B) 5-mm length classes, and their environmental factors. Species and length classes are represented by open triangles and factor gradients are represented by arrows. For clarity, the eight environmental factors (A and B = slope, shoreline sinuosity, substrate particle size, ledge, sunny, cloudy, partly cloudy, rain) and one or two spatial CoVs (A = sandbar type, depth class; B = sandbar type) with lowest percent of total variation explained (%TVE) were omitted from the graph. Temporal CoVs (month and diel) always accounted for greater than 1.1% TVE and were therefore included in the graph (labeled with italics). Each axis is labeled with TVE and partial percent of total variation explained (pTVE). Length classes are labeled by shortest length within each class, e.g., 10 = fishes ranging from 10 to 14 mm TL. See Table 2.1 for species code definitions.	15
3.3. Partial canonical correspondence analysis (pCCA) showing relationships	

among (A) species (CPUE) and environmental factors (EFs) (controlling

v to c ra	represented by open triangles and factors by arrows. Each axis is labeled with percent of total variation explained (%TVE) and partial percent of otal variation explained (%pTVE) specific to each set of factors. Length classes are labeled by shortest length within each class, e.g., 10 = fishes ranging from 10 to 14 mm TL. See Table 2.1 for species code definitions.	146
a ((() a la p fa	al canonical correspondence analysis (pCCA) showing relationships among (A) length classes (CPUE) and environmental factors (EFs) controlling for effect of spatiotemporal factors), and (B) length classes (CPUE) and spatiotemporal factors (controlling for effect of EFs). Fishes are represented by open triangles and factors by arrows. Each axis is abeled with percent of total variation explained (%TVE) and partial percent of total variation explained (%pTVE) specific to each set of factors. Length classes are labeled by shortest length within each class, e.g., 10 = fishes ranging from 10 to 14 mm TL	.147

for effect of spatiotemporal factors), and (B) species (CPUE) and spatiotemporal factors (STs) (controlling for effect of EFs). Fishes are

ASSEMBLAGE STRUCTURE AND SHALLOW-WATER HABITAT USE BY SMALL-BODIED FISHES AT LOWER MISSOURI RIVER SANDBARS

Clayton J. Ridenour

Dr. David L. Galat, Thesis Supervisor ABSTRACT

Populations of many native big-river fishes have declined since channelization and flow regulation contributed to losses of shallow-water habitat (SWH) on lower Missouri River (LMOR). Existing point and wing-dike sandbars represent a potentially important source of SWH to fishes during early ontogeny within the main channel of LMOR. Small-bodied fishes were sampled using pre-positioned electrofishing devices from 0.0-0.5 m water depths adjacent to four point and four wing-dike sandbars on LMOR between July and October, 2005. A suite of associated environmental factors were also measured. Habitat use and assemblage structure relative to three spatial (sandbar type, region within sandbars, and distance from shoreline within region) and two temporal (month, diel), and environmental factors were evaluated using Analysis of Variance, Detrended Correspondence Analysis, and Canonical Correspondence Analysis.

Samples yielded 49 species from 13 families in depths 0.0-0.5 m; most fishes were ≤105 mm TL. Fish mean length increased but abundance decreased from July to October. Ordination analyses revealed that the assemblage was organized into bodylength subgroups. Fish assemblages were not different between point and wing-dike sandbars. Instead, fishes aligned along a depth-velocity gradient relative to body length. Shallow (*ca.* 0.12m), near-shore areas were dominated by fishes <35 mm TL during the day, but larger fishes (e.g., 70 mm TL) moved nearer to shore at night. This research shows that main-channel sandbars provide nursery to many fluvial fishes during early ontogeny and that sandbars play an important role as nursery in large regulated rivers.

CHAPTER I

Native Fish Ecology and the Effects of Large-river Ecosystem Degradation

Introduction

Channelization and flow regulation have degraded many large rivers and their habitats for fluvial fishes around the world (Dynesius and Nilsson 1994; Bayley 1995; Ward et al. 1999; Bunn and Arthington 2002). River biota have been negatively impacted by human manipulation of hydrology and geomorphology in Australia (Doupé and Pettit 2002; Humphries et al. 2002; Arthington and Pusey 2003), Europe (Schiemer and Spindler 1989; Garner 1996; Aarts et al. 2004; Hirzinger et al. 2004;), Africa (King and Louw 1998; Winemiller and Jepsen 1998), North America (Koebel 1995; Sparks 1995; Bernhardt et al. 2005; Galat et al. 2005a), and South America (Ponton and Copp 1997; Mérona and Albert 1999). Native fishes that adapted under pre-modification conditions are at risk because degradation acts as a disturbance to reduce habitats important for completing life history stages (Junk et al. 1989; Gore and Shields 1995; Lytle and Poff 2004), and alters timing and quantity of seasonal flows used as reproductive cues to many fluvial fishes (Poff et al. 1997; Modde and Irving 1998; Galat et al. 1998). Disturbance often increases abundances of other species (e.g., introduced, non-native) that are more suited for survival and acquisition of recourses in the modified environment (Brown and Ford 2002) and affects trophic web dynamics (Power 1990; Power et al. 1996; Winemiller and Jepsen 1998; Dettmers et al. 2001a).

Human societies are becoming more aware of the value potential from self sustaining ecologically intact natural resources. The paradigm governing human-resource interaction is shifting from exploitation and degradation to conservation and co-existence between humans and the environment because competition for natural resources (e.g., water) is becoming more intense and the value of ecosystem integrity is more realized by society (Grumbine 1994; Barmuta 2003; Cullen 2003; Dole and Niemi 2004; Hulse et al. 2004). Ecosystem services such as clean water, a diverse mix of species, and recreational opportunities contribute far more to quality of life and overall standard of living than clear-cut forests, industrialization, and polluted rivers (Neimi et al. 1999). Large rivers are ecologically complex and among the most impacted ecosystems; therefore, much attention has been given to conservation and restoration of these systems (Karr et al. 1985; Sparks 1995; Johnson et al. 1995; Richter et al. 2003; Nilsson et al. 2005; Palmer et al. 2005).

Small-bodied fishes

A small-fish assemblage can be described by their age or body size. However, to be conclusive a small-fish assemblage must be defined using both factors, a variety of descriptive terms exist in the literature. *Young-of-the-year* (YoY, Harvey 1987; Jurajda 1995; Barko et al. 2004a), age-0 (Tyus and Haines 1991; Michaletz 1997; Barko et al. 2004b), 0+ (Garner 1996; Jurajda 1999), 0+ *juvenile* (Copp 1992; Copp et al. 1994), and 0-group (Ellis and Gibson 1995; Grift et al. 2003) are generally used to refer to fishes that are small, within their first year of life, or in the larvae/juvenile life stage, and are often used in discussions of nursery habitat. However, because some species remain in

the juvenile stage (i.e., reproductively immature) for longer than the first year of life, and because adults (i.e., reproductively mature) of small-bodied species also are small, the need exists for a more inclusive term than those listed above to describe a small fish assemblage.

I have selected two terms to use in this thesis; first I use the term 'small-bodied' (empirically defined in Chapter 2 based on lengths of fishes collected) to include individuals from species that do not grow to large adult size (e.g., many Cyprinidae), and small individuals of species that grow to large adult size (e.g., Catostomidae, Ictaluridae, Lepisosteidae). Second, I use the term 'age-0' to refer to fishes that are within the first year of life and are small-bodied, these include species that grow to both large and small adult size. Therefore, 'age-0' is nested within 'small-bodied' and each is used to identify a specific group of fishes. Finally, I define nursery habitat as where age-0 fishes congregate.

Fluvial fishes

Small-bodied fishes are an important component of large river ecology. They represent one strand in the food web and interact in aquatic trophic dynamics consuming invertebrates and in turn serving as prey for larger predators (Lindeman 1942; Diana 1995; Motta and Uieda 2005). Small-bodied fishes can have a significant top-down effect on abundances of algae, zooplankton, and invertebrates in the trophic cascade of small streams (Power 1992). Abundance and diversity of zooplankton and benthic invertebrates within the main channel of two large Midwestern rivers were hypothesized to be sufficient to support a functional food web for age-0 and adult fishes (Dettmers et

al. 2001a). The position of small-bodied fishes in the trophic cascade reflects their ecological significance and makes them suitable surrogates as a measure of ecological biodiversity in large rivers (Simon and Emery 1995; Emery et al. 2003).

Native small-bodied adult fishes serve as good biotic indicators of the ecological state of fluvial systems (Jurajda 1999; Schiemer 2000; Neumann 2002). They are relatively easy to collect, identify, and often have unique ecomorphology; small-bodied fish are abundant and diverse, age-0 in particular have narrow habitat tolerances relative to adults, are specially adapted for survival through the final bottle-neck life stage to reproductive age in their native environments, and are conducive for classification into various functional guilds (Griffiths 1992; Schiemer et al. 2001; Kozłowski and Gawelczyk 2002; Emery et al. 2003). Micro-environments generally associated with age-0 fluvial fishes are shallow water depth with gradually sloping banks and low flow velocity (Schiemer et al. 1991; Aadland 1993; Copp et al. 1994; Humphries et al. 1999; Grift et al. 2003). These microhabitats generally provide warmer water temperature and opportunity for foraging and growth because little energy is allocated to swimming costs in maintaining position (Pavlov 1994; Humphries et al. 1999; King 2004). Growth and survival of fishes from hatch to juvenile stage are enhanced with increasingly warmer water paralleling the natural spring rise in river temperature (Keckeis et al. 2001; Nunn et al. 2003).

Turbidity plays a role in predator-prey interactions, and thus the distribution and abundance of fishes, because low water transparency aids in predator avoidance by prey fishes (Bonner and Wilde 2002). However, many species in turbid systems have developed sensory adaptations to low light such as increased use of lateral line and

external sensory organs (e.g., taste buds) on the leading edge of fins and the snout to detect prey (Rodríguez and Lewis 1997; Dieterman and Galat 2005).

Local weather conditions may affect proximate distribution of fishes in shallow areas. Direct sunshine on shallow habitats warms water at a fast rate, results in high primary productivity (Morin et al. 1999), and may support a high density of young feeding fishes. High winds may increase wave amplitude, increase turbidity thereby decreasing visual predation risk. Wind may also re-suspend coarse organic materials that are consumed by macroinvertebrates, which would be consumed by small-bodied fishes (Dudgeon 1991; Garman and Moring 1993) in shallow areas. Rain may introduce new coarse organic material and macroinvertebrates into shallow areas as forage to small-bodied fishes. Shallow habitat may serve a significant role in growth of, and as refuge from predation to, small-bodied fishes.

Harvey and Stewart (1991) show that piscivorous fishes are more effective hunters in deeper pools of small headwater streams, but that significant predation risk from wading/diving animals exists in shallower habitats. In addition, larger fishes have greater risk to wading/diving predators in shallow habitats than smaller fishes (Power 1984; Power 1987; Schlosser 1987), possibly because larger fishes are easier for these predators to detect (Helfman et al. 1997). In general, a system with high habitat heterogeneity or abundant refuge patches has greater survival and diversity of small-bodied fishes (Townsend 1989; Beukers and Jones 1997), and indicates high ecological integrity in large fluvial systems (Ward and Stanford 1989; Ward and Stanford 1995; Ward et al. 1999).

Transitional zones are gradients of intermediate habitat between adjacent habitat types (or patches) that structure community dynamics in many aquatic systems (Naiman et al. 1988; Rundle et al. 1998). Transitions in fluvial systems occur over large spatial scales like the longitudinal gradient between upstream headwaters and the downstream confluence (Hynes 1975; Vannote et al. 1980), and over small spatial scales like the lateral gradient between a river and its floodplain (Junk et al. 1989), (Bretschko 1995; Kolasa and Zalewski 1995). The aquatic terrestrial transition zone (ATTZ) is the spatially and temporally dynamic lateral border between the river and its floodplain that provides important spawning and nursery habitats for many fluvial fishes in large rivers (Junk et al. 1989; see also Tockner et at. 2000). The ATTZ is a unique habitat gradient important during the early life stage of many riverine fishes (Schiemer et al. 1995) and often support distinct fish assemblages which are distributed along that gradient (Rahel and Hubert 1991; Gutreuter et al. 1999; Willis and Magnuson 2000; Petry et al. 2003). In this thesis I adopt an extended definition of ATTZ to include the interface between the aquatic and terrestrial zone of sandbars within main-channel borders of large rivers, hereafter called sandbar ATTZ (Reeves 2006; Tracy-Smith 2006). I use 'floodplain ATTZ' to refer to the river-floodplain transition described by Junk et al. (1989), 'sandbar ATTZ' to refer to the river-sandbar transition within main channel borders, and 'ATTZ' to refer to a general aquatic-terrestrial transition zone in large rivers.

Declines of floodplain dependent riverine fishes are thought to be closely related to lost spawning and nursery habitat where a river is isolated from its floodplain (Copp 1997: Neumann 2002). However, many imperiled fluvial fishes rarely or never use off-channel habitats (Dettmers et al. 2001b; Galat and Zweimüller 2001). Many fishes that

occur in rivers have been classified into one of three macrohabitat use guilds (Kinsolving and Bain 1993). Fluvial specialists require flowing water to complete all parts of their life history cycle; *fluvial dependents* require flow to complete at least one part of their life history; and macrohabitat generalists do not require flow to complete any part of their life history (Galat and Zweimüller 2001; Galat et al. 2005a). Keckeis et al. (2001) suggest that low recruitment of native fluvial specialists is more a function of limited suitable spawning and nursery area than altered environmental factors (e.g., temperature) within main-channel borders of large regulated rivers. It logically follows that timing of availability is important because habitat must be available during the period it is needed by age-0 fish (Caley and John 1996; Mérigoux and Ponton 1999). To illustrate, many fluvial dependents use the floodplain ATTZ as nursery during early ontogeny, but return to the river channel for the adult life stage; if availability and need of the floodplain ATTZ are not synchronized, survival through early ontogeny may be low for these species. Similarly, sandbar ATTZ may play a critical role in early ontogeny of obligate riverine species. Therefore, information on the spatial and temporal variability of habitat use by fishes in sandbar ATTZ during a critical early developmental period may be a key component to fisheries restoration in large degraded river systems.

Missouri River

Degradation

The Missouri River is highly degraded relative to its unregulated state (Galat et al. 2005b). Acts of Congress authorized channelization of the river downstream of Sioux City, IA, hereafter called lower Missouri River (LMOR), and construction of six main-

stem dams upstream of Sioux City, IA, between 1912 and 1981 (Figure 1.1). The final and most notable along a lineage of Congressional acts was the Missouri River Bank Stabilization and Navigation Project (*BSNP*, USACE 2003). This and preceding legislation were to provide flood protection and encourage the navigation industry to transport goods from agricultural states in the upper and middle Missouri basin to distribution centers in the lower basin and eastward through the Mississippi River basin (Ferrell 1996).

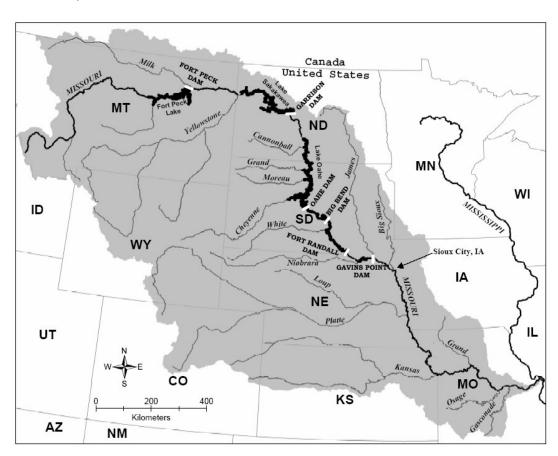


Figure 1.1 Missouri River basin (shaded area) showing major tributaries to Missouri River and location of six main-stem dams with associated reservoirs upstream of Sioux City, IA. Dams are represented by thick white lines at the downstream end of each reservoir. Dams and associated reservoirs (in parentheses) from upstream to downstream are: Fort Peck Dam (Fort Peck Lake), Garrison Dam (Lake Sakakawea), Oahe Dam (Lake Oahe), Big Bend Dam (Lake Sharpe), Fort Randall Dam (Lake Francis Case), Gavins Point Dam (Lewis and Clark Lake). The reach of Missouri River from Gavins Point Dam to its confluence with Mississippi River is defined as lower Missouri River.

The pre-modification Missouri River was characterized by a network of shallow, migrating, braided channels that continuously created and destroyed numerous shifting sandbars across a wide channel (Galat et al. 1998; Galat et al. 2005a), wide fluctuations in flow (Galat and Lipkin 2000), and high turbidity (Pflieger and Grace 1987). Continuously eroding and shifting banks were overtopped by annual floods that deposited rich organic sediments onto the floodplain and transported organic energy and sediments back to the river as floods receded. Channelization of LMOR resulted in a structurally different system that shortened its length by 73.4 kilometers, reduced water-surface area by 50%, reduced island surface area by 98%, and disconnected the river from much of its floodplain from Rulo, NE to the mouth; lost chutes and sloughs - associated with lost islands - that were once favored fishing places of recreational anglers are now silted in and largely annexed into private ownership of adjacent landowners (Funk and Robinson 1974). Flow is now concentrated within stable rip-rap banks of the comparatively narrow navigation channel rather than spread across numerous secondary channels and around actively eroding sandbars (Nestler and Sutton 2000). A nearly fourfold decrease in turbidity has occurred since significant flow regulation was implemented when dams became operational in the 1940s (Pflieger and Grace 1987; Johnson et al. 1996). Existing sandbars represent an important source of shallow-water habitat (SWH) within mainchannel borders to native fishes that adapted to the free flowing, braided and meandering channel network of the pre-modification Missouri River.

Mitigation

The Water Resources Development Act of 1986 (WRDA86) authorized the original Missouri River Fish and Wildlife Mitigation Project to mitigate the ecological effects of the BSNP completed by U.S. Army Corps of Engineers (USACE) in 1980 on LMOR. A modified Missouri River Fish and Wildlife Mitigation Project was reauthorized by Congress in 1999 (WRDA99) and charged to the USACE. The modified action plan included creation of 7,000-20,000 acres of SWH over at least 30 years with estimated cost up to \$1.33 billion (USACE 2003; USACE 2004). The U.S. Fish and Wildlife Service (USFWS) submitted an Amended Biological Opinion report to USACE in 2003 recommending 20,000 acres of SWH creation and improvement to achieve a goal of 20-30 SWH acres per mile needed to recover three endangered Missouri River species (USFWS 2003). The biological opinion defined SWH as water less than 5 ft (1.5 m) deep with flow velocity less than 2 ft/s (0.6 m/s). A total 6,020 acres of SWH creation and restoration of emergent sandbar habitat during nesting periods of endangered interior least turn (Sterna antillarum) and piping plover (Charadrius melodus) are planed in the reach from Kansas City, MO (rkm 591) to the mouth of Osage River (rkm 210).

Pallid sturgeon (*Scaphirhynchus albus*) is a large-bodied, long-lived large-river fish that was listed as endangered in 1990 (Quist et al. 2004). Their decline is thought to be directly related to "destruction and alteration" of habitats and flows that were historically present in Missouri River. Habitat and flow degradation is also blamed for population declines in other native small-bodied species that appear to be important food resources for pallid sturgeon (USFWS 2003). Sandbars are hypothesized to compose part of the habitat used by pallid sturgeon during some of its early life history (USFWS 2003),

and the shallow waters adjacent to sandbars appear to be important habitat to many other native fishes. Sturgeon chub (*Macrhybopsis gelida*) and sicklefin chub (*M. meeki*) are specialized native small-bodied large-river species that have declined in LMOR in response to river degradation (Galat et al. 2005a; but see Pflieger and Grace 1987; Gelwicks et al. 1996; Grady and Milligan 1998). These two species composed 79% of hatchery-reared juvenile pallid sturgeon diet after release to upper Missouri River above Fort Peck Reservoir, therefore a need exists to recover declining populations of these and other native forage fishes to aid recovery of pallid sturgeon (Gerrity 2005; Gerrity et al. 2006).

In addition to pallid sturgeon, five small-bodied species are currently monitored on LMOR from Gavins Point Dam near Sioux City, IA (rkm 1,305) downstream to its confluence with Mississippi River (rkm 0): sturgeon chub, sicklefin chub, speckled chub (*M. aestivalis*), sand shiner (*Notropis stramineus*), and fishes in the genus *Hybognathus*. The USFWS-Fisheries Resource Office in Region 3 is monitoring these and other native fish species in LMOR segment 13 (mouth of Grand River at rkm 403 to mouth of Osage River at rkm 210) under the Pallid Sturgeon Population Assessment Program (PSPAP) and Habitat Assessment and Monitoring Program (HAMP). Sampling occurred under these programs at selected river bends (called sample units), but bends were further partitioned and sampled as macro-, meso-, and microhabitats (Starostka et al. 2005). The finest level of data resolution possible by these programs is limited by gears used to collect fishes in each broad habitat type. Bag seines (9.1-m wide, 3.175-mm mesh), a variety of boat towed beam and otter trawls, and mini-fyke nets (3.175-mm mesh) were used to collect target and other small-bodied fishes along sandbars (defined as depth <

1.2 m), channel borders (depth > 1.2 m), in scour holes, and across island tips (Utrup et al. 2006). A typical 9-m wide bag seine haul may cover a wide depth range and sweep across many small-scale geomorphic features that may be important for hierarchically explaining differential habitat use, or niche separation, by small-bodied fishes (e.g., Frissell et al. 1986; Tonn 1990; Tillman 1994; Wu and Loucks 1995). Therefore, PSPAP and HAMP study designs may lack sufficient resolution to tease apart small-scale relationships between fishes, particularly small-bodied fishes, and their microhabitats to determine what specific geomorphic processes must be restored to create and maintain habitats for imperiled fishes (e.g., see Copp 1992; Poizat ant Pont 1996; Schiemer 2000).

It is unclear how creation of SWH will influence pallid sturgeon. Preliminary telemetry data from adults (A. Delonay, U.S. Geological Survey, personal communication) and catches from PSPAP and HAMP programs (Starostka et al. 2005; Utrup et al. 2006) indicate that they are not frequently observed or collected in water shallower than 1.5-m in LMOR. However, these monitoring techniques do not account for individuals too small to implant with transmitters or collect with PSPAP and HAMP sampling gears. Reeves (2006) collected a small number of larval *Scaphirhynchus* sturgeon (0.1 larval sturgeon fish per 100m³ of water, vs. 14.3 larvae per 100m³ of water averaged across all fish species) in the shallow waters adjacent to sandbars during 2002, but none during 2003 or 2004. His results indicated that SWH adjacent to sandbars may be of some use as habitat for larval *Scaphirhynchus*. Previous sampling surveys indicate sandbars may be important habitat to many other native small-bodied fishes (Grace 1985; Grace and Pflieger 1985; Gelwicks et al. 1996; Grady and Milligan 1998; Reeves 2006). However, detailed fine-scale relationships among small-bodied fishes and sandbar

environments have never been quantified to determine how they use these few remaining SWHs within main-channel borders of LMOR. Therefore, even if pallid sturgeon are not immediately located in or directly use SWHs associated with main-channel sandbars, sandbars may be important to pallid sturgeon recovery if they serve as habitat to support production of many native small-bodied fishes important in their diet.

Thesis objectives

I developed a series of research objectives to study the relationship among small-bodied fishes and their habitats in LMOR sandbar ATTZ. I had two objectives for Chapter 2. First was to quantify how abundance and body length of the small-bodied fish assemblage and a suite of environmental factors vary in the context of three spatial and two temporal scales at sandbar ATTZ. As part of this objective, I quantified sandbar ATTZ depth and velocity use profiles for five select species currently targeted under monitoring programs of the U.S. Fish and Wildlife Service. Second, I tested if the lower Missouri River small-bodied fish assemblage in shallow-waters adjacent to sandbars was composed of a series of taxonomically related sub-assemblages (species), of sub-assemblages that parallel habitat use guilds (habitat use), and/or by sub-assemblages of similar body length (body length).

My objective for Chapter 3 was to quantify the interactions between small-bodied fishes and their environment and determine the relative contributions of spatiotemporal and environmental factors explaining the observed variation in the small-bodied fish assemblage composition organized by (1) species and (2) body length. This objective addresses two questions: (1) do spatiotemporal and environmental factors equally

explain the variation in species and body length assemblages? and (2) what factor, or suite of factors, explains the most variation in composition for each assemblage type? Results from these objectives will directly contribute to scientific information needed by state and federal agencies to manage and create SWH for pallid sturgeon and associated fishes recovery. It differs from previous surveys to fill important information gaps about small-bodied fishes and habitats at sandbars in two fundamental ways: (1) focusing on a narrower and shallower depth range within the 0.0-1.5 m partial definition of SWH developed by the USFWS, and (2) reducing the spatial scope to specific microhabitats within sandbars to provide high resolution detail of post-larvae fishes and the environmental conditions associated with their habitats.

Literature Cited

- Aadland, L. P. 1993. Stream habitat types: their fish assemblages and relationship to flow. North American Journal of Fisheries Management 13: 790-806.
- Aarts, B. G. W., F. W. B. Van Den Brink, and P. H. Nienhuis. 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated rivers in Europe: the transversal floodplain gradient. River Research and Applications 20: 3-23.
- Arthington, A. H. and B. J. Pusey. 2003. Flow restoration and protection in Australian rivers. River Research and Applications 19: 377-395.
- Barko, V. A., M. W. Palmer, D. P. Herzog, and B. S. Ickes. 2004a. Influential environmental gradients and spatiotemporal patterns of fish assemblages in the unimpounded upper Mississippi River. The American Midland Naturalist 152: 369-385.
- Barko, V. A., D. P. Herzog and R. A. Hrabik. 2004b. Relationship among fish assemblages and main-channel-border physical habitats in the unimpounded Upper Mississippi River. Transactions of the American Fisheries Society 133: 371-384.
- Barmuta, L. A. 2003. Imperilled rivers of Australia: challenges for assessment and conservation. Aquatic Ecosystem Health and Management 6: 55-68.
- Bayley, P. B. 1995. Understanding large river-floodplain ecosystems. BioScience 45: 153-158.
- Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308: 636-637.
- Beukers, J. S. and G. P. Jones. 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114: 50-59.
- Bonner, T. H. and G. R. Wilde. 2002. Effects of turbidity on prey consumption by prairie stream fishes. Transactions of the American Fisheries Society 131: 1203-1208.
- Bretschko, G. 1995. River/land ecotones: scales and patterns. Hydrobiologia 303: 83-91.
- Brown, L. R. and T. Ford. 2002. Effects of flow on the fish communities of a regulated California river: implications for managing native fishes. River Research and

- Applications 18: 331-342.
- Bunn, S. E. and A. H. Arthington. 2002. Basic principles and ecologic consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30(4): 492-507.
- Caley, M. J. and J. S. John. 1996. Refuge availability structures assemblages of tropical reef fishes. Journal of Animal Ecology 65: 414-428.
- Copp, G. H. 1992. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. Environmental Biology of Fishes 33: 181-193.
- Copp, G. H. 1997. Importance of marinas and off-channel water bodies as refuges for young fishes in a regulated lowland river. Regulated Rivers: Research and Management 13: 303-307.
- Copp, G. H., G. Guti, B. Rovny and J. Cerny. 1994. Hierarchical analysis of habitat use by 0+ juvenile fish in Hungarian/Slovak floodplain of the Danube River. Environmental Biology of Fishes 40: 329-348.
- Cullen, P. 2003. Challenges to the conservation of Australian freshwater biodiversity: an epilogue. Aquatic Ecosystem Health and Management 6: 97-101.
- Dettmers, J. M., D. H. Wahl, D. A. Soluk and S. Gutreuter. 2001a. Life in the fast lane: fish and foodweb structure in the main channel of large rivers. Journal of the North American Benthological Society 20: 255-265.
- Dettmers, J. M., S. Gutreuter, D. H. Wahl and D. A. Soluk. 2001b. Patterns in abundance of fishes in main channels of the upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences 58: 933-942.
- Diana, J. S. 1995. Biology and ecology of fishes. Cooper Publishing Group LLC, USA.
- Dieterman, D. J. and D. L. Galat. 2005. Variation in body form, taste buds, and brain patterns of the sicklefin chub, *Macrhybopsis meeki*, in the Missouri River and lower Yellowstone River, USA. Journal of Freshwater Ecology 20: 561-573.
- Dole, D. and E. Niemi. 2004. Future water allocation and in-stream values in the Willamette River basin: a basin-wide analysis. Ecological Applications 14: 355 367.
- Doupé, R. G. and N. E. Pettit. 2002. Ecological perspectives on regulation and water allocation for the Ord River, Western Australia. River Research and Applications 18: 307-320.
- Dudgeon, D. 1991. An experimental study of the effects of predatory fish on

- macroinvertebrates in a Hong Kong stream. Freshwater Biology 25: 321-330.
- Dynesius, M. and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266: 753-762.
- Ellis, T. and R. N. Gibson. 1995. Size-selective predation of 0-group flatfishes on a Scottish coastal nursery ground. Marine Ecology Progress Series 127: 27-37.
- Emery, E. B., T. P. Simon, F. H. McCormick, P. L. Angermeier, J. I. Deshon, D. L. Yoder, R. E. Sanders, W. D. Pearson, G. D. Hickman, R. J. Reash and J. A. Thomas. 2003. Development of a multimetric index for assessing the biological condition of the Ohio River. Transactions of the American Fisheries Society 132: 791-808.
- Ferrell, J. 1996. Soundings: one hundred years of the Missouri River Navigation Project. US Army Corps of Engineers, Kansas City District, Kansas City.
- Frissell, C. A., W. J. Liss, C. E. Warren and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10: 199-214.
- Funk, J. L. and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series Report 11. Jefferson City.
- Galat, D. L. and I. Zweimüller. 2001. Conserving large-river fishes: is the highway analogy an appropriate paradigm? Journal of the North American Benthological Society 20: 266-279.
- Galat, D. L. and R. Lipkin. 2000. Restoring ecological integrity of great rivers: historical hydrographs aid in defining reference conditions for the Missouri River. Hydrobiologia 422: 29-48.
- Galat, D.L., C.R. Berry, W.M. Gardner, J.C. Hendrickson, G.E. Mestl, G.J. Power, C. Stone, and M.R. Winston. 2005a. Spatiotemporal patterns and changes in Missouri River fishes. American Fisheries Society Symposium 45: 249-291.
- Galat, D. L., C. R. Berry, Jr., E. J. Peters, and R. G. White. 2005b. Missouri River basin. Pages 427-480 *in* A.C. Benke and C.E. Cushing, editors. Rivers of North America. Elsevier, Amsterdan.
- Galat, D. L., L. H. Fredrickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, G. T. Gelwicks, J. E. Havel, D. L. Helmers, J. B. Hooker, J. R. Jones, M. F. Knowlton, J. Kubisiak, J. Mazourek, A. C. McColpin, R. B. Renken and R. D. Semlitsch. 1998. Flooding to restore connectivity of regulated, largeriver wetlands. Bioscience 48: 721-733.

- Garman, G. C. and J. R. Moring. 1993. Diet and annual production of two boreal river fishes following clearcut logging. Environmental Biology of Fishes 36: 301-311.
- Garner, P. 1996. Microhabitat use and diet of 0+ cyprinid fishes in a lentic, regulated reach of the river Great Ouse, England. Journal of Fish Biology 48: 367-382.
- Gelwicks, G. T., K. Graham and D. L. Galat. 1996. Status survey for sicklefin chub, sturgeon chub, and flathead chub in the Missouri River, Missouri. Final Report. Missouri Department of Conservation, Columbia, MO. 23p.
- Gerrity, P. C. 2005. Habitat use, diet, and growth of hatchery-reared juvenile pallid sturgeon and indigenous shovelnose sturgeon in the Missouri River above Fort Peck Reservoir. Master's thesis. Montana State University, Bozeman, Montana.
- Gerrity, P. C., C. S. Guy, and W. M. Gardner. 2006. Juvenile pallid sturgeon are piscivorous: a call for conserving native cyprinids. Transactions of the American Fisheries Society 135: 604-609.
- Gore, J. A. and F. D. Shields, Jr. 1995. Can large rivers be restored? BioScience 45: 142-152.
- Grace, T. B. 1985. The status and distribution of commercial and forage fish in the Missouri river and their utilization of selected habitats: Evaluation of sand island habitat in the Missouri River. Final Report. Missouri Department of Conservation, Columbia, MO. National Marine Fisheries Service Program 2-363-R, Project IV, Job II. 34p.
- Grace, T. B. and W. L. Pflieger. 1985. Fish survey of the Missouri and Mississippi rivers. Missouri Department of Conservation, Columbia, Missouri. National Marine Fisheries Service Program 2-363-R, Project IV, Job I. 56pp.
- Grady, J. M. and J. Milligan. 1998. Status of Selected cyprinid species at historic lower Missouri River sampling sites. U.S. Fish and Wildlife Service Report, Columbia Fisheries Resource Office, Columbia, MO.
- Griffiths, D. 1992. Size, abundance, and energy use in communities. Journal of Animal Ecology 61: 307-315.
- Grift, R. E., A. D. Buijse, W. L. T. Van Densen, M. A. M. Machiels, J. Dranenbarg, J. G. P. Klein Breteler and J. J. G. M. Backx. 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. River Research and Applications 19: 353-374.
- Grumbine, R. E. 1994. What is ecosystem management? Conservation Biology 8: 27-38.

- Gutreuter, S., A. D. Bartles, K. Irons, and M. B. Sandheinrich. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences 56: 2282-2291.
- Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116: 851-855.
- Harvey, B. C. and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. Oecologia 87: 336-342.
- Helfman, G. S., B. B. Collette, and D. E. Facey. 1997. Fishes as prey. Pages 334-347 *in* Helfman, G.S., B.B. Collette, and D.E. Facey. The diversity of fishes. Blackwell Science, London.
- Hulse, D. W., A. Branscomb, and S. G. Payne. 2004. Envisioning alternatives: using citizen guidance to map future land and water use. Ecological Applications 14: 325-341.
- Hirzinger, V., H. Keckeis, H. L. Nemeschkal, and F. Schiemer. 2004. The importance of inshore areas for adult fish distribution along a free-flowing section of the Danube, Austria. River Research and Applications 20: 137-149.
- Humphries, P., L. G. Serafini, and A. J. King. 2002. River regulation and fish larvae: variation through space and time. Freshwater Biology 47: 1307-1331.
- Humphries, P., A. J. King, and J. D. Koehn. 1999. Fish, flows and floodplains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. Environmental Biology of Fishes 56: 129-151.
- Hynes, H. N. B. 1975. The stream and its valley. Verh. Internat. Verein. Limnol. 19:1-15.
- Johnson, R. R., C. L. Milewski and K. F. Higgins. 1996. Summary and selected annotated bibliography of the upper Mississippi and Missouri River drainage basins with emphasis on wetlands and riparian zones and the impact of flood control and flooding on the ecosystem. Pages 113-149 *in* Galat, D. L., and Frazier, A. G., editors, Overview of river-floodplain ecology in the Upper Mississippi River Basin, v. 3 *of* Kelmelis, J. A., editor, Science for floodplain management into the 21st century: Washington, D.C., U.S. Government Printing Office.
- Johnson, B. L., W. B. Richardson, and T. J. Naimo. 1995. Past, present, and future concepts in large river ecology. BioScience 45: 134-141.

- Junk, W. J., P. B. Bayley and R. E. Sparks. 1989. The flood pulse concept in riverfloodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences Ottawa 106: 110-127.
- Jurajda, P. 1999. Comparative nursery habitat use by 0+ fish in a modified lowland river. Regulated Rivers: Research and Management 15: 113-124.
- Jurajda, P. 1995. Effect of channelization and regulation on fish recruitment in a flood plain river. Regulated Rivers: Research and Management 10: 207-215.
- Karr, J. R., L. A. Toth, and D. R. Dudley. 1985. Fish communities of midwestern rivers: a history of degradation. BioScience 35: 90-95.
- Keckeis, H., E. Kamler, E. Bauer-Nemeschkal, and K. Schneeweiss. 2001. Survival, development and food energy partitioning of nase larvae and early juveniles at different temperatures. Journal of Fish Biology 59: 45-61.
- King, A. J. 2004. Ontogenetic patterns of habitat use by fishes within the main channel of an Australian floodplain river. Journal of Fish Biology 65: 1582-1603.
- King, J. and D. Louw. 1998. Instream flow assessments for regulated rivers in South Africa using the building block methodology. Aquatic Ecosystem Health and Management 1: 109-124.
- Kinsolving, A. D. and M. B. Bain. 1993. Fish assemblage recovery along a riverine disturbance gradient. Ecological Applications 3: 531-544.
- Koebel, J. W. 1995. A historical perspective on the Kissimmee River restoration project. Restoration Ecology 3: 149-159.
- Kolasa, J. and M. Zalewski. 1995. Notes on ecotone attributes and functions. Hydrobiologia 303: 1-7.
- Kozłowski, J. and A.T. Gawelczyk. 2002. Why are species' body size distributions usually skewed to the right? Functional Ecology 16: 419-432.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23: 399-418.
- Lytle, D. A. and N. L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19: 94-100.
- Michaletz, P. H. 1997. Factors affecting abundance, growth, and survival of age-0 gizzard shad. Transactions of the American Fisheries Society 126: 84-100.
- Mérigoux, S. and D. Ponton. 1999. Spatio-temporal distribution of young fish in

- tributaries of natural and flow-regulated section of a neotropical river in French Guiana. Freshwater Biology 42: 177-198.
- Mérona, B. D. and P. Albert. Ecological monitoring of fish assemblages downstream of a hydroelectric dam in French Guiana (South America). Regulated Rivers: Research and Management 15: 339-351.
- Modde, T. and D. B. Irving. 1998. Use of Multiple Spawning Sites and Seasonal Movement by Razorback Suckers in the Middle Green River, Utah. North American Journal of Fisheries Management 18: 318-326.
- Morin, A., W. Lamoureux and J. Busnarda. 1999. Empirical models predicting primary productivity from chlorophyll *a* and water temperature for stream periphyton and lake and ocean phytoplankton. Journal of the North American Benthological Society 18: 299-307.
- Motta, R. L. and V. S. Uieda. 2005. Food web structure in a tropical stream ecosystem. Austral Ecology 30: 58-73.
- Naiman, R. J., H. Decamps, J. Pastor, and C. A. Johnston. 1988. The potential importance of boundaries of fluvial ecosystems. Journal of the North American Benthological Society 7: 289-306.
- Nestler, J. and V. K. Sutton. 2000. Describing scales of features in river channels using fractal geometry concepts. Regulated Rivers: Research and Management 16: 1-22.
- Neumann, D. 2002. Ecological rehabilitation of a degraded large river system considerations based on case studies of macrozoobenthos and fish in the lower Rhine and its catchment area. International Review of Hydrobiology 87: 139-150.
- Niemi, E., M. Gall, and A. Johnston. 1999. An economy in transition: the Klamath-Siskiyou ecoregion. Final Report: The Klamath-Siskiyou Alliance. ECONorthwest, Eugene, OR.
- Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. Science 308: 405-408.
- Nunn, A. D., I. G. Cowx, P. A. Frear, and J. P. Harvey. 2003. Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers? Freshwater Biology 48: 579-588.
- Palmer, M. A., E. S. Bernhardt, J. D. Allan, P. S. Lake, G. Alexander, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad Shah, D. L. Galat, S. Gloss, P. Goodwin, D. H. Hart, B. Hassett, R. Jenkinson, G. M. Kondolf, R. Lave, J. L. Meyer, T. K.

- O'Donnell, L. Pagano, P. Srivastava and E. Sudduth. 2005. Standards for ecologically successful river restoration. Journal of Applied Ecology 42:208-217.
- Pavlov, D. S. 1994. The downstream migration of young fishes in rivers: mechanisms and distribution. Folia Zoologica 46: 193-208.
- Petry, P., P. B. Bayley, and D. F. Markle. 2003. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. Journal of Fish Biology 63: 547-579.
- Pflieger, W. L. and Grace. 1987. Changes in the fish fauna of the lower Missouri River, 1940-1983. Pages 166-177 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press.
- Poff, L. N., A. J. David, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. Bioscience 47: 769-784.
- Poizat, G. and D. Pont. 1996. Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. Freshwater Biology 36: 611-622.
- Ponton, D. and G. H. Copp. 1997. Early dry-season community structure and habitat use of young fish in tributaries of the River Sinnamary (French Guiana, South America) before and after hydrodam operation. Environmental Biology of Fishes 50: 235-256.
- Power, M. E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. Ecology 73: 1675-1688.
- Power, M. E. 1990. Effects of fish in river food webs. Science 250: 811-814.
- Power, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pages 333-351 *in* W.C. Kerfoot and A. Sih, editors. Predation. Direct and indirect effects on aquatic communities. University Press of New England, Hanover, NH.
- Power, M. E. 1984. Depth distributions of armored catfish: predator-induced resource avoidance? Ecology 65: 523-528.
- Power, M. E., W. E. Dietrich, and J. C. Finlay. 1996. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. Environmental Management 20: 887-895.
- Quist, M. C., A. M. Boelter, J. M. Lovato, N. M. Korfanta, H. L. Bergman, D. C. Latka, C. Korschgen, D. L. Galat, S. Krentz, M. Oetker, M. Olson, C. M. Scott, and J.

- Berkley. 2004. Research and Assessment Needs for Pallid Strugeon Recovery in the Missouri River. Final report to the U.S. Geological Survey, U.S. Army Corps of Engineers, U.S. Fish and Wildlife Service, and U.S. Environmental Protection Agency. William D. Ruckelshaus Institute of Environmental and Natural Resources, University of Wyoming, Laramie. Available online at: http://infolink.cr.usgs.gov/Science/PallidSturgeon/PSWorkshop04.pdf
- Rahel, F. J. and W. A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: biotic zonation and additive patterns of community change. Transactions of the American Fisheries Society 120: 319-332.
- Reeves, K. 2006. Use of main channel and shallow-water habitats by larval fishes in the lower Missouri River. Doctoral dissertation. University of Missouri, Columbia, Missouri.
- Richter, B. D., R. Mathews, D. L. Harrison, and R. Wigington. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. Ecological Applications 13: 206-224.
- Rodríguez, M. A. and W. M. Lewis, Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. Ecological Monographs 67: 109-128.
- Rundle, S. D., M. J. Attrill, and A. Arshad. 1998. Seasonality in macroinvertebrate community composition across a neglected ecological boundary, the freshwater estuarine transition zone. Aquatic Ecology 32: 211-216.
- Schiemer, F. 2000. Fish as indicators for the assessment of the ecological integrity of large rivers. Hydrobiologia 422/423: 271-278.
- Schiemer, F., H. Keckeis, G. Winkler, and L. Flore. 2001. Large rivers: the relevance of ecotonal structure and hydrological properties for the fish fauna. Archiv für Hydrobiologie Supplement 135: Large Rivers 12: 487-508.
- Schiemer, F. and T. Splinder. 1989. Endangered fish species of the Danube River in Austria. Regulated Rivers Research and Management 4: 397-407.
- Schiemer, F., T. Spindler, H. Wintersberger, A. Schneider, and A. Chovanec. 1991. Fish fry associations: important indicators for the ecological status of large rivers. Verhandlungen International Vereinigung der Limnologie 24: 2497-2500.
- Schiemer, F., M. Zalewski, and J. E. Thorpe. 1995. Land/inland water ecotones: intermediate habitats critical for conservation and management. Hydrobiologia 303: 259-264.
- Schlosser, I. J. 1987. The role of predation in age- and size-related habitat use by stream

- fishes. Ecology 68: 651-659.
- Simon, T. P. and E. B. Emery. 1995. Modification and assessment of an index of biotic integrity to quantify water resource quality in great rivers. Regulated Rivers: Research and Management 11: 283-298.
- Sparks, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. Bioscience 45: 168-182.
- Starostka, A., N. Frohnauer, W. Doyle, and T. Hill. 2005. Habitat assessment and monitoring program: initial year of biological monitoring. 2005 Annual Report. U.S. Fish and Wildlife Service-Columbia Fisheries Resource Office, Columbia, MO.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75: 2-16.
- Tockner, K., F. Malard, and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes 14: 2861-2883.
- Tonn, W. M. 1990. Climate change and fish communities: a conceptual framework. Transactions of the American Fisheries Society 119: 337-352.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8: 36-50.
- Tracy-Smith, E. 2006. Relation of Missouri River flows to sandbar morphology with implications for selected biota. Master's Thesis. University of Missouri, Columbia, Missouri.
- Tyus, H. M. and G. B. Haines. 1991. Distribution, habitat use, and growth of age-0 Colorado squawfish in the Green River basin, Colorado and Utah. Transactions of the American Fisheries Society 120: 79-89.
- USACE. 2004. Missouri River bank stabilization and navigation project, fish and wildlife mitigation project: annual implementation report. U.S. Army Corps of Engineers. Available: https://www.nwd.usace.army.mil (March 2007).
- USACE. 2003. Final supplemental environmental impact statement for the Missouri River fish and wildlife mitigation project. U.S. Army Corps of Engineers, Kansas City District, Kansas City, MO, Omaha District, Omaha, NE.
- USFWS. 2003. U.S. Fish and Wildlife Service 2003 amendment to the 2000 Biological Opinion on the operation of the Missouri River main stem reservoir system, operation and maintenance of the Missouri River bank stabilization and navigation project, and operation of the Kansas River reservoir system. U.S. Fish

- and Wildlife Service. Available: https://www.nwd.usace.army.mil (March, 2007).
- Utrup, N., W. Doyle, C. Lee, A. Plauck, and T. Hill. 2006. Pallid sturgeon population assessment project and associated fish community monitoring for the Missouri River: segment 13. 2005 Annual Report. U.S. Fish and Wildlife Service Columbia Fisheries Resource Office, Columbia, MO.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.
- Ward, J. V. and J. A. Stanford. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers: Research and Management 11: 105-119.
- Ward, J. V. and J. A. Stanford. 1983. The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic systems. Pages 347-356. *in* T. D. Fontaine and S. M. Baretell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, U.S.A.
- Ward, J. V., K. Tockner and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management 15: 125-139.
- Willis, T. V. and J. J. Magnuson. 2000. Patterns in fish species composition across the interface between streams and lakes. Canadian Journal of Fisheries and Aquatic Sciences 57: 1042-1052.
- Winemiller, K. O. and D. B. Jepsen. 1998. Effects of seasonality and fish movement on tropical river food webs. Journal of Fish Biology 53 (Supp. A): 267-296.
- Wu, J. and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. The Quarterly Review of Biology 70: 439-466.

CHAPTER II

Patterns of Distribution and Abundance by Small-bodied Fishes at Lower Missouri River Sandbars: The Importance of Body Length

Introduction

Shallow, slow current-velocity habitats (SSVH) are used by many small-bodied riverine fishes (Copp 1992; Copp et al. 1994; Jurajda 1999; Bowen et al. 2003; Grift et al. 2003; Hirzinger et al. 2004; Nunn et al. 2007). They provide benign environmental conditions and a productive area as nursery for age-0 fishes and may serve as refuge to other small-bodied fishes (Johnson and Covich 2000; Roussel and Bardonnet 1999). Brown and Coon (1994) suggested that the lower reaches of tributary streams were essential during early ontogeny of lower Missouri River (LMOR) fishes because they were the only low-velocity habitats available. However, many age-0 and small-bodied fishes were found in adjacent connected scour basins where velocity was low relative to main channel flow (Tibbs and Galat 1997; Galat et al. 2004; Whitledge et al. 2005) and larvae of many species were found in shallow areas adjacent to sandbars (Reeves 2006) in LMOR. In light of these recent findings, existing sandbars represent a potentially important source of SSVH within the channelized and flow regulated LMOR. Early life stages represent periods of high population mortality before fishes become reproductively mature adults. Native fish conservation will benefit from studies of small-bodied fishes and their microhabitat use to improve recruitment through this population bottle neck.

Two types of sandbars dominate sandbar composition (98%) on LMOR (Reeves 2006). Point sandbars, hereafter called *point bars* (PB), form on the inside of channel bends; wing-dike sandbars, hereafter called *wing-dike bars* (WD), form behind man made wing-dikes. Point bars more closely mimic natural sandbars from the historic river channel; they are larger but less abundant than wing-dike bars (Tracy-Smith 2006). Physical differences between and within these two sandbar types may be important factors in how fishes are distributed. For example, side channels on the upper Mississippi River differentially provide suitable habitat for fishes based on individual side channel characteristics. There, fluvial specialists are more abundant in side-channels that are highly influenced by main-channel flows than in side-channels that are characterized by more macrohabitat generalists and minimally influenced by main channel flows (Ellis et al. 1979). Differences may similarly exist in fish assemblages of sandbars on LMOR, however little information exists on whether small-bodied fishes differentially use point and wing-dike sandbar types, or habitats at smaller scales around sandbars.

Body size may play an important role in fish survival because size is related to ability to compete for resources and avoid predation (Kerr 1989; Griffiths 1992). Larger fishes consume more resources at a higher rate than smaller fishes. Rapid ontogeny during early life reduces predation risk because development of locomotor features help early life stage fishes escape predators; rapid growth reduces predation risk because most aquatic piscivores are gape limited (Brown and Maurer 1986; Webb and Weihs 1986; Schlosser 1988; Sogard 1997). However, a tradeoff may exist with body size relative to predation risk. Power (1984, 1987) found that terrestrial predators selected larger sized small-bodied fish while hunting shallow waters in an Amazon Basin stream; possibly

because smaller fish were more cryptic or more likely to escape after capture. In response, larger fishes avoided shallow water despite high abundance of food resources, which set up a size-based assemblage and habitat use structure. Similarly, the small-bodied fish assemblage at LMOR sandbar ATTZ may differentially use distinct habitats by species and/or along a body length gradient.

Ontogenetic habitat shifts of many riverine fishes correspond to changing environmental conditions during the first year of life (Bischoff and Freyhof 1999; Dettmers et al. 2001; Wolter and Bischoff 2001). Wide fluctuations in discharge control seasonal availability of many habitats and play a significant role in survival of many fluvial fishes (Junk et al. 1989; Freeman et al. 2001). Many fishes may not have access to floodplain ATTZ where the river is disconnected from its floodplain or during low discharge. High discharge submerges sandbar ATTZ under relatively deep and fast flowing water rendering sandbar ATTZ unavailable to fluvial specialists. Therefore, it may be important to synchronize fish use with habitat availability relative to discharge in large rivers (Copp 1992; Garner 1997; Childs et al. 1998; Flore and Keckeis 1998) where native fish populations may be depressed due to flow regulation (Stanford et al. 1996; Propst and Gido 2004).

Suitable habitats for age-0 fishes may be available during only a short time period (Yu and Peters 2003), indicating they must undergo rapid ontogenetic habitat shifts to survive. However, ontogenetic driven shifts from age-0 to adult habitat often occur on a seasonal scale (Garner 1996; Bischoff and Freyhof 1999; Wolter and Bischoff 2001) suggesting that many fluvial species have specially adapted life history strategies or use surrogate habitats to cope with short-term wide fluctuations in flow (Strange et al. 1993;

Freeman et al. 2001). To illustrate, LMOR was historically a complex mosaic of shifting channels and sandbars that probably provided suitable small-bodied fish habitat over a wide range of flows; if fishes were displaced with increasing discharge, it is likely they had a reasonably good chance of settling in a similarly suitable habitat (e.g., higher elevation sandbar). Today, these same native fishes, especially age-0, may be vulnerable to flashy unpredictable flows because much of the sandbar ATTZ was lost when LMOR was channelized and straightened. Results of similar studies on small streams (Harvey 1987; Pearsons et al. 1992; Strange et al. 1993; Dolloff et al. 1994) support this hypothesis suggesting it is reasonable to expect greater survival in a large river like LMOR where decision makers realize the importance native fish conservation and are working to restore some semblance of diversity and abundance of habitat patches toward pre-regulation levels.

Diel habitat use patterns of fishes are comparatively less studied than diurnal patterns in lotic systems primarily because rough terrain in many streams, sampling methods, and logistic limitations are not conducive to nocturnal sampling (Johnson and Covich 2000). Nevertheless, diel studies are important to obtain complete and accurate fisheries data (Brewer et al. 2005). Diel habitat use studies on fluvial small-bodied fishes indicate that day-night shifts are generally attributed to foraging patterns (Yu and Peters 2003), or trade-offs between feeding opportunity and predation risk (Culp 1989; Copp and Jurajda 1993; Gries et al. 1997; Baras and Nindaba 1999a,b; Roussel and Bardonnet 1999). Shallow, near-shore areas are often occupied by smaller fishes during the day, but abundance of larger fishes may increase at night (Kneib 1987; Pratt and Fox 2001; Arrington and Winemiller 2003; Wolter and Freyhof 2004), possibly because

vulnerability to terrestrial predators is reduced (Power 1987; Schlosser 1988). This suggests that if abundance of larger fishes increases in sandbar ATTZ at night in response to lower terrestrial predation risk, then aquatic predation risk to smaller fishes may increase at night. Therefore, it is reasonable to expect small-bodied fishes that use SSVH in sandbar ATTZ diurnally to use different habitats nocturnally (e.g., see Jacobsen and Berg 1998). The use of sandbar habitats by small-bodied fishes may vary by diel period for subgroups of fishes based on body size.

Lack of suitable habitat may serve a significant role in the decline of native fish species on LMOR. Sicklefin chub (Macrhybopsis meeki), sturgeon chub (M. gelida), speckled chub (M. aestivalis), plains minnow (Hybognathus placitus), and sand shiner (Notropis stramineus) are archetypical big-river small-bodied fishes that are native to LMOR. Their abundance, size structure, and habitat use at sandbar ATTZ is not well understood, particularly at a fine resolution. Sicklefin and sturgeon chub may have direct implications to the recovery of endangered pallid sturgeon and therefore are important component of LMOR fish ecology. The USFWS-Fisheries Resource Office in Region 3 is monitoring these five small-bodied native fish species to determine their response to habitat creation. Other species such as channel catfish (Ictalurus punctatus) and freshwater drum (Aplodinotus grunniens) are important recreational species, while gizzard shad (Dorosoma cepedianum) and other minnows (e.g., red shiner Cyprinella *lutrensis*) are important forage fishes. My goal was to determine how small-bodied fishes use existing shallow-water sandbar habitats and how the assemblage was structured during the time of year small-bodied fishes are expected to be most abundant. Achieving this goal will provide information to improve and increase availability of SSVH in the

main-channel of the channelized LMOR for conservation of many native fluvial fishes. I focused quantitative high resolution sampling effort in waters adjacent to sandbars in the depth range 0.0-0.5 m to provide detailed information about this ecologically important, yet little studied, transition zone.

My first objective was to quantify how abundance and body length of the small-bodied fish assemblage and a suite of environmental factors vary in the context of three spatial and two temporal scales at sandbar ATTZ. As part of this objective I quantified sandbar ATTZ depth and velocity use profiles for many species, including the five species currently targeted under monitoring programs of the U.S. Fish and Wildlife Service. My second objective was to test if the small-bodied fish assemblage at sandbar ATTZ was composed primarily of sub-assemblages of taxonomically related species, of sub-assemblages that parallel habitat use guild, and/or by sub-assemblages with similar body length.

Study Area

This study occurred along a 128-km reach of LMOR in central Missouri between the confluences of Moniteau Creek (rkm 254) and Chariton Creek (rkm 381) with Missouri River (river kilometers begin at zero and increase upstream from the confluence with Mississippi River; Figure 2.1). I selected eight sandbars, four point bars and four wing-dike bars, within this reach. These two sandbar types were selected because they compose 98% of LMOR sandbars in the study area (Reeves 2006) and were likely to have connected secondary channels during the period July-October (Reeves 2006; Tracy-Smith 2006). Mean distance between sandbars was 15.9 km; the furthest distance

between adjacent sandbars was 35.4 km from Petite Saline sandbar (rkm 285) to Boonville sandbar (rkm 320), shortest distance was 3.2 km from Marion sandbar (rkm 253) to Hartsburg sandbar (rkm 256).

Methods

In the sections that follow I first describe the spatial and temporal components of a sampling design to collect small-bodied fishes in a structured and repeatable framework. Second, I present the technique used to collect fishes within the sampling framework to accomplish objectives. Finally, I describe how data were processed and analyzed to address objectives.

Sample Design

Spatial

Sandbar morphology is largely controlled by river discharge (Tracy-Smith 2006), and a diversity of habitats exists at smaller spatial scales around sandbars. I developed a sampling design that (1) was repeatable over a range of discharge; (2) sampled the same relative positions on sandbars over a range of discharge for spatially consistent comparison over time; (3) provided information on multiple scales, yet was sensitive enough to distinguish units of smaller scale that developed within constraints of its larger parent scale, and; (4) objectively distributed sampling effort over the spatiotemporal range of shallow-water depths, water velocities, and substrate types present at sandbars.

The spatial distribution and abundance of fishes that use LMOR sandbar habitats and associated environmental factors was quantified within a hierarchically nested

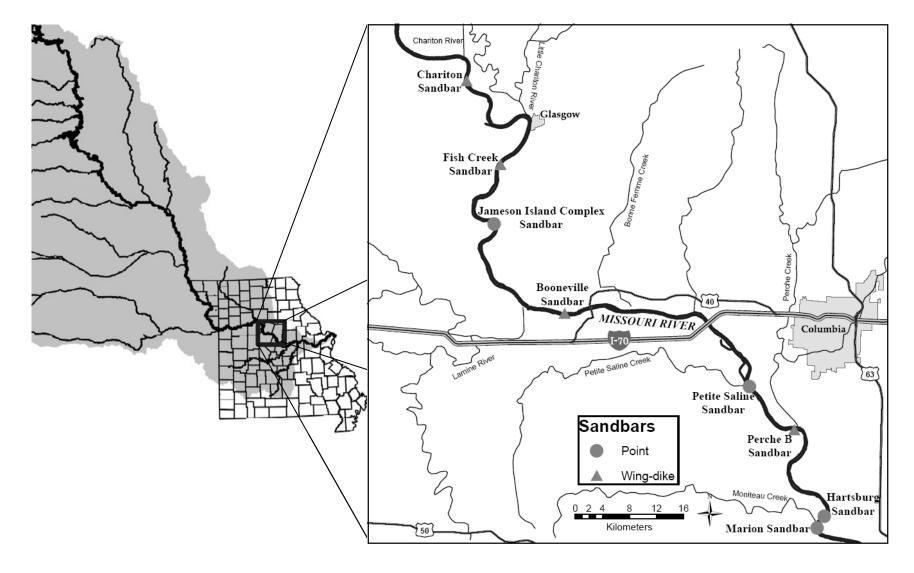


Figure 2.1. Map of study reach along Missouri River in central Missouri showing sandbars studied and major tributaries.

framework (Figure 2.2). The largest spatial extent was termed sandbar type, defined here to consist of (1) four point bars and (2) four wing-dike bars. At the next lower spatial scale, termed region, six individual regions were delineated around the sandbar perimeter to capture the range of SWH that occurred adjacent to each sandbar. In rare cases where a tertiary channel dissected the sandbar, it was sampled and categorized as a seventh region. Each region was composed of two transects perpendicular to the shoreline and up to three sample units were distributed along each transect relative to distance from shore to incorporate both the spatial and depth diversity present. Fish collections and environmental factors measured at these sample units composed the smallest spatial scale, termed sample unit. The standard protocol used to delineate space and distribute sample units as described in the following subsections was a consistent method for sampling the same relative position on emergent sandbars over a range of discharges. It was objective and minimized personal sampling bias in the field (e.g., where to place sample units), and a template to quantify differences in habitat use by fishes across the diversity of SWH associated with sandbars. A similar method that met these criteria was used if sandbars were small or submerged due to high discharge (see Appendix A). Region scale-

The following procedure was used to delineate regions and was the basis for effectively distributing sample units around sandbars. Length of the midline on each sandbar was measured traveling from the most upstream to downstream point with a handheld global positioning system (GPS) unit. In cases where the bar midline did not follow a straight line, measurements were taken incrementally by traveling along the midline being cognizant of relative lateral position on the bar to remain centered. A 1x1-

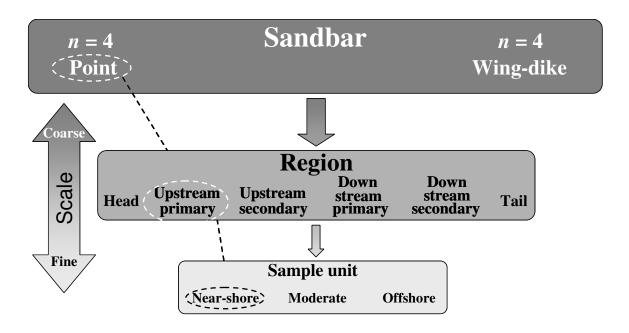


Figure 2.2. Flow chart illustrating nested spatial scale design for sampling lower Missouri River (LMOR) sandbars. Sandbars are the largest spatial scale and contain regions; sample units are the smallest scale and compose regions.

m reference cross was placed at one-third and two-thirds the length along the sandbar with the axes angled approximately 45° from the sandbar midline. These axes were used to direct sight-lines to the sandbar-water interface to mark the location of transects which extended perpendicular from the shoreline into the water. The submerged area between transects from the same reference cross represent one region (Figure 2.3). The upstream and downstream ends of sandbars were also delineated into discrete regions and sampled.

Regions were labeled with respect to relative position on the sandbar as either up or downstream and primary or secondary channel side. Region names with code in parenthesis are as follows: head region (HR), upstream primary channel region (UP), upstream secondary channel region (US), downstream primary channel region (DP), downstream secondary channel region (DS), tail region (TR), and tertiary channel (TC) when present.

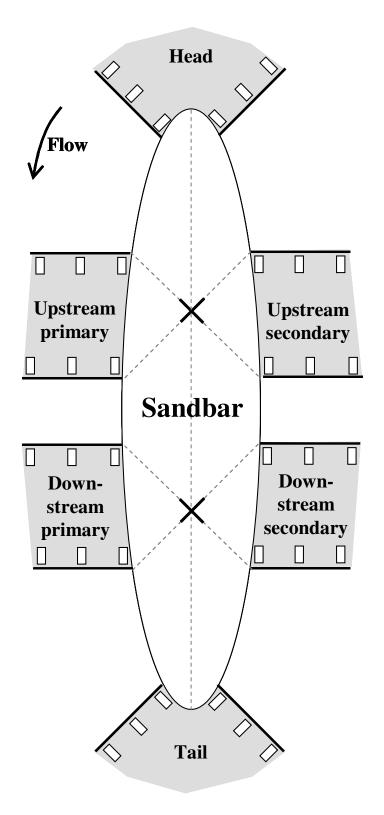


Figure 2.3. Idealized lower Missouri River sandbar showing spatial delineation design used to collect small-bodied fishes. "X" represent reference crosses used to sight (dashed lines) position of transects (solid dark lines) to place sample units (white boxes) within regions (shaded area between transects).

Sample unit scale-

The sample unit was, by definition, the finest level of spatial resolution in this study and was defined by the gear used to collect fishes (PAED, see below Fish collection and handling). Up to three sample units were placed on each transect relative to distance from shore within the depth range 0.0-0.5 m. This depth range was limited to 0.5-m by effectiveness of the gear to ensure equal effort across all samples, and will be detailed below under Fish collection and handling. One sample unit was located with the PAED inside edge place at the sandbar-water interface, termed *nearr-shore*; one offshore where depth was 0.5-m; and a third, termed moderate, between the first and second at a depth approximately one-half the distance between near-shore and offshore units. Less than three samples were collected along transects where shoreline slope was steep to avoid sample units overlapping or being too close to one another to be considered independent. In these instances, each sample unit was moved 5 m up or downstream or until they were 10 m apart. Only one collection was made along particularly steep transects where the 0.0-0.5 m depth range was covered by a single sample unit. A seventh sample unit was reserved as a "wildcard" in regions to sample unique habitat features (e.g., large woody debris, vegetation, etc.), when present, that were not covered by transects; wildcards were also classified as near-shore, moderate, or offshore.

Temporal

Month-

Fishes were collected during the warmer water period July-October, 2005, when post larval age-0 fishes were expected to be most abundant (Galat et al. 1998). Sandbar types were sampled in a stratified random order within three week periods during the four-month sampling period. Stratified sampling order was randomly selected for each period, and sampling alternated between point and wing-dike sandbars on consecutive trips. Sandbars were randomly reselected in the alternating stratified manner for each three week period. Regions were also sampled in a randomly selected order that differed each day. Transects and PAEDs within each region were sampled in order from most downstream to upstream and from near-shore to offshore. Although not random, this approach minimized disturbance of un-sampled units and maximized time efficiency during sampling. Collection times for monthly temporal comparisons were restricted to daylight hours from 45 minutes after sunrise to 45 minutes before sunset to minimize catches associated with the crepuscular period.

Diel-

I used a reduced sampling design on one point bar (Petite Saline sandbar, rkm 287, see Figure 2.1) to study the effect of diel period on abundance and body length of small-bodied fishes, and how they relate to depth, velocity, and temperature by sample unit category. I selected Petite Saline sandbar because it was a relatively large and well studied sandbar (see Grace 1985; Gelwicks et al. 1996; Grady and Milligan 1998, Reeves 2006, Tracy-Smith 2006) and had regions on opposite sides (primary vs. secondary channel) with relatively shallow slopes. The shallow sloping banks of the upstream

primary and downstream secondary regions provided a good natural laboratory to test the effect of depth on abundance and body size of small-bodied fishes between light and dark diel periods. Diel samples were collected on three occasions spaced approximately monthly from July to September, 2005. On these occasions, upstream primary and downstream secondary regions were each sampled once every 4 hours for 24 consecutive hours during each sampling trip. Fishes, depth, velocity, and temperature data were collected for each four hour block within each of these regions using protocol as described below.

Fish collection and handling

I used a prepositioned areal electrofishing device (PAED) with bottom parallel electrodes as the sample unit to quantitatively sample fishes across the range of habitats present in shallow areas adjacent to sandbars. This gear samples a known discrete area that is relatively small so that samples can be compared among adjacent PAEDs in close proximity and is more consistent and quantitative than seining. General PAED design (e.g., Bain et al. 1985; Peters et al. 1989; Fisher and Brown 1993; Gelwicks et al. 1996) includes a rectangular frame placed on the substrate with two sides (opposite) representing the anode and cathode. The bottom parallel electrode design sampled fishes within a defined area concentrating current between electrodes that were pre-positioned to sample a discrete microhabitat. Investigator effect associated with other electrofishing methods (e.g., Copp and Peňáz 1988) was minimized because PAEDs were left undisturbed for at least 11 minutes to allow re-colonization before being sampled (Bain et al. 1985; Bain and Finn 1991). Janáč and Jurajda (2005) found this method (termed

remote electrofishing) was more efficient and less species selective for collecting age-0 fishes than other microhabitat electrofishing techniques.

Bottom parallel electrode PAED area was 3.75 m² (2.5 m X 1.5 m). Electrodes consisted of two 62-cm sections of 5.08-cm outside diameter DWV copper pipes linked by 61-cm lengths of 4.76-mm diameter aircraft cable separated by 2.54-cm diameter PVC tubing (Figure 2.4). A 4,400 watt alternating current (AC) generator fitted with a heavyduty safety shut-off switch was used to supply nearly instant power consistently to PAEDs. The use of AC electrofishing reduces positive electro-taxis (Fisher and Brown 1993), so that risk of biasing samples with fishes outside the defined PAED area was low. The heavy-duty switch was an important detail to reduce human bias and consistently produce similar effort during initiation of electrofishing at each PAED. Conceptually, there was variability and lag to maximum power output each time the generator was started because it may not start on the first ignition attempt or run intermittently for a moment after ignition. This variability and lag would have been directly transferred to the water and may have allowed fishes time to flee the increasing electrical field and escape capture if a switch was not used. With the switch, however, the generator was started and allowed to stabilize to maximum power before the switch was flipped to deliver immediate full power to PAEDs during initiation of electrofishing.

A general voltage gradient (volts/cm) range required to immobilize fishes is 0.14-0.30 v/cm (Reynolds 2000), and many agree that 0.20 v/cm is sufficient (Bain et al. 1985; Fisher and Brown 1993; Schwartz and Herricks 2004). I adopted a minimum standard effort of 0.20 v/cm and tested voltage gradient produced by PAEDs near the surface in 1.0-m deep water over a range of conductivity. Voltage gradient near the surface was

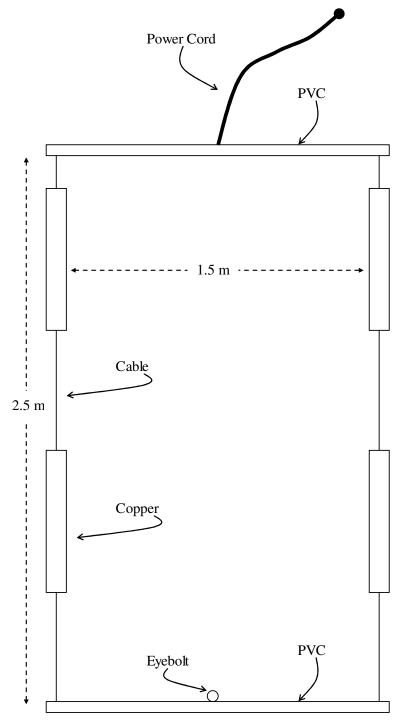


Figure 2.4. Diagram of Missouri River prepositioned areal electrofishing device (PAED) depicting DWV-copper and aircraft cable linkages of electrodes, PVC, stabilizing eyebolt, and 12-guage power cord. PAEDs were staked through eye bolt for stability and to indicate location of downstream terminal end.

0.375 v/cm at the highest conductivity encountered during tests (740 uS/cm) in water 1.0 m deep. Extrapolation indicated that PAEDs would effectively sample small-bodied fishes in LMOR waters up to 975 uS/cm; only one sample unit had conductivity over this threshold (1153 uS/cm) during fish sampling. Since voltage gradient decreases with distance from electrodes, water near the surface and half way between electrodes represented where the lowest voltage gradient occurred throughout the PAED sample volume. I conservatively restricted fish sampling with PAEDs to water depths ranging from 0.0 to 0.5m to assure that the minimum effective voltage gradient (i.e., effort) required to immobilize fish (0.2 v/cm) was achieved for all collections.

PAEDs were deployed with the long axis parallel to the shoreline and left undisturbed for at least 11 minutes (Bain and Finn 1991; Baras 1995; Cowx et al. 2001). They were energized for no longer than 45-s and immobilized fishes were collected in a 3.175-mm mesh seine net held immediately downstream. A D-frame net (mesh 3.175 mm) was used to sweep the sampled volume toward the seine net if no visually identifiable current was present. Thus, the minimum size of small-bodied fishes evaluated in this study was those retained by 3.175-mm mesh. Collections were processed in the field immediately after each PAED was sampled. Large fishes that were easily identifiable were measured (TL) to the nearest millimeter and released. All small-bodied fishes were preserved in 10% formalin and transported to the lab. Fixed specimens were repeatedly rinsed with tap water in the lab, identified using Pflieger (1997), total length (TL) measured to the nearest millimeter, and specimens then transferred to 80% ethanol and stored until completion of the study. Early life stage

fishes that had not fully developed adult identification characteristics were identified using a key developed by K. Reeves (see Reeves 2006).

Habitat data collection

Environmental Factors

Environmental factors were measured at each sample unit in a region after all units of the region were sampled for fishes. Factors hypothesized to be important to the distribution of riverine fishes that were measured included sandbar shoreline slope (Copp and Jurajda 1993), sandbar shoreline sinuosity (Hirzinger et al. 2004), turbidity (Rodríguez and Lewis 1997; Bonner and Wilde 2002; Quist et al. 2004), depth (Childs et al. 1998), velocity (Pavlov 1994), temperature (Keckeis et al. 2001), and substrate particle size composition (Copp 1992; Jurajda 1999). Slope and shoreline sinuosity are relevant at the sandbar or region scales. Turbidity, velocity, temperature, and substrate composition were discrete point measures collected at the sample unit scale; these and depth (not a discrete sample unit measure) were then averaged up to region and sandbar scales to reflect mean conditions at these levels.

Region scale

Sandbar slope of the submerged portion of sandbar ATTZ is directly related to area of shallow-water habitat. Since this study focuses on small-bodied fish use of shallow-water habitat it was important to quantify this environmental factor. Slope was quantified by measuring distance between sandbar shoreline and sample units with a laser rangefinder (accuracy \pm 1.0-m) and later divided into mean sample unit depth (see below)

for each unit and the shoreline; sample unit slopes were then averaged to reflect region and sandbar scales.

As with slope, shoreline sinuosity was measured to reflect shallow-water habitat at sandbar ATTZ. Highly sinuous shorelines indicate that numerous pockets of SSVH extend inland towards the sandbar where back-flow eddies or no-flow areas may be important to fishes. Shoreline sinuosity was quantified as the ratio of (1) length of the shoreline between transects that composed a region measured with a walking wheel to follow the contour of the water-sandbar interface, and (2) the straight-line distance between the same two points measured with the laser rangefinder. Shoreline sinuosity was collected primarily at upstream primary, upstream secondary, downstream primary, and downstream secondary regions, but not head or tail regions. The straight-line distance between transects of head and tail regions crossed the sandbar from primary to secondary channel side and would have given misleadingly high sinuosity values not comparable to other regions. Equations for slope and shoreline sinuosity are detailed under *Data processing* below.

Sample unit scale

Parameters recorded at each PAED included turbidity, sample unit mean depth, current velocity, temperature, conductivity, and substrate composition. Turbidity (NTU) was collected prior to any other measurements by standing downstream and to the side of the PAED (or on the sandbar shoreline if possible) to avoid biasing the sample by disturbing sediments. A water sample was taken from the center of the PAED at approximately half the water's depth and turbidity measured in the field using a Hach

model 2100P trubidimeter. Sample unit mean depth (hereafter depth) was measured to the nearest 0.1 m at each of the PAED corners with a standard metric top set wading rod and later averaged to one value representing mean depth for the sample-unit area. Near bed (NBV) and mean column (MCV) current velocities (m/s) were measured at the center of the PAED using a Marsh McBirney Model 2000 electromagnetic flow meter on the wading rod. Near bed velocity was measured approximately 25-mm above the substrate as the distance from the foot of the wading rod to the midpoint of meter probe when set at the lowest possible position on the wading rod. Mean column velocity was measured at 60% the depth below the water surface (McMahon et al. 1996). Water temperature (C^{o}) and conductivity (μ S/cm) were measured at the center of the sample unit area with a YSI Model 30 SCT meter. All meters were calibrated before field collections began and were maintained throughout the sampling season to meet manufacturer recommendations.

Substrate type and composition was visually estimated and categorized according to the modified Wentworth scale (McMahon et al. 1996) simplified into four particle size classes: (1) clay and silt = < 0.0625 mm diameter (silt hereafter), (2) sand = 0.0625-2.0 mm diameter, (3) gravel = 2.0-64.0 mm diameter, (4) cobble and boulder = > 64.0 mm diameter (hereafter cobble). A substrate sample was collected and classified from the center of each PAED at the same point velocity was measured by grasping a handful of sediments and visually estimating relative proportions of each size class present (e.g., % silt + % sand + % gravel + % cobble = 100). Substrate samples were later converted to the geometric mean of substrate size (G_s), hereafter *substrate particle size index*. This index is detailed under "Data processing" below, and Table 1C in Appendix C can be used to convert G_s to particle size classes on the modified Wentworth scale.

A set of reference substrate size-class vials was prepared by sieving substrate samples into each of the four particle-size classes to promote consistency in visual estimates. These standards were then used as the standard to train field technicians before the sampling season and as a field reference guide throughout the season. One technician was designated for substrate classification duties and I periodically (approximately 2-4 times per day) classified substrate from a PAED as a verification check to see how closely our estimates agreed. Samples were also periodically (approximately monthly) sieved in the field to visually show relative proportions of each particle size class for estimate calibration and retraining if necessary.

Data processing

I developed a relational database (Microsoft Access XP) to store and query all collected data (these data and metadata can be obtained by contacting the author or his advisor). Catch-per-unit-effort (CPUE) was used to standardize catch data and report relative abundance among sample units. Area sampled was constant (3.75 m²), however depth varied among sample units and catch data needed to be standardized to directly compare abundance among sample units of different volume. Volumetric CPUE was calculated to depict density of fishes that could be distributed throughout water columns of varying depths. Volumetric CPUE for each PAED was calculated as:

CPUE (N/m³) =
$$\frac{N}{A \times D_M}$$
,

where N was the number of individuals, A was sample unit area (3.75 m²), and D_M was sample unit mean depth (m). All sample units that composed a region were averaged to

obtain a region scale CPUE for among region comparisons; all regions that composed a sandbar were averaged to obtain a sandbar scale CPUE for comparisons between point and wing-dike bars; point and wing-dike sandbar CPUEs were averaged to obtain overall sandbar CPUE. Temporal comparisons of CPUE were made by averaging by month or diel period for each spatial scale. The same averaging method was used to obtain means for fish body length, slope, shoreline sinuosity, and substrate particle size index at appropriate spatial scales; and these parameters by month and diel period at appropriate spatial scales.

Slope ($S_{\%}$) was calculated between each sample unit and the sandbar-water interface as:

$$S_{\%} = (D_{M}/D_{S})*100$$
,

where D_M was mean sample unit depth (m) and D_S was distance from sample unit to sandbar-water interface (depth = 0.0 m). Shoreline sinuosity (S_S) was calculated along the sandbar-water interface between the two transects that composed a region as:

$$S_s = (1-(T_I/S_L))*100$$
,

where T_L was the straight-line distance between transects at the sandbar-water interface, and S_L was length of the sandbar-water interface shoreline. This index ranged from zero (straight shoreline) to approaching, but never reaching, 100 as the most sinuous shoreline. Sample unit mean depth, here after 'depth', (D_M) was calculated as:

$$D_M = (D_1 + D_2 + D_3 + D_4)/4$$
,

where D_i was the water depth (m) measured at each corner of the sample unit. Substrate particle size index (G_s) was calculated from visual estimates of relative proportions of four size classes present in substrate samples as:

$$G_s = (D_1^{w_1}) (D_2^{w_2}) \dots (D_i^{w_i}),$$

where D_i was the mean diameter of size range i, and w_i was the proportion of size range i in the sample (Sappington et al. 1998); D_i for each size range was taken from Galat et al. (2001) since our studies were both in Missouri River.

To address my second objective fishes were grouped into 5-mm length classes based on body length (TL) to reduce the dataset and simplify interpretation of results.

Length classes were labeled with respect to the low value from each length class range so that fishes with body length in the range of 5 to 9 mm were labeled as length class '5', 10 14 mm were labeled as length class '10', and so on.

Analyses

ANOVA

To test if fish abundance, body length, and environmental factors varied relative to the spatial and temporal scales studied, collections were classified into four monthly categories (July, August, September, October) for samples collected under monthly temporal design, and two diel periods (light, dark) for samples collected under the diel sample design. Data collected under the monthly sample design were analyzed using *Proc Mixed* in SAS (2004) as a split-split-split plot analysis of variance (ANOVA) with alpha probability set to 0.05 to test for differences in means of fish CPUE, fish body length, water temperature, velocity, slope, shoreline sinuosity, turbidity, and substrate particle size index. The main-plot contained the effect of sandbar type. The sub-plot contained the effects of region and the interaction sandbar type*region. The sub-sub-plot contained the effects of sample unit and interactions with sandbar type and region. The

sub-sub-plot contained the effects of month and interactions with sandbar type, region, and sample unit.

Data collected under the diel sample design were analyzed using *Proc Mixed* in SAS (2004) as a split-split plot ANOVA with alpha probability set to 0.05 to test for differences in fish CPUE, fish body length, water temperature, and velocity between light and dark diel periods. The main-plot contained the effect of region. The sub-plot contained the effects of sample unit and the interaction region*sample unit. The sub-sub-plot contained the effects of diel period and interactions with region and sample unit. Variance was pooled within effects for both ANOVA designs since field data often contain unequal *n* among effects (Steel et al. 1996). See Appendix B for SAS codes used.

Fisher's least significant difference (LSD) was used in both ANOVA designs to test mean differences using the appropriate error term as discussed by Steel et al. (1996) with significance set at alpha probability 0.05. An average LSD value was calculated to provide the reader an ability to compare means of CPUE and body length within or among effects. It was necessary to calculate the average LSD because there was unequal *n* among effects (Steel et al. 1996). For example, more near-shore samples were collected than offshore because some regions had steeper slope and only one (i.e., near-shore) PAED was required to sample the 0.0-0.5-m depth range. The average LSD is based on the mean standard error within effects. If the difference between two means is greater than the average LSD value reported Tables, they are significant at alpha 0.05. However, statistics reported in Results text below are based on standard errors from specific (i.e., not mean) LSD comparisons.

Depth-velocity use profiles for species were developed by averaging body length among individuals and calculating standard errors for each of the five species monitored by USFWS and five other species that are important recreationally or as forage fishes and/or were abundant in samples (i.e., red shiner, river carpsucker, gizzard shad, channel catfish, freshwater drum) to display graphically. Means and standard errors were calculated for depth and water velocity measured from sample units to develop a depth-velocity-body length use profile for each species. In addition to the 10 species highlighted graphically, I developed a table listing depth-velocity use profiles for all species collected in $\geq 1\%$ of samples.

Length-at-age data were collected and summarized to estimate age of fishes collected in this study. Data were collected from reports for as many of the species collected in this study as possible. However, only data developed for species where specimens were collected from Missouri River were used.

Turbidity, depth, velocity, and slope were square-root transformed to better meet assumptions of normality for analyses. These factors were transformed before being entered into analyses, and resulted in more normal distributions for each factor. Results of tests were reported below with transformed data as mean \pm SE in regular font and back-transformed data as mean in *italic* font.

It was important to keep fishes collected under the diel sample design segregated from fishes collected under the monthly sample design while testing for differences in abundance and body size at the two temporal scales because sampling effort was not equal between the two designs. For example, including all fishes collected under the monthly design into the light diel period of a "light vs. dark" test of CPUE would bias the

test towards the light diel pattern. Therefore, only fishes collected during diel specific sampling trips were used to test for differences between light and dark periods. Likewise, fishes collected during dark periods were excluded from tests of abundance or body size among months.

If results of tests for the effect of diel period on abundance and body length were significant, I partitioned small-bodied fishes' total lengths into 5, 25, 75, and 95 percentiles according to diel period to determine how the distribution of small-bodied fish total length changed and at whichever spatial level (i.e., sandbar, region, sample unit scales) means differed. This allowed me to determine if a change (if present) in fish mean length between the light and dark period was due to an increase or decrease in abundance of smaller or larger size fishes at that spatial level.

DCA

Detrended correspondence analysis (DCA; ter Braak and Šmilauer 2002) was used to address my objective of determining if the small-bodied fish assemblage in sandbar ATTZ was composed of taxonomically related species, of fishes in the same habitat use guild, and/or by fishes of similar body size. For clarity, species, habitat use guilds, and length classes represent groups; units compose each group. For example, species units S_1 , S_2 ,..., S_i compose the species group (where i is the total number of species); guild units G_1 , G_2 , G_3 compose the habitat use guild group; and lengths class units L_5 , L_{10} ,..., L_i compose the length class group (where i is the maximum length class included).

Detrended correspondence analysis is an indirect gradient analysis that reflects how units within groups relate to each other within ordination (i.e., theoretical) space. The results plotted in ordination space provide a visualization to illustrate how the fish assemblage is structured because units in close proximity to each other tend to be from the same samples; that is they tend to occur together in sample space. Detrended correspondence analysis provides an estimate of the total amount of variance (hereafter total inertia, λ) in a fish assemblage dataset. Low total inertial indicates that units were consistently aligned along relatively few ordination gradients, and that points within units have short distances among them. For example, low total inertia indicates that L_{5-a} was consistently associated with L_{5-b} , but not L_{80-a} , where L_i represents length class units, and -a and -b represent points within units. High total inertia indicates that points within units were more randomly distributed in ordination space and that they were aligned along more ordination gradients (e.g., L_{5-a} marginally associated with L_{5-b} and L_{80-a}). Total inertia was compared among the three datasets to determine which provided the simplest (i.e., lowest total inertia) explanation for how the assemblage was structured.

Detrended correspondence analysis scores for the first three ordination axes from the group that best explained assemblage structure were imported to ArcGIS 9.1 (2005) for spatial statistics analyses to quantify the distribution of units in ordination space. Quantifying the distribution of units provided an objective way to determine which units were associated with each other. Units that were close together in ordination space were interpreted to co-occur more frequently than units spaced further apart (ter Braak and Šmilauer 2002). Spatial cluster analyses were run to quantify the distribution of units. First, mean nearest neighbor distance (MMN) and Moran's *I* for spatial autocorrelation

were measured among units to determine if a pattern consistent with clustering existed within the distribution. If clustering was detected, Getis-Ord general *G* test was used, and standard distance among units was measured, to estimate how units were clustered in DCA ordination space to address the question of which units more frequently co-occurred than others. Additional methods required to determine where among units clustering occurred depending upon results, are explained in Results under *Small-bodied fish* assemblage structure.

Dataset selection for analyses

Given the high frequency, fine resolution sampling approach of PAEDs, I considered the number of times a species or length class was collected to be more telling of its membership to the sandbar ATTZ fish assemblage than the number of individuals collected. Therefore, the complete fish dataset was partitioned for inclusion in analyses as follows: (1) species (first objective) or length classes (second objective) that occurred in at least 1% of all samples collected and (2) individuals that were "small-bodied". I decided on the 1% criteria based on the total number of samples collected (see Results) because it included a sufficient number of individuals per species for statistical analyses while omitting only the rarest species.

Length (mm TL) parameters to empirically define "small-bodied" in this study were obtained with length-frequency analysis. Frequencies of individuals within 5-mm length classes (total length) were counted and are presented in results. Some carpsuckers (*Carpiodes* spp.) were classified as "unidentified carpsucker" (UCS) because they were either too small (approximately 12 mm TL) or too damaged during collection to be

positively identified to species. UCS could be one of three *Carpiodes*: (1) river carpsucker (*C. carpio*), (2) quillback (*C. cyprinus*), or (3) highfin carpsucker (*C. velifer*). Therefore, USC were excluded from DCA analysis because they represent a confounding problem for understanding true differences in ordination space among known *Carpiodes* spp. from the species group. These were likewise excluded from the macrohabitat use guild and length class groups so that analyses were run with the same number of individuals and results of total inertia were comparable among groups.

Each individual fish used DCA was a species, was in length class, and belonged to a macrohabitat use guild; these were its attributes. All three datasets are from the same samples, but simply organized by their specific attribute. Therefore, data points used in spatial cluster analyses were identical among all three groups. Analysis of datasets differed by testing only one attribute at a time. If the species group best explained assemblage structure, its DCA scores would be spatially analyzed by testing among all unique species while ignoring the length class and habitat use guild attributes. Likewise, length class DCA scores would be analyzed by testing among all unique length classes while ignoring the species and macrohabitat use guild attributes. Finally, macrohabitat use guild DCA scores would be analyzed by testing among the three unique guilds while ignoring the species and length class attributes.

Results

Distribution, abundance, and environment

I collected 24,500 individuals using PAEDs from 49 species and 13 families in 968 samples at sandbar ATTZ between July and October 2005. Species were distributed

among all three macrohabitat use guilds with 11 fluvial specialists, 12 fluvial dependent and 25 macrohabitat generalist species (Table 2.1). Orangethroat darter (*Etheostoma spectabile*, *n*=1) was not classified into a macrohabitat use guild by Galat et al. (2005) as they considered it a tributary species. Seven species (14% of total richness) are state or federally listed as imperiled and five species are introduced. River carpsucker (*Carpiodes carpio*) was the species most abundant in collections, followed by red shiner, channel catfish, and emerald shiner (*Notropis atherinoides*). However, red shiner was the most frequently collected species (i.e., occurred in most number of sample units), followed by channel catfish, emerald shiner, and river carpsucker (Table 2.1).

Length-frequency distributions of all fishes collected show that 74.5 % (18,260 individuals) were <35mm TL, 91.2% (22,355 individuals) were <60-mm TL, and only 0.03% (7 individuals) were longer than 500-mm TL. Fishes ≤105-mm TL composed 99.4% of all fishes collected (Figure 2.5). Therefore, I selected ≤105-mm TL as the maximum body length for inclusion in all subsequent analyses. Hereafter, 'small-bodied' fish refers to a specimen ≤105 mm TL. This 105-mm maximum length criterion included in analyses age-0 (e.g., juvenile) and older (e.g., adult) specimens of small genera such as *Macrhybopsis*, *Hybognathus*, *Notropis*, and *Cyprinella*, and small-size (including age-0) specimens of "large-bodied" genera such as *Carpiodes*, *Dorosoma*, *Ictalurus*, and *Aplodinotus*. Fishes ≤105-mm TL numbered 24,348 individuals (including UCS; 21,142 excluding UCS), and there were 25 species (excluding UCS) that occurred in ≥9 sample units. These two criteria together further reduced the dataset to 22,522 individuals used to test for differences in abundance and body length of small-bodied fishes.

Table 2.1. Fish species collected at sandbar ATTZ with family and species name, common name, four letter species code, number (#) of individuals in all samples and number of samples species present in, collected on lower Missouri River (LMOR). Heritage status to LMOR and membership to a habitat use guild defined by Galat et al. (2005).

Family & species name	Common name	Code	# of fish	# of samples	Heritage status	Habitat use guild
Acipenseridae	Common name	Code	11511	samples	Status	use guna
Scaphirhynchus platorynchus	shovelnose sturgeon	SNSG	3	2	Native	Fluvial Specialist
Lepisosteidae						
Lepisosteus osseus	longnose gar	LNGR	6	6	Native	Fluvial Dependent
Lepisosteus platostomus	shortnose gar	SNGR	4	4	Native	Macrohabitat Generalist
Hiodontidae						
Hiodon alosoides	goldeye	GDEY	11	9	Native	Fluvial Dependent
Clupeidae						
Alosa chrysochloris	skipjack herring	SJHR	2	2	Native	Fluvial Dependent
Dorosoma cepedianum	gizzard shad	GZSD	1055	187	Native	Macrohabitat Generalist
Cyprinidae						
Macrhybopsis meeki	sicklefin chub	SFCB	20	14	Native	Fluvial Specialist
Macrhybopsis gelida	sturgeon chub	SGCB	25	17	Native	Fluvial Specialist
Macrhybopsis aestivalis	speckled chub	SKCB	671	197	Native	Fluvial Specialist
Macrhybopsis storeriana	silver chub	SVCB	115	72	Native	Macrohabitat Generalist
Platygobio gracilis	flathead chub	FHCB	1	1	Native	Fluvial Specialist

Table 2.1. Continued.

Family & species name	Common name	Code	# of fish	# of samples	Heritage status	Habitat use guild
Phenacobius mirabilis	suckermouth minnow	SMMW	5	4	Native	Fluvial Specialist
Hybognathus placitus	plains minnow	PNMW	154	39	Native	Fluvial Dependent
Hybognathus argyritis	western silvery minnow	WSMW	2	1	Native	Fluvial Dependent
Hybognathus hankinsoni	brassy minnow	BSMW	1	1	Uncertian	Macrohabitat Generalist
Pimephales notatus	bluntnose minnow	BNMW	30	21	Native	Macrohabitat Generalist
Pimephales vigilax	bullhead minnow	BHMW	232	115	Native	Macrohabitat Generalist
Pimephales promelas	fathead minnow	FHMW	3	3	Native	Macrohabitat Generalist
Notropis dorsalis	bigmouth shiner	BMSN	21	15	Native	Fluvial Specialist
Notropis stramineus	sand shiner	SNSN	130	61	Native	Fluvial Specialist
Notropis blennius	river shiner	RVSN	212	86	Native	Fluvial Specialist
Cyprinella lutrensis	red shiner	RDSN	4033	435	Native	Macrohabitat Generalist
Notropis atherinoides	emerald shiner	ERSN	1525	357	Native	Macrohabitat Generalist
Luxilus cornutus	common shiner	CMSN	3	1	Native	Not Classified
Cyprinus carpio	common carp	CARP	4	4	Introduced	Macrohabitat Generalist
Hypophthalmicthys nobilis	bighead carp	ВНСР	1	1	Introduced	Fluvial Dependent
Catostomidae						
Carpiodes cyprinus	quillback	QLBK	125	30	Native	Macrohabitat Generalist
Carpiodes velifer	highfin carpsucker	HFCS	57	8	Native	Fluvial Specialist

Table 2.1. Continued.

Family & species name	Common name	Code	# of fish	# of samples	Heritage status	Habitat use guild
Carpiodes carpio	river carpsucker	RVCS	9583	252	Native	Macrohabitat Generalist
Carpiodes spp.	carpsucker	UCS	3358	23	Native	Macrohabitat Generalist
Catostomus spp.	sucker	UCT	12	2	Native	Fluvial Dependent
Ictiobus cyprinellus	bigmouth buffalo	BMBF	11	9	Native	Macrohabitat Generalist
Ictiobus bubalus	smallmouth buffalo	SMBF	1	1	Native	Macrohabitat Generalist
Ictiobus niger	black buffalo	BKBF	1	1	Native	Macrohabitat Generalist
Moxostoma spp.	redhorse	RDHS	2	2	Native	Not Classified
Ictaluridae						
Ictalurus punctatus	channel catfish	CNCF	2325	376	Native	Macrohabitat Generalist
Ictalurus furcatus	blue catfish	BLCF	18	12	Native	Fluvial Specialist
Pylodictis olivaris	flathead catfish	FHCF	2	2	Native	Fluvial Dependent
Poecilliidae						
Gambusia affinis	western mosquitofish	MQTF	231	64	Introduced	Macrohabitat Generalist
Atherinidae Labidesthes sicculus	brook silverside	BKSS	3	3	Native	Macrohabitat Generalist
Moronidae						
Morone saxatilis	striped bass	SDBS	12	10	Introduced	Fluvial Dependent
Morone chrysops	white bass	WTBS	2	2	Native	Fluvial Dependent
Morone americana	white perch	WTPH	12	11	Introduced	Fluvial Dependent

Table 2.1. Continued.

F1 0			и с	ш с	TT 1:	TT 1 %
Family &	~	~ .	# of	# of	Heritage	Habitat
species name	Common name	Code	fish	samples	status	use guild
Centrarchidae						
Lepomis cyanellus	green sunfish	GNSF	20	17	Native	Macrohabitat
Lepomis cyaneius	green sumsn	ONSI	20	17	rative	Generalist
Lepomis	hhaaill	BLGL	78	47	Native	Macrohabitat
macrochirus	bluegill	BLUL	70	4/	Nauve	Generalist
T : 1:1:-	orangespotted	OCCE	6	5	Matina	Macrohabitat
Lepomis humilis	sunfish	OSSF	6	3	Native	Generalist
Micropterus	1	LMDC	0	0	NT - 4th	Macrohabitat
salmoides	largemouth bass	LMBS	8	8	Native	Generalist
D	1.5	WECD	4	2	NT	Macrohabitat
Pomoxis annularis	white crappie	WTCP	4	3	Native	Generalist
Percidae						
Etheostoma	orangethroat	0.555			Not	Not
spectabile	darter	OTDR	1	1	Classified	Classified
Sciaenidae						
	freshwater					Macrohabitat
Aplodinotus		FWDM	359	177	Native	
grunniens	drum			,		Generalist

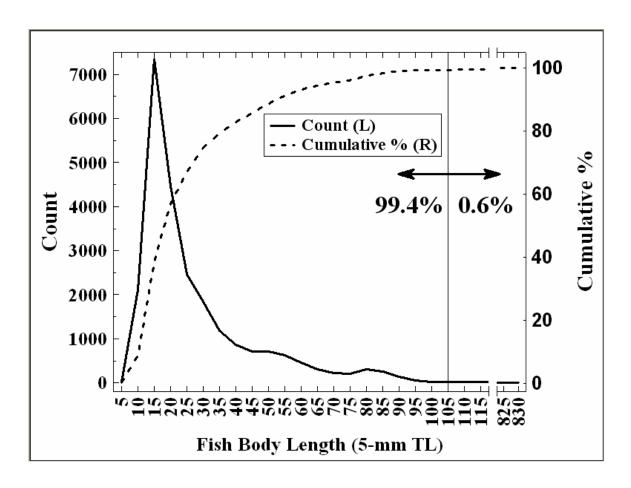


Figure 2.5. Length frequency distribution for all fishes collected from all sample units at sandbar ATTZ in lower Missouri River. Frequencies of individuals were counted within 5-mm length classes labeled by the smallest value within each class (e.g., 5 to 9-mm is '5'). Fish lengths ranged from 8 to 830-mm total length (TL). Fishes shorter than or equal to 105-mm TL (solid vertical line) composed 99.4% of all fishes collected and were included in further analyses.

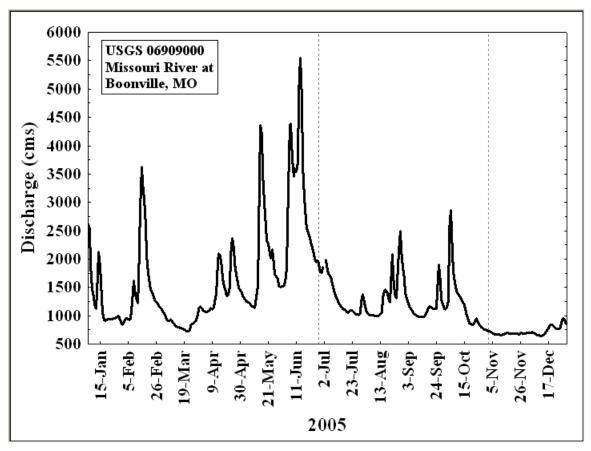


Figure 2.6 Annual hydrograph showing mean daily discharge (m3/s) on lower Missouri River (LMOR) measured at Boonville, MO (rkm 316) near midpoint of the study reach. Area inside vertical dotted lines represents the period fish were collected in shallow waters adjacent to LMOR sandbars. Data are from USGS-NWIS web interface available online at http://waterdata.usgs.gov/nwis.

River discharge at Boonville, Missouri, (rkm 316), near the midpoint of the study reach, ranged from 733 to 2860 m³/s, and exceeded 2,500 m³/s twice during the study period (Figure 2.6). Submerged sandbars or tertiary channels were rarely encountered. Submerged sandbars were sampled on three occasions (Fish Creek sandbar, rkm 356, 11 July 2005 and 27 September 2005; Hartsburg sandbar, rkm 258, 16 August 2005) and yielded 441 individuals from 13 species in 41 samples. One wing-dike sandbar on one occasion (Perche B sandbar, rkm 277, 11 October 2005) and no point bars that had a

tertiary channel crossing the bar. The wing-dike bar's tertiary channel yielded 65 individuals from 7 species in 3 samples. Submerged bar or tertiary channel samples were not included in ANOVA because numbers of observations for each were low relative to emergent sandbar samples. However, all except four of these fishes were ≤105-mm TL and were included in DCA to examine assemblage structure.

Abundance and body length in space and time

Small-bodied fishes CPUE and body length differed by region, sample unit, and month (Table 2.2). Abundance was higher in August than September or October and size increased from July to October across the three spatial scales (Table 2.3). Fishes tended to be smaller and more abundant during July and August, then less abundant but larger during September and October (Figure 2.7). No difference existed in abundance (F = 1.6, P = 0.26) or body size (F = 3.1, P = 0.13) of small-bodied fishes between point and wingdike sandbars. There was no consistent pattern between abundance and body length by region (Figure 2.8); except that fish mean length was shorter at upstream secondary regions than other regions during July, August, and October (Table 2.3). Near-shore sample units had higher abundance and were composed of shorter fishes than moderate or offshore samples over the study period (Table 2.3). Mean abundance in the near-shore zone was more than 5 times higher in July and August than in September and October and more than 24 times higher than the offshore zone in July and August. Fish were larger in offshore than in near-shore samples units during all months (|t| = 12.2, P < 0.01; Figure 2.9).

Table 2.2. Spit-split-split plot ANOVA table for fish catch-per-unit-effort (CPUE #/m³), fish body length (mm TL), and environmental factors for spatial and temporal scales and their interactions. Shoreline sinuosity has fewer degrees of freedom for effects involving region because head and tail regions were not tested. Effect codes: SB=sandbar, RG=region, SC=sample unit category, MN=month.

		C	PUE	Bod	y length	ı D	epth	Ve	elocity	Temp	erature	Tu	rbidity	Sub	strate	Sl	ope	Shor	eline
		(m^3)	(m	mTL)	((m)	(m/s)	((C^{0})	(\)	NTU)	((G_s)	(%)	sinuc	osity
Effect	df	\overline{F}	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	df F	P
SB	1	1.6	0.26	3.1	0.13	2.0	0.21	4.1	0.09	0.1	0.81	0.1	0.83	0.4	0.53	6.8	0.04	1 7.2	0.04
RG	5	0.2	0.97	5.0	< 0.01	1.8	0.15	21	< 0.01	1.3	0.29	1.8	0.14	1.8	0.15	1.1	0.39	3 0.5	0.70
SB*RG	5	0.4	0.86	2.3	0.07	2.0	0.10	1.5	0.22	2.0	0.11	2.6	0.04	0.4	0.87	2.3	0.07	3 0.8	0.49
SC	2	9.4	< 0.01	80	< 0.01	614	< 0.01	76	< 0.01	16.4	< 0.01	0.5	0.62	0.3	0.72	N	//A	Ν	V/A
SB*SC	2	2.5	0.09	3.0	0.06	3.4	0.04	4.4	0.02	2.7	0.08	0.9	0.43	0.2	0.81	N	//A	Λ	V/A
RG*SC	10	0.2	0.99	0.8	0.62	1.1	0.35	2.0	0.04	0.8	0.63	0.5	0.88	0.4	0.93	N	//A	Λ	V/A
SB*RG*SC	10	0.4	0.92	0.6	0.81	2.2	0.03	0.8	0.64	0.4	0.93	0.2	1.00	0.2	0.99	N	//A	Λ	V/A
MN	3	2.6	0.05	29	< 0.01	2.3	0.07	8.1	< 0.01	1702	< 0.01	74	< 0.01	1.9	0.13	1.3	0.26	3 11	<0.01
MN*SB	3	1.5	0.22	2.3	0.07	6.2	< 0.01	3.4	0.02	10.9	< 0.01	91	< 0.01	0.3	0.80	6.5	< 0.01	3 12	<0.01
MN*RG	15	0.7	0.80	1.8	0.03	0.6	0.90	2.4	< 0.01	2.9	< 0.01	1.6	0.08	1.3	0.20	1.2	0.26	9 13	<0.01
MN*SB*RG	15	1.2	0.31	0.9	0.52	1.4	0.13	1.0	0.48	2.1	< 0.01	1.7	0.04	1.6	0.08	1.1	0.34	9 8.4	<0.01
MN*SC	6	2.8	0.01	3.5	< 0.01	1.9	0.08	0.3	0.94	1.1	0.39	0.7	0.65	0.4	0.88	N	//A	Λ	V/A
MN*SB*SC	6	1.6	0.15	0.6	0.70	2.1	0.05	0.6	0.70	1.1	0.38	1.4	0.21	0.7	0.69	N	//A	Λ	V/A
MN*RG*SC	30	0.7	0.85	0.8	0.84	0.6	0.96	0.8	0.79	0.3	1.00	0.5	0.99	0.5	0.99	N	//A	Ν	V/A
MN*SB*RG*SC	30	1.2	0.23	1.0	0.41	0.6	0.97	0.4	1.00	0.4	1.00	0.4	1.00	0.5	0.99	N	//A	Λ	V/A

Table 2.3. Means of catch-per-unit-effort (CPUE #/m³) and body length (mm TL) \pm standard error (pooled variance) of fishes (\geq 9 sample units, \leq 105-mm TL) pooled across all spatial scales and months, and by sandbar, region, and sample unit category among months. Fisher's least significant difference (*LSD*) is listed under each spatial scale to determine significance between means^{1, 2}. Codes for sandbar and region: PB = point sandbar, WD = wing-dike sandbar, HR = head region, UP = upstream primary region, US = upstream secondary region, DP = downstream primary region, DS = downstream secondary region, TR = tail region.

	All m	onths	J	ul	A	ug	S	ep	O	ct
		Body		Body		Body		Body		Body
Place	CPUE	length	CPUE	length	CPUE	length	CPUE	length	CPUE	length
All Places	48.6 ± 15.9	41.0 ± 1.1	73.4 ± 27.4	31.3 ± 1.9	83.0 ± 24.5	39.2 ± 1.5	18.0 ± 25.1	45.4 ± 1.5	19.8 ± 27.5	47.9 ± 1.7
LSD			61.8	3.4	61.8	3.4	61.8	3.4	61.8	3.4
Sandbar										
PB	70.5 ± 23.9	43.2 ± 1.7	136.7 ± 32.3	34.3 ± 2.3	98.8 ± 36.1	39.2 ± 2.2	31.1 ± 33.3	47.3 ± 2.1	15.5 ± 36.6	52.0 ± 2.3
WD	26.6 ± 25.9	38.7 ± 1.9	10.0 ± 44.3	28.3 ± 3.1	67.3 ± 33.1	39.1 ± 2.1	4.9 ± 37.6	43.5 ± 2.3	24.2 ± 41.0	43.8 ± 2.5
LSD	69.1	5.0	95.8	5.8	95.8	5.8	95.8	5.8	95.8	5.8
Region										
HR	64.0 ± 33.4	41.8 ± 2.2	111.4 ± 64.0	34.1 ± 4.7	86.3 ± 55.5	40.8 ± 3.0	29.5 ± 47.0	46.0 ± 2.7	28.9 ± 55.7	46.4 ± 3.4
UP	32.8 ± 33.5	44.1 ± 2.1	52.3 ± 54.6	38.6 ± 3.9	36.3 ± 57.6	41.9 ± 3.0	17.6 ± 52.9	46.9 ± 2.9	25.0 ± 52.4	49.1 ± 2.8
US	32.5 ± 38.4	32.0 ± 2.3	18.2 ± 80.5	16.3 ± 5.3	70.2 ± 63.4	30.3 ± 3.3	30.8 ± 56.5	44.0 ± 2.9	10.9 ± 70.6	37.3 ± 3.7
DP	51.1 ± 34.2	43.1 ± 2.1	154.0 ± 59.4	31.1 ± 4.2	18.2 ± 49.6	46.0 ± 2.7	26.9 ± 58.0	46.8 ± 3.0	5.2 ± 57.9	48.4 ± 3.1
DS	47.8 ± 34.8	42.2 ± 2.0	29.9 ± 52.6	36.1 ± 3.1	118.5 ± 49.0	37.6 ± 2.6	11.0 ± 58.9	41.6 ± 3.1	31.8 ± 70.1	53.7 ± 3.6
TR	63.2 ± 33.7	42.5 ± 2.0	74.4 ± 56.2	31.6 ± 3.2	169.0 ± 48.6	38.5 ± 2.6	7.6 ± 56.9	47.2 ± 3.1	17.2 ± 61.9	52.6 ± 3.2
LSD	90.7	5.1	156.8	8.7	156.8	8.7	156.8	8.7	156.8	8.7
Sample unit										
Near-shore	126.2 ± 23.9	28.9 ± 1.6	210.4 ± 40.4	23.2 ± 2.8	219.1 ± 35.3	28.0 ± 1.9	40.7 ± 36.5	31.0 ± 2.0	34.4 ± 39.8	33.5 ± 2.2
Moderate	14.9 ± 28.1	44.1 ± 1.7	7.1 ± 49.3	34.4 ± 3.1	21.0 ± 44.1	44.6 ± 2.4	12.8 ± 44.6	47.2 ± 2.4	18.6 ± 47.7	50.2 ± 2.7
Offshore	4.7 ± 25.4	49.8 ± 1.6	2.6 ± 43.2	36.3 ± 3.0	9.1 ± 37.6	44.9 ± 2.1	0.5 ± 38.2	58.1 ± 2.1	6.5 ± 45.6	60.0 ± 2.5
LSD	64.1	3.5	110.2	6.1	110.2	6.1	110.2	6.1	110.2	6.1

Differences in means within a column are significant $(P \le 0.05)$ if $\ge LSD$.

² Differences in means among or within individual months are significant (P < 0.05) if $\geq LSD$.

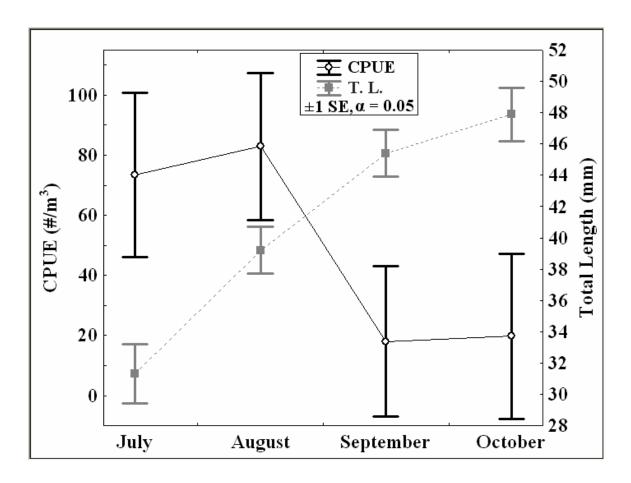


Figure 2.7. Relationship between catch-per-unit-effort (CPUE $\#/m^3$, dark bars) and mean body length (mm TL, light bars) of small-bodied fishes collected in sandbar ATTZ on lower Missouri River from July through October. Data are means \pm SE (pooled variance).

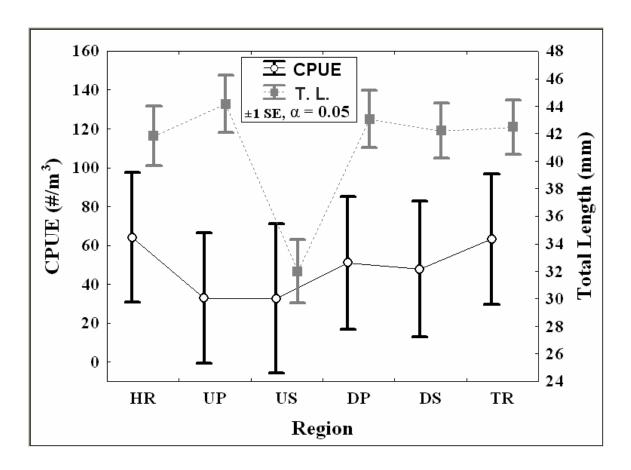


Figure 2.8. Catch-per-unit-effort (CPUE $\#/m^3$, dark bars) and body length (mm TL, light bars) of small-bodied fishes around sandbar ATTZ by region in lower Missouri River. Data are means \pm SE (pooled variance).

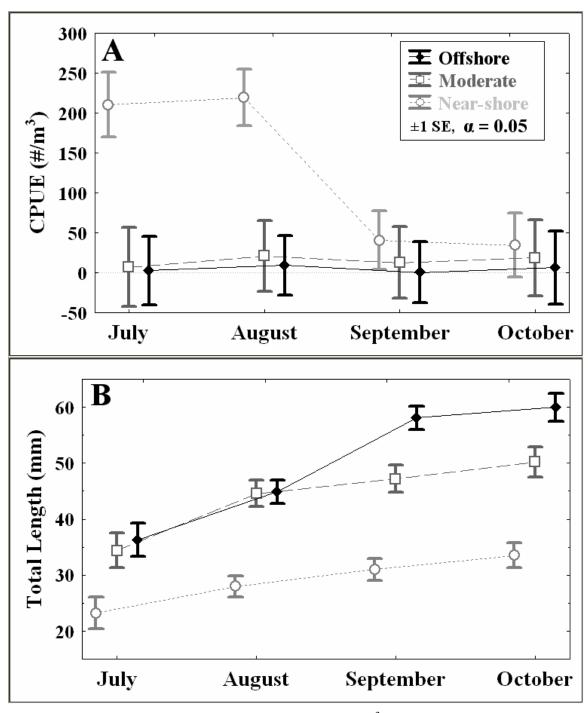


Figure 2.9. Plots of (A) catch-per-unit-effort (CPUE $\#/m^3$) and (B) body length of small-bodied fishes by sample unit category distance from shore among months. Data are means \pm SE (pooled variance).

There was no overall effect of diel period on CPUE (F = 0.80, P = 0.37) or body length (F = 0.04, P = 0.84) of fishes. However, there was significance for body length (F= 4.97, P = 0.01) in the interaction between diel period and sample unit category (Table 2.4). Mean abundance increased by 39%, and fish mean body length by 29%, in the nearshore zone from the light to dark period (Table 2.5). In contrast, fish mean body length decreased by 14% in the offshore zone from light to dark periods (Figure 2.10). Ninetypercent of fishes collected near-shore during the day were within the 14-26 mm TL range; this near-shore range widened to 14-49 mm TL during the night (Figure 2.11). Maximum length of fish in the P_{75} - P_{95} TL (mm) range increased near-shore and decreased offshore from day to night (Figure 2.11). Median fish size was 10-mm longer offshore at night than near-shore during the day; however, modal fish size did not change (Table 2.6). Mean abundance of fishes in length class 45 more than tripled in the nearshore zone at night, and length classes 60-70 mm TL were not collected from the nearshore zone during the day but averaged 7.5 fish/m³ near shore at night (Table 2.7). Table D2 in Appendix D lists abundance and body length by species between light and dark diel periods.

Abundance, body length, and habitat use of select species

River carpsucker mean CPUE was highest during July-August then decreased to less than 1.0 CPUE during September-October (Table 2.8). Red shiner mean CPUE was low during July-August then more than doubled during September-October. Mean CPUE of chubs (*Macrhybopsis spp.*) was <2.0 during all months; however, speckled chub (*M. aestivalis*) CPUE increased from <0.05 in July and August to 1.8 in September and

Table 2.4. Spit-split plot ANOVA table for fish catch-per-unit-effort (CPUE #/m³), fish body length, water depth, water velocity, and water temperature for effects diel period (DL), region (RG), sample unit category (SC), and their interactions.

			UE 1 ³)	-	length TL)		pth n)		ocity /s)	Tempe (C	_
Effect	df	\overline{F}	\overline{P}	\overline{F}	P	\overline{F}	P	\overline{F}	\overline{P}	\overline{F}	P
DL	1	0.80	0.37	0.04	0.84	0.96	0.33	0.24	0.63	14.44	<0.01
RG	1	8.37	0.01	2.03	0.16	0.43	0.51	85.7	0.01	0.67	0.42
SC	2	11.8	0.01	11.9	0.01	905	0.01	69.0	0.01	1.91	0.15
DL*RG	1	0.70	0.40	0.88	0.35	0.12	0.73	0.15	0.70	2.05	0.15
DL*SC	2	0.67	0.51	4.97	0.01	0.27	0.76	0.62	0.54	3.66	0.03
DL*RG*SC	2	0.64	0.53	0.07	0.93	0.29	0.75	0.33	0.72	0.06	0.94

Table 2.5. Means \pm standard error (SE, pooled variance) of fish (\geq 9 sample units, \leq 105-mm TL) catch-per-unit-effort (CPUE #/m³), fish body length (mm TL), water depth (m), water velocity (m/s), and water temperature (C°) between light and dark diel period among region and sample unit scale in water adjacent to Petite Saline sandbar in lower Missouri River. Factors were tested with split-split plot ANOVA and Fisher's least significant difference post hoc comparison ($P \leq 0.05$); water depth and water velocity were tested under square-root transformation, *italic* values below square root transformed mean \pm SE are back-transformed means. Asterisk indicates significance between means.

Factor	Light	Dark
Diel period		
CPUE	48.92 ± 22.40	79.83 ± 26.27
Body length	38.12 ± 1.55	38.60 ± 1.72
Depth (sqrt)	0.50 ± 0.01	0.50 ± 0.01
	0.25	0.25
Velocity (sqrt)	0.28 ± 0.01	0.27 ± 0.01
	0.08	0.08
Temperature	29.19 ± 0.16	$*$ 28.24 \pm 0.19
Region		
Upstream primary		
CPUE	13.40 ± 31.67	15.44 ± 36.61
Body length	38.69 ± 2.24	41.34 ± 2.45
Depth (sqrt)	0.51 ± 0.01	0.50 ± 0.01
	0.26	0.25
Velocity (sqrt)	0.36 ± 0.02	0.35 ± 0.02
	0.13	0.13
Temperature	29.11 ± 0.23	28.52 ± 0.27
Downstream secondary	y	
CPUE	84.43 ± 31.67	144.22 ± 37.69
Body length	37.56 ± 2.14	35.86 ± 2.42
Depth (sqrt)	0.50 ± 0.01	0.50 ± 0.01
	0.25	0.25
Velocity (sqrt)	0.21 ± 0.02	0.19 ± 0.02
	0.04	0.04
Temperature	29.27 ± 0.23	* 27.95 ± 0.27

Table 2.5. Continued.

Factor	Light		Dark
Sample unit			
Near-shore			
CPUE	139.45 ± 38.50		227.02 ± 46.16
Body length	26.10 ± 2.66	*	36.65 ± 2.98
Depth (sqrt)	0.31 ± 0.01		0.30 ± 0.01
	0.09		0.09
Velocity (sqrt)	0.16 ± 0.02		0.13 ± 0.02
	0.03		0.02
Temperature	30.00 ± 0.28	*	28.10 ± 0.34
Moderate			
CPUE	5.55 ± 38.50		8.91 ± 44.86
Body length	39.62 ± 2.65		37.19 ± 2.94
Depth (sqrt)	0.52 ± 0.01		0.51 ± 0.01
	0.27		0.26
Velocity (sqrt)	0.32 ± 0.02		0.31 ± 0.02
	0.10		0.10
Temperature	28.90 ± 0.28		28.32 ± 0.33
Offshore			
CPUE	1.75 ± 39.37		3.56 ± 45.48
Body length	48.64 ± 2.74		41.97 ± 3.04
Depth (sqrt)	0.68 ± 0.01		0.68 ± 0.01
	0.47		0.46
Velocity (sqrt)	0.37 ± 0.02		0.38 ± 0.02
	0.14		0.15
Temperature	28.66 ± 0.29		28.29 ± 0.33

Table 2.6. Descriptive statistics for the distribution of small-bodied fishes body lengths (mm TL) collected in near-shore, moderate, and offshore sample units between light and dark diel periods for fishes collected in ≥ 9 sample units and ≤ 105 -mm TL. Statistic 'n' is the number of fish collected ≤ 105 -mm TL, median, mode, and percentile (P_i) are relative to total length of fishes rounded to the nearest millimeter. Percentiles indicate the body length that i percent of fishes collected were shorter than.

	Near-	shore	Mo	derate	Of	fshore
Statistic	light	dark	light	dark	light	dark
n	1,966	1,886	269	290	115	200
Median	18	20	31	31	44	28
Mode	18	18	20	22	22	18
P_5	14	14	17	16	17	17
P_{25}	16	17	20	23	25	20
P 75	20	24	47	45	63	44
P 95	26	49	66	63	95	72

Table 2.7. Mean catch-per-unit-effort (CPUE $\#/m^3$) \pm standard error of small-bodied fishes (i.e., ≤ 105 mm TL) by length class that were collected in near-shore, moderate, and offshore samples in light and dark periods during diel sampling. Length classes are 5-mm and labeled by the shortest length within each class (e.g., '10' is 10-14 mm TL).

			Sample Unit C	Category	·	<u> </u>
Length	Near	-shore		erate	Offs	hore
class	Light	Dark	Light	Dark	Light	Dark
10	40.74 ± 14.19	177.77 ± 120.26	1.09 ± 0.17	1.43 ± 0.31		0.55 ± 0.06
15	150.37 ± 57.34	222.14 ± 163.72	4.89 ± 3.65	1.92 ± 0.35	1.40 ± 0.69	1.92 ± 0.65
20	58.17 ± 17.51	117.46 ± 50.76	3.87 ± 2.36	2.55 ± 0.56	0.92 ± 0.13	1.19 ± 0.19
25	10.50 ± 2.36	24.26 ± 10.38	1.90 ± 0.48	2.94 ± 0.81	0.64 ± 0.06	0.95 ± 0.14
30	7.15 ± 2.05	18.24 ± 8.05	2.04 ± 0.48	2.50 ± 0.70	0.57 ± 0.05	0.94 ± 0.32
35	3.62 ± 0.91	8.53 ± 2.50	1.70 ± 0.45	1.76 ± 0.23	0.56 ± 0.04	0.91 ± 0.23
40	3.98 ± 0.62	9.80 ± 2.51	1.90 ± 0.58	2.04 ± 0.43	0.66 ± 0.11	0.91 ± 0.13
45	3.04 ± 0.42	9.38 ± 2.59	1.47 ± 0.40	1.85 ± 0.46	0.53 ± 0.03	0.55 ± 0.04
50	2.13 ± 0.23	7.74 ± 2.08	1.73 ± 0.80	1.79 ± 0.28	0.64 ± 0.11	0.62 ± 0.07
55	2.43 ± 0.00	5.82 ± 1.15	1.28 ± 0.33	1.34 ± 0.18	0.55 ± 0.04	0.60 ± 0.04
60		6.94 ± 1.69	1.16 ± 0.18	0.94 ± 0.06	0.69 ± 0.10	0.73 ± 0.16
65		4.09 ± 1.00	1.00 ± 0.07	1.27 ± 0.23	0.58 ± 0.07	0.57 ± 0.03
70		11.53 ± 0.00	1.58 ± 0.70	0.83 ± 0.07	0.61 ± 0.05	0.61 ± 0.06
75			0.92 ± 0.05	0.89 ± 0.09	0.62 ± 0.06	0.60 ± 0.07
80				0.86 ± 0.12	1.81 ± 0.00	0.58 ± 0.06
85			0.99 ± 0.00		0.55 ± 0.06	
90					0.52 ± 0.00	0.62 ± 0.09
95			0.78 ± 0.00		1.00 ± 0.48	
100			0.81 ± 0.00		0.86 ± 0.31	

Table 2.8. Mean catch-per-unit-effort (CPUE $\#/m^3$) and body length (mm TL) \pm standard error (SE, pooled variance) of species (\geq 9 sample units, \leq 105-mm TL) collected in sandbar ATTZ on lower Missouri River by month. An asterisk preceding mean or SE value indicates the value is greater than 0.0 and less than 0.05.

	J	ul	A	ug	S	ер	C	Oct
Family &		Body		Body		Body		Body
species	CPUE	length	CPUE	length	CPUE	length	CPUE	length
Hiodontidae								
goldeye	*0.1 ± *0.1	48.3 ± 3.7						
Clupeidae								
gizzard shad	0.5 ± 0.1	57.3 ± 1.6	0.9 ± 0.3	64.4 ± 1.3	0.5 ± 0.2	82.7 ± 0.9	2.7 ± 0.8	85.7 ± 0.2
Cyprinidae								
sicklefin chub	*0.1 ± *0.1	28.4 ± 2.3	*0.1 ± *0.1	26.6 ± 3.0	*0.1 ± *0.1	17.3 ± 2.6	*0.1 ± *0.1	28.9 ± 7.7
sturgeon chub	*0.1 ± *0.1	18.0 ± 0.5	*0.1 ± *0.1	23.2 ± 0.0	*0.1 ± *0.1	21.1 ± 1.6	*0.1 ± *0.1	25.0 ± 1.4
speckled chub	*0.1 ± *0.1	22.1 ± 1.2	$0.1 \pm *0.1$	26.1 ± 1.5	0.8 ± 0.3	26.6 ± 0.6	1.8 ± 0.5	31.3 ± 0.5
silver chub	$0.1 \pm *0.1$	32.7 ± 1.1	*0.1 ± *0.1	43.0 ± 6.4	*0.1 ± *0.1	69.4 ± 3.0	*0.1 ± *0.1	81.1 ± 4.9
plains minnow	0.9 ± 0.7	25.5 ± 1.1	0.7 ± 0.5	38.5 ± 1.3	*0.1 ± *0.1	55.4 ± 2.3		
bluntnose minnow	*0.1 ± *0.1	28.9 ± 4.9	*0.1 ± *0.1	13.9 ± 0.0	*0.1 ± *0.1	36.3 ± 7.1	0.1 ± 0.1	18.6 ± 3.2
bullhead minnow	0.1 ± 0.1	22.7 ± 1.7	0.2 ± 0.1	25.7 ± 1.0	0.4 ± 0.1	30.8 ± 0.7	0.2 ± 0.1	36.7 ± 1.2
bigmouth shiner	*0.1 ± *0.1	31.0 ± 8.1	0.1 ± 0.1	36.8 ± 2.8	0.1 ± 0.1	36.4 ± 3.3	*0.1 ± *0.1	47.7 ± 0.0
sand shiner	0.3 ± 0.1	17.5 ± 0.5	0.4 ± 0.1	27.9 ± 1.5	0.1 ± *0.1	34.5 ± 2.8	$0.1 \pm *0.1$	38.9 ± 4.4
river shiner	0.1 ± 0.1	21.0 ± 1.7	1.3 ± 0.3	27.8 ± 0.6	0.4 ± 0.1	31.9 ± 1.6	0.3 ± 0.1	31.0 ± 1.9
red shiner	0.9 ± 0.3	33.4 ± 1.3	5.7 ± 1.8	22.6 ± 0.4	16.1 ± 2.5	29.0 ± 0.1	15.0 ± 2.8	32.0 ± 0.2
emerald shiner	2.8 ± 1.6	23.9 ± 0.9	1.5 ± 0.5	27.6 ± 1.1	2.9 ± 0.8	42.1 ± 0.6	2.4 ± 0.4	45.7 ± 0.7

Table 2.8. Continued.

	J	ul	A	ug	S	ep	C	Oct
Family &		Body		Body		Body		Body
species	CPUE	length	CPUE	length	CPUE	length	CPUE	length
Catostomidae								
quillback	0.7 ± 0.5	20.8 ± 0.7	0.3 ± 0.1	30.5 ± 1.9	*0.1 ± *0.1	38.0 ± 6.6		
river carpsucker	43.5 ± 12.3	18.8 ± 0.1	71.9 ± 30.6	21.1 ± 0.1	0.7 ± 0.2	45.4 ± 1.3	0.3 ± 0.1	64.9 ± 1.9
bigmouth buffalo	$0.1 \pm *0.1$	20.2 ± 2.5	*0.1 ± *0.1	15.1 ± 0.0				
Ictaluridae								
channel catfish	0.3 ± 0.1	46.2 ± 1.0	3.8 ± 0.7	54.7 ± 0.3	1.2 ± 0.2	60.6 ± 0.6	1.8 ± 0.4	67.6 ± 0.7
blue catfish			*0.1 *0.1	68.6 4.5				
Poecilliidae								
western mosquitofish	0.3 ± 0.1	29.4 ± 1.2	1.4 ± 0.4	22.9 ± 0.7	0.6 ± 0.3	22.2 ± 0.6	*0.1 ± *0.1	16.0 ± 0.0
Moronidae								
striped bass	*0.1 ± *0.1	55.0 ± 6.3	*0.1 ± *0.1	67.1 ± 7.4				
white perch	*0.1 ± *0.1	39.4 ± 2.5	*0.1 ± *0.1	49.7 ± 2.3				
Centrarchidae								
green sunfish	*0.1 ± *0.1	32.3 ± 4.6	$0.1 \pm *0.1$	38.6 ± 4.6	*0.1 ± *0.1	36.4 ± 0.0		
bluegill	*0.1 ± *0.1	22.6 ± 2.2	$0.2 \pm *0.1$	30.5 ± 2.2	$0.2 \pm *0.1$	27.4 ± 1.0	$0.1 \pm *0.1$	36.8 ± 4.0
Sciaenidae								
freshwater drum	$0.2 \pm *0.1$	39.1 ± 1.4	0.5 ± 0.1	59.5 ± 1.0	0.1 ± *0.1	81.0 ± 2.3	0.1 ± *0.1	91.0 ± 5.6

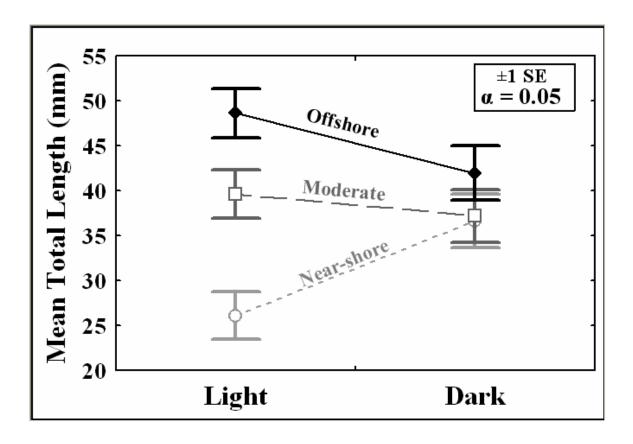


Figure 2.10. Plot of mean small-bodied fishes total length \pm standard error (pooled variance) collected in near-shore, moderate, and offshore sample units at sandbar ATTZ between light and dark diel periods on lower Missouri River. Data were analyzed as split-split plot ANOVA.

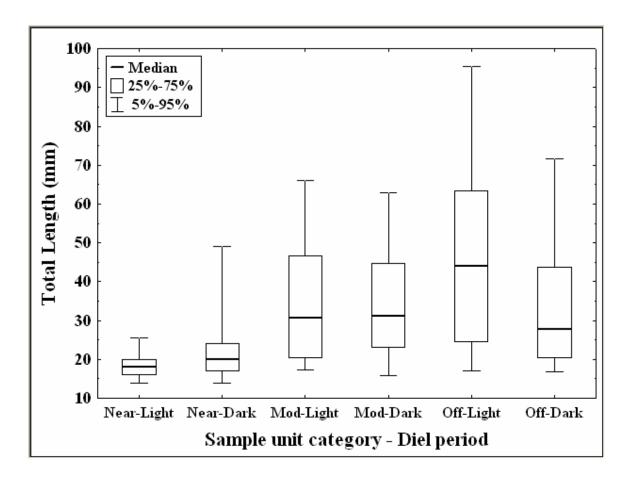


Figure 2.11. Box plots displaying the size distribution of small-bodied fishes to the nearest millimeter (TL) collected in near-shore, moderate, and offshore sample units between light and dark diel periods. Whiskers represent the middle 90%, rectangles the middle 50%, and horizontal line within rectangles the median of size fishes collected. See Table 2.6 for additional descriptive statistics related to this plot.

October. Plains minnow and sand shiner mean CPUE was highest during July and August, and then they were less abundant during September and October; plains minnows were not collected in October.

Length-at-age data developed from fishes collected in Missouri River was available for 14 of the species collected in this study (Peirce et al. 2003; Hesse 2004; Hay 2006). Lengths-at-age by species were variable among reports, age-0 ranged from 26 to 60 mm TL and age-1 from 32-170 mm TL (Table 2.9). Length-at-age-0 from more than one report was available for only five species: silver chub (*Macrhybopsis storeriana*), bigmouth shiner (*Notropis dorsalis*), sand shiner, river shiner (*N. blennius*), and red shiner. However, most data show that fishes ≤35 mm TL were shorter than length-at-age-1; except sand shiner from Pierce et al. (2003) and bigmouth shiner from Hesse (2004) (Table 2.9). I interpreted lengths shorter than those reported at age-1 to be age-0.

Individuals ≤105 mm TL for the six most abundant species collected were generally shorter than length-at-age-1 criteria (Table 2.9) and thus are mostly age-0. These included 99.8% of river carpsuckers, 86.5% of red shiners, 85.6% of channel catfish, 68.3% of emerald shiners, all gizzard shad, and at least 89.2% of speckled chubs. In addition, all sicklefin and sturgeon chubs, 70% of sand shiners, and 81.2% of plains minnows were shorter than the minimum length-at-age-1.

Species showed a general depth-velocity use gradient relative to body size (Figure 2.12). For visual simplicity I selected the species shown in Figure 2.12 because they represented the pattern for all species that larger fishes used deeper and faster water than smaller fishes. The depth and velocity profiles for all species (n = 25) that occurred in at least 1% of sample units are listed in Table 2.10. The five small-bodied species

monitored by USFWS programs (sturgeon chub, sicklefin chub, speckled chub, plains minnow, sand shiner) had short mean body lengths (<35 mm TL) but occurred over a range of depths and velocities (Table 2.10). Of these species, sicklefin chub used the greatest and plains minnow the lowest mean depth and velocity.

Table 2.9. Summary of available reports for length-at-age-0 and age-1 for 14 Missouri River species. See Literature Cited for full citation to each report.

			Length (m	m) at age-		
		0			1	
	Pierce			Pierce		
	et al.	Hesse	Hay	et al.	Hesse	Hay
Species	(2003)	(2004)	(2006)	(2003)	(2004)	(2006)
gizzard shad					130	
sicklefin chub				40		
sturgeon chub		42			67	
speckled chub		39				
silver chub		55	60		137	117
plains minnow		35		47	45	
bigmouth shiner		24	34		31	50
sand shiner		32	30	32	48	42
river shiner		41	45		62	61
red shiner		35	33		44	44
emerald shiner			26	45	75	54
river carpsucker			38	79	79	73
channel catfish				70	170	
freshwater drum				100	103	

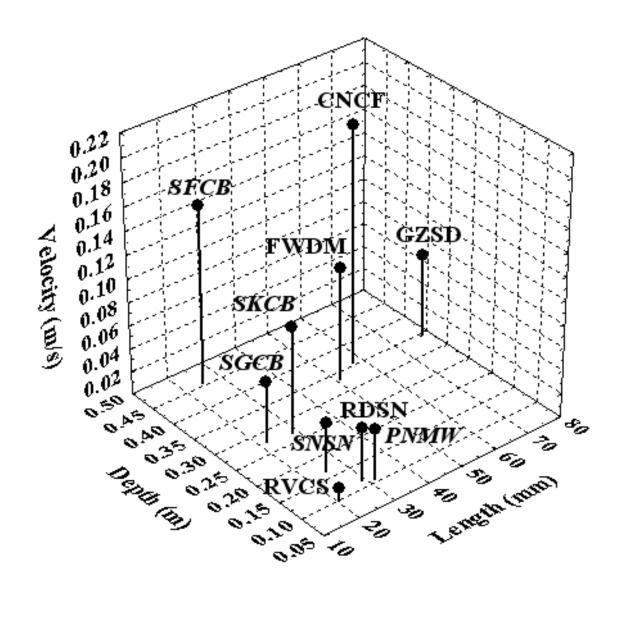


Figure 2.12. Mean body length, depth, and velocity used by 10 fish species collected in sandbar ATTZ on lower Missouri River. Select species labeled in *italics* are currently monitored by U.S Fish and Wildlife Service programs. Depth and velocity were square-root transformed for ANOVA test then back-transformed for display here. See Table 2.1 for species code definition and Table 2.10 for mean values of body length, depth, and velocity by species.

Table 2.10. Body length, depth, and velocity profiles (mean \pm standard error, SE; pooled variance) of species (\geq 9 sample units, \leq 105-mm TL) of small-bodied fishes collected at sandbar ATTZ on lower Missouri River. Select species labeled in *italics* are those currently monitored by U.S Fish and Wildlife Service programs. Depth and velocity were square-root transformed for ANOVA test and are reported here as such; *italic* values below square root transformed mean \pm SE are back-transformed means.

	Body length	Depth	Velocity
Common name	(mm)	(m)	(m/s)
goldeye	48.30 ± 3.16	0.585 ± 0.036	0.427 ± 0.051
		0.343	0.183
gizzard shad	77.69 ± 0.32	0.588 ± 0.004	0.268 ± 0.005
		0.346	0.072
sicklefin chub	25.10 ± 3.01	0.674 ± 0.034	0.390 ± 0.049
		0.454	0.152
sturgeon chub	21.96 ± 2.35	0.525 ± 0.026	0.227 ± 0.038
		0.276	0.051
speckled chub	28.67 ± 0.47	0.535 ± 0.005	0.303 ± 0.008
		0.286	0.092
silver chub	42.10 ± 0.99	0.525 ± 0.011	0.259 ± 0.016
		0.275	0.067
plains minnow	31.68 ± 0.96	0.325 ± 0.011	0.207 ± 0.016
		0.106	0.043
bluntnose minnow	30.06 ± 2.67	0.494 ± 0.030	0.256 ± 0.044
		0.244	0.066
bullhead minnow	29.42 ± 0.70	0.541 ± 0.008	0.175 ± 0.011
		0.293	0.031
bigmouth shiner	36.27 ± 2.35	0.325 ± 0.026	0.133 ± 0.038
		0.106	0.018
sand shiner	25.12 ± 0.97	0.405 ± 0.011	0.204 ± 0.016
		0.164	0.042
river shiner	28.06 ± 0.69	0.393 ± 0.008	0.164 ± 0.011
		0.155	0.027
red shiner	29.16 ± 0.17	0.380 ± 0.002	0.215 ± 0.003
		0.144	0.046
emerald shiner	35.99 ± 0.27	0.458 ± 0.003	0.268 ± 0.004
		0.210	0.072
quillback	23.90 ± 0.90	0.396 ± 0.010	0.074 ± 0.015
		0.157	0.005

Table 2.10. Continued.

	Body length	Depth	Velocity
Common name	(mm)	(m)	(m/s)
river carpsucker	20.32 ± 0.10	0.314 ± 0.001	0.106 ± 0.002
		0.099	0.011
bigmouth buffalo	19.67 ± 3.16	0.368 ± 0.036	0.107 ± 0.051
		0.136	0.011
channel catfish	57.57 ± 0.23	0.594 ± 0.003	0.452 ± 0.004
		0.353	0.204
blue catfish	68.63 ± 3.33	0.621 ± 0.037	0.462 ± 0.054
		0.386	0.213
western mosquitofish	23.80 ± 0.67	0.372 ± 0.008	0.046 ± 0.011
		0.138	0.002
striped bass	61.03 ± 3.16	0.473 ± 0.036	0.340 ± 0.051
		0.224	0.116
white perch	44.53 ± 2.88	0.461 ± 0.032	0.123 ± 0.047
		0.212	0.015
green sunfish	36.83 ± 2.29	0.503 ± 0.026	0.203 ± 0.037
		0.253	0.041
bluegill	28.86 ± 1.19	0.460 ± 0.013	0.067 ± 0.019
		0.212	0.004
freshwater drum	50.99 ± 0.55	0.575 ± 0.006	0.311 ± 0.009
		0.331	0.097

Environmental factors in space and time

Results of analysis for factors that were square-root transformed (depth, velocity, turbidity, slope) are reported below as transformed mean ± SE, followed by the back-transformed mean in *italics* in text. Tables 2.5, 2.11 and 2.12 referred to below have back transformed means listed in *italic* below transformed mean ± SE. For brevity, factors turbidity, substrate particle size, slope, and shoreline sinuosity are reported under one subheading in text below, but are reported in greater detail separately in tables. Values reported in text below represent averages for spatial and temporal scales, but were decomposed to finer resolution in Tables. All statements of difference below were determined from main effects ANOVA tables (*F*-statistic; i.e., Table 2.2, 2.4) or Fisher's LSD post-hoc comparison (*t*-statistic).

Depth-

There was no difference in water depth between point and wing-dike bars, by month (Table 2.2; Table 2.11), or diel period (Table 2.4; Table 2.5). Water depth was shallower in near-shore $(0.359 \pm 0.007, 0.13 \text{ m})$ than moderate $(0.505 \pm 0.008, 0.25 \text{ m}; |t| = 15.2, P < 0.01)$ or offshore $(0.672 \pm 0.007, 0.45 \text{ m}; |t| = 35.0, P < 0.01)$ sample units; moderate sample units were shallower (|t| = 17.1, P < 0.01) than offshore sample units (Table 2.12). Near-shore sample units had shallower depth (|t| = 2.6, P = 0.01) at point bars $(0.343 \pm 0.009, 0.12 \text{ m})$ than at wing-dike bars $(0.376 \pm 0.009, 0.14 \text{ m})$. Depths at moderate (|t| = 1.1, P = 0.27) or offshore (|t| = 0.9, P = 0.36) sample units were not different between point and wing-dike sandbars.

Table 2.11. Means ± standard error (SE, pooled variance) of environmental factors measured in sandbar ATTZ among months, between point and wing-dike sandbars among months, and among regions within and between point and wing-dike sandbars among months. Means for successively higher levels of organization are estimable by averaging up from the lower level. Depth, velocity, turbidity and slope were square-root transformed (sqrt) for ANOVA and are reported here as such; *italic* values below square root transformed means ± SEs are back-transformed means. Sinuosity ranges from approaching zero (straight) to approaching 100 (sinuous). Low substrate (Gs) values correspond to substrates dominated by small diameter particles (e.g., silt and sand), high values indicate large particles are dominant (e.g., gravel and cobble); see Appendix Table D1 to reference index values for proportions of silt, sand, gravel, and cobble. Region codes: HR = head; UP = upstream primary; US = upstream secondary; DP = downstream primary; DS = downstream secondary; TR = tail.

		J	ul	A	ug	S	ep	O	ct
	Month &	Point	Wing-	Point	Wing-	Point	Wing-	Point	Wing-
Factor	Region	bar	dike bar						
Depth s	qrt (m)								
•	Month	0.52 ± 0.01	0.51 ± 0.01	0.47 ± 0.01	0.53 ± 0.01	0.51 ± 0.01	0.52 ± 0.01	0.53 ± 0.01	0.52 ± 0.01
		0.27	0.26	0.22	0.28	0.26	0.27	0.28	0.27
	HR	0.47 ± 0.02	0.54 ± 0.03	0.46 ± 0.02	0.53 ± 0.02	0.50 ± 0.02	0.53 ± 0.02	0.51 ± 0.02	0.54 ± 0.02
		0.22	0.29	0.21	0.28	0.25	0.28	0.26	0.29
	UP	0.51 ± 0.02	0.52 ± 0.03	0.43 ± 0.02	0.55 ± 0.02	0.47 ± 0.02	0.53 ± 0.03	0.49 ± 0.02	0.51 ± 0.02
		0.26	0.27	0.19	0.31	0.23	0.28	0.24	0.26
	US	0.55 ± 0.02	0.42 ± 0.04	0.46 ± 0.03	0.52 ± 0.02	0.49 ± 0.02	0.52 ± 0.02	0.50 ± 0.03	0.53 ± 0.03
		0.31	0.18	0.21	0.27	0.24	0.27	0.25	0.28
	DP	0.53 ± 0.02	0.56 ± 0.03	0.53 ± 0.02	0.55 ± 0.02	0.55 ± 0.03	0.53 ± 0.02	0.55 ± 0.02	0.53 ± 0.02
		0.29 0.32		0.28	0.30	0.30	0.28	0.31	0.28
	DS	0.52 ± 0.02	0.52 ± 0.03	0.50 ± 0.02	0.50 ± 0.02	0.52 ± 0.02	0.48 ± 0.03	0.55 ± 0.03	0.49 ± 0.03
		0.27	0.27	0.25	0.25	0.27	0.23	0.30	0.24
	TR	0.50 ± 0.02	0.50 ± 0.03	0.47 ± 0.02	0.50 ± 0.02	0.52 ± 0.02	0.53 ± 0.02	0.55 ± 0.02	0.50 ± 0.02
		0.25	0.25	0.22	0.25	0.27	0.29	0.30	0.25
Velocity	sqrt (m/s)								
	Month	0.26 ± 0.03	0.20 ± 0.03	0.35 ± 0.03	0.22 ± 0.03	0.33 ± 0.03	0.32 ± 0.03	0.33 ± 0.03	0.28 ± 0.03
		0.068	0.039	0.123	0.050	0.112	0.100	0.107	0.080
	HR	0.32 ± 0.06	0.24 ± 0.06	0.41 ± 0.06	0.20 ± 0.05	0.47 ± 0.04	0.35 ± 0.05	0.40 ± 0.05	0.25 ± 0.06
		0.104	0.055	0.166	0.041	0.224	0.120	0.162	0.064
	UP	0.42 ± 0.03	0.28 ± 0.06	0.43 ± 0.06	0.28 ± 0.05	0.42 ± 0.04	0.38 ± 0.06	0.40 ± 0.04	0.31 ± 0.05
		0.173	0.081	0.186	0.078	0.180	0.141	0.159	0.099
	US	0.09 ± 0.06	0.04 ± 0.09	0.19 ± 0.06	0.13 ± 0.05	0.17 ± 0.05	0.31 ± 0.06	0.03 ± 0.06	0.11 ± 0.07
		0.008	0.002	0.037	0.017	0.030	0.099	0.001	0.012
	DP	0.28 ± 0.05	0.30 ± 0.06	0.50 ± 0.05	0.37 ± 0.05	0.41 ± 0.06	0.36 ± 0.05	0.41 ± 0.06	0.41 ± 0.05
		0.076	0.091	0.249	0.135	0.171	0.129	0.168	0.169
	DS	0.25 ± 0.04	0.14 ± 0.06	0.21 ± 0.04	0.15 ± 0.05	0.16 ± 0.04	0.19 ± 0.07	0.28 ± 0.06	0.25 ± 0.07
		0.063	0.018	0.045	0.021	0.024	0.038	0.080	0.060
	TR	0.21 ± 0.05	0.28 ± 0.06	0.36 ± 0.05	0.21 ± 0.04	0.37 ± 0.05	0.30 ± 0.06	0.44 ± 0.06	0.37 ± 0.06
		0.043	0.078	0.132	0.045	0.135	0.093	0.194	0.135

Table 2.11. Continued.

					San	dbar			
			ul	A	ug	Se	ер	O	ct
	Month &	Point	Wing-	Point	Wing-	Point	Wing-	Point	Wing-
Factor	Region	bar	dike bar	bar	dike bar	bar	dike bar	bar	dike bar
Temper	rature (C°)								
-	Month	30.1 ± 0.4	30.7 ± 0.4	28.9 ± 0.4	29.9 ± 0.4	26.4 ± 0.4	26.6 ± 0.4	17.1 ± 0.4	15.9 ± 0.4
	HR	29.2 ± 0.7	30.9 ± 0.7	29.0 ± 0.7	29.7 ± 0.6	26.1 ± 0.6	26.4 ± 0.6	16.5 ± 0.6	15.9 ± 0.7
	UP	29.9 ± 0.5	31.1 ± 0.8	30.1 ± 0.7	29.8 ± 0.6	27.4 ± 0.6	26.6 ± 0.7	17.3 ± 0.6	16.1 ± 0.7
	US	30.0 ± 0.7	30.3 ± 1.0	30.1 ± 0.8	30.6 ± 0.7	27.2 ± 0.6	26.1 ± 0.7	19.6 ± 0.7	14.9 ± 0.8
	DP	31.7 ± 0.6	30.5 ± 0.7	27.9 ± 0.6	29.8 ± 0.6	25.5 ± 0.7	26.4 ± 0.6	17.4 ± 0.7	17.1 ± 0.7
	DS	29.5 ± 0.5	30.8 ± 0.7	28.0 ± 0.6	29.6 ± 0.6	27.4 ± 0.6	28.0 ± 0.8	16.3 ± 0.7	15.2 ± 0.8
	TR	30.3 ± 0.6	30.5 ± 0.7	28.4 ± 0.6	30.2 ± 0.6	24.9 ± 0.6	26.1 ± 0.7	15.7 ± 0.7	16.3 ± 0.7
Turbidit	y sqrt (NTU)							
	Month	7.09 ± 0.97	7.12 ± 1.01	13.9 ± 0.98	8.96 ± 0.97	7.33 ± 0.97	9.8 ± 0.99	7.97 ± 0.98	11.6 ± 1.00
		50.29	50.70	191.96	80.34	53.66	95.42	63.48	135.06
	HR	8.40 ± 1.24	5.37 ± 1.31	15.9 ± 1.25	8.22 ± 1.15	7.56 ± 1.14	9.6 ± 1.14	7.93 ± 1.16	11.6 ± 1.24
		70.48	28.83	253.20	67.62	57.09	92.41	62.85	133.80
	UP	7.90 ± 1.05	5.68 ± 1.32	14.1 ± 1.25	8.90 ± 1.18	7.43 ± 1.10	9.4 ± 1.25	7.63 ± 1.11	10.6 ± 1.23
	***	62.40	32.21	199.88	79.15	55.18	89.18	58.23	113.13
	US	5.62 ± 1.26	5.96 ± 1.65	14.2 ± 1.32	9.48 ± 1.21	6.54 ± 1.19	10.3 ± 1.25	8.36 ± 1.28	12.2 ± 1.41
	DD	31.53	35.50	200.63	89.94	42.79	105.66	69.94	149.99
	DP	6.04 ± 1.20	7.93 ± 1.26	13.9 ± 1.16	8.03 ± 1.14	7.46 ± 1.28	8.0 ± 1.16	7.17 ± 1.24	10.8 ± 1.21
	DS	<i>36.51</i> 8.19 ± 1.07	62.90 9.34 ± 1.29	193.25 12.0 ± 1.13	<i>64.45</i> 9.74 ± 1.17	55.59 7.78 ± 1.10	64.64 12.1 ± 1.38	51.38 8.59 ± 1.28	115.74 13.2 ± 1.38
	טט	6.19 ± 1.07 67.09	9.34 ± 1.29 87.14	12.0 ± 1.13 143.18	9.74 ± 1.17 94.81	60.59	12.1 ± 1.36 145.94	6.39 ± 1.26 73.73	13.2 ± 1.36 174.37
	TR	6.40 ± 1.15	8.45 ± 1.26	13.0 ± 1.16	9.41 ± 1.13	7.19 ± 1.19	9.2 ± 1.25	8.13 ± 1.25	174.37 11.3 ± 1.25
	111	41.01	71.47	170.24	88.57	51.67	83.77	66.09	128.04

Table 2.11. Continued.

					San	dbar				
		Jul		A	ug	S	ер	C	Oct	
	Month &	Point	Wing-	Point	Wing-	Point	Wing-	Point	Wing-	
Factor	Region	bar	dike bar							
Substrat	$te(G_s)$									
	Month	2.70 ± 1.72	1.29 ± 2.39	1.51 ± 1.92	1.54 ± 1.73	6.30 ± 1.75	3.33 ± 1.99	1.56 ± 1.95	1.25 ± 2.19	
	HR	6.68 ± 4.72	7.57 ± 5.43	0.86 ± 4.85	2.10 ± 3.95	30.3 ± 3.75	4.66 ± 3.81	3.00 ± 4.03	3.84 ± 4.80	
	UP	2.42 ± 2.77	1.34 ± 5.45	3.26 ± 4.87	0.78 ± 4.26	2.27 ± 3.34	11.5 ± 4.86	1.56 ± 3.56	0.79 ± 4.70	
	US	0.87 ± 4.88	0.19 ± 7.75	0.56 ± 5.47	1.95 ± 4.52	1.63 ± 4.27	0.79 ± 4.76	1.18 ± 5.08	0.09 ± 6.16	
	DP	2.89 ± 4.45	0.38 ± 5.00	1.35 ± 4.04	2.45 ± 3.86	1.11 ± 5.17	1.10 ± 3.94	0.58 ± 4.76	0.89 ± 4.46	
	DS	1.13 ± 3.00	0.44 ± 5.18	2.15 ± 3.72	1.08 ± 4.11	0.95 ± 3.37	0.78 ± 5.81	1.70 ± 5.18	1.06 ± 5.93	
	TR	2.21 ± 3.92	0.49 ± 4.99	0.88 ± 4.05	0.89 ± 3.71	1.52 ± 4.34	1.20 ± 4.77	1.34 ± 4.93	0.98 ± 4.92	
Slope so	qrt (%)									
	Month	0.21 ± 0.02	0.35 ± 0.03	0.23 ± 0.02	0.31 ± 0.02	0.24 ± 0.02	0.32 ± 0.02	0.29 ± 0.02	0.31 ± 0.03	
		0.044	0.126	0.055	0.095	0.057	0.100	0.081	0.094	
	HR	0.14 ± 0.05	0.45 ± 0.05	0.23 ± 0.05	0.33 ± 0.04	0.18 ± 0.04	0.29 ± 0.04	0.24 ± 0.04	0.34 ± 0.05	
		0.019	0.201	0.051	0.112	0.034	0.086	0.056	0.118	
	UP	0.17 ± 0.04	0.38 ± 0.05	0.14 ± 0.05	0.34 ± 0.04	0.20 ± 0.04	0.37 ± 0.05	0.22 ± 0.04	0.33 ± 0.05	
		0.030	0.142	0.019	0.118	0.042	0.140	0.048	0.109	
	US	0.17 ± 0.05	0.24 ± 0.07	0.23 ± 0.05	0.34 ± 0.05	0.20 ± 0.05	0.37 ± 0.05	0.28 ± 0.05	0.37 ± 0.06	
		0.029	0.059	0.052	0.118	0.041	0.139	0.079	0.135	
	DP	0.30 ± 0.05	0.41 ± 0.05	0.29 ± 0.04	0.30 ± 0.04	0.37 ± 0.05	0.31 ± 0.05	0.34 ± 0.05	0.32 ± 0.05	
		0.087	0.164	0.086	0.092	0.136	0.096	0.118	0.099	
	DS	0.22 ± 0.04	0.32 ± 0.05	0.23 ± 0.04	0.26 ± 0.05	0.21 ± 0.04	0.23 ± 0.06	0.30 ± 0.05	0.23 ± 0.06	
		0.049	0.100	0.053	0.067	0.044	0.055	0.088	0.051	
	TR	0.26 ± 0.04	0.34 ± 0.05	0.29 ± 0.04	0.27 ± 0.04	0.26 ± 0.05	0.31 ± 0.05	0.34 ± 0.05	0.26 ± 0.05	
		0.066	0.115	0.084	0.071	0.068	0.099	0.113	0.066	

Table 2.11. Continued.

			Sandbar Sen Oct										
		Jul		A	aug	S	ер		Oct				
	Month &	Point	Wing-	Point	Wing-	Point	Wing-	Point	Wing-				
Factor	Region	bar	dike bar	bar	dike bar	bar	dike bar	bar	dike bar				
Shorelin	e sinuosity												
	Month	31.5 ± 3.7	9.5 ± 4.1	24.0 ± 3.7	14.2 ± 3.7	31.1 ± 3.7	11.7 ± 3.8	13.0 ± 3.8	10.8 ± 4.0				
	HR	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A				
	UP	35.5 ± 7.0	22.2 ± 7.7	27.6 ± 7.5	11.2 ± 7.2	15.6 ± 7.1	9.5 ± 7.5	25.5 ± 7.1	5.5 ± 7.5				
	US	42.8 ± 7.8	8.0 ± 9.7	26.8 ± 7.7	8.5 ± 7.5	54.0 ± 7.4	4.8 ± 7.7	7.2 ± 7.8	9.4 ± 8.1				
	DP	22.4 ± 7.4	3.7 ± 7.5	16.6 ± 7.2	17.9 ± 7.2	10.7 ± 7.7	11.5 ± 7.3	8.6 ± 7.5	13.8 ± 7.4				
	DS	25.4 ± 7.1	4.0 ± 7.8	24.9 ± 7.2	19.2 ± 7.4	44.2 ± 7.2	21.2 ± 8.1	10.6 ± 7.8	14.7 ± 8.8				
	TR	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A				

Table 2.12. Means ± standard error (SE, pooled variance) of environmental factors measured in sandbar ATTZ among sample units within and among regions by month. Means for successively higher levels of organization are estimable by averaging up from the lower level. Depth, velocity, turbidity and slope were square-root transformed (sqrt) for ANOVA and are reported here as such; *italic* values below square root transformed means ± SEs are back-transformed means. Sinuosity ranges from approaching zero (straight) to approaching 100 (sinuous). Low substrate (Gs) values correspond to substrates dominated by small diameter particles (e.g., silt and sand), high values indicate large particles are dominant (e.g., gravel and cobble); see Appendix Table D1 to reference index values for proportions of silt, sand, gravel, and cobble. Region codes: HR = head; UP = upstream primary; US = upstream secondary; DP = downstream primary; DS = downstream secondary; TR = tail.

	Sample unit category												
		Jul			Aug Sep					Oct			
Factor	Near-		Off	Near-		Off	Near-	•	Off	Near-		Off	
Region	shore	Moderate	shore	shore	Moderate	shore	shore	Moderate	shore	shore	Moderate	shore	
Depth so	qrt (m)												
HR	0.39 ± 0.03	0.50 ± 0.03	0.63 ± 0.03	0.35 ± 0.02	0.48 ± 0.03	0.66 ± 0.03	0.37 ± 0.02	0.49 ± 0.02	0.70 ± 0.02	0.37 ± 0.02	0.51 ± 0.03	0.69 ± 0.03	
	0.15	0.25	0.39	0.13	0.23	0.43	0.13	0.24	0.49	0.14	0.26	0.47	
UP	0.36 ± 0.02	0.53 ± 0.03	0.66 ± 0.02	0.35 ± 0.02	0.46 ± 0.03	0.66 ± 0.03	0.37 ± 0.02	0.47 ± 0.03	0.67 ± 0.02	0.33 ± 0.02	0.50 ± 0.03	0.67 ± 0.02	
	0.13	0.28	0.43	0.12	0.22	0.44	0.14	0.23	0.45	0.11	0.25	0.44	
US	0.36 ± 0.04	0.47 ± 0.04	0.62 ± 0.04	0.33 ± 0.03	0.50 ± 0.04	0.65 ± 0.03	0.37 ± 0.03	0.46 ± 0.03	0.69 ± 0.02	0.33 ± 0.03	0.53 ± 0.04	0.69 ± 0.03	
	0.13	0.23	0.39	0.11	0.25	0.42	0.14	0.21	0.47	0.11	0.28	0.47	
DP	0.39 ± 0.03	0.00	0.68 ± 0.03	0.40 ± 0.02		0.70 ± 0.02	0.38 ± 0.02		0.70 ± 0.03			0.72 ± 0.03	
	0.15	0.32	0.46	0.16	0.27	0.48	0.15	0.28	0.48	0.13	0.29	0.52	
DS	0.33 ± 0.02	0.53 ± 0.03	0.69 ± 0.03	0.33 ± 0.02	0.51 ± 0.02	0.66 ± 0.02	0.30 ± 0.03		0.70 ± 0.03	0.33 ± 0.03	0.55 ± 0.03	0.69 ± 0.04	
	0.11	0.28	0.48	0.11	0.26	0.43	0.09	0.24	0.49	0.11	0.30	0.48	
TR	0.38 ± 0.02		0.63 ± 0.03			0.65 ± 0.02			0.66 ± 0.03		0.50 ± 0.03		
	0.14	0.24	0.40	0.13	0.20	0.42	0.14	0.29	0.43	0.15	0.25	0.48	
Velocity	sqrt (m/s)												
HR						0.41 ± 0.06							
	0.0240	0.1134	0.1195	0.0143	0.1512	0.1657	0.0912	0.1796	0.2538	0.0579	0.0663	0.2361	
UP			0.41 ± 0.05			0.46 ± 0.06			0.47 ± 0.05		0.38 ± 0.06		
	0.0741	0.1385	0.1656	0.0461	0.1502	0.2150	0.0494	0.2593	0.2201	0.0324	0.1414	0.2629	
US		0.01 ± 0.10				0.18 ± 0.06			0.29 ± 0.05		0.10 ± 0.08		
	0.0005	0.0001	0.0064	0.0058	0.0499	0.0341	0.0175	0.0946	0.0842	0.0061	0.0094	0.0007	
DP			0.41 ± 0.06			0.53 ± 0.05			0.47 ± 0.06		0.48 ± 0.07		
	0.0310	0.0805	0.1647	0.1104	0.1930	0.2792	0.0904	0.1475	0.2254	0.0475	0.2258	0.2899	
DS			0.25 ± 0.06			0.24 ± 0.05			0.27 ± 0.06		0.26 ± 0.08		
	0.0134	0.0471	0.0604	0.0118	0.0349	0.0585	0.0039	0.0379	0.0721	0.0376	0.0656	0.1168	
TR			0.37 ± 0.06		0.24 ± 0.06				0.45 ± 0.06		0.43 ± 0.07		
	0.0372	0.0291	0.1335	0.0476	0.0560	0.1669	0.0803	0.0747	0.2025	0.0901	0.1851	0.2316	

Table 2.12. Continued.

	Sample unit category											· · · · · · · · · · · · · · · · · · ·
	Jul				Aug			Sep		Oct		
Factor	Near-		Off	Near-		Off	Near-	•	Off	Near-		Off
Region	shore	Moderate	shore	shore	Moderate	shore	shore	Moderate	shore	shore	Moderate	shore
Tempera	ature (C°)											
HR	30.3 ± 0.69	29.7 ± 0.80	30.1 ± 0.69	30.3 ± 0.61	29.1 ± 0.69	28.7 ± 0.63	26.6 ± 0.55	26.4 ± 0.55	25.8 ± 0.58	17.1 ± 0.59	15.3 ± 0.67	16.1 ± 0.68
UP	31.2 ± 0.57	30.0 ± 0.72	30.2 ± 0.57	30.8 ± 0.58	29.7 ± 0.74	29.2 ± 0.67	27.3 ± 0.51	27.1 ± 0.75	26.5 ± 0.54	18.1 ± 0.58	15.8 ± 0.68	16.1 ± 0.58
US	30.2 ± 0.85	30.2 ± 1.04	30.1 ± 0.85	30.7 ± 0.65	30.8 ± 0.87	29.5 ± 0.65	26.9 ± 0.62	26.6 ± 0.74	26.4 ± 0.60	17.5 ± 0.74	17.3 ± 0.86	16.9 ± 0.82
DP	31.6 ± 0.63	31.0 ± 0.73	30.8 ± 0.70	29.2 ± 0.52	28.6 ± 0.66	28.7 ± 0.57	26.1 ± 0.59	26.0 ± 0.77	25.8 ± 0.64	17.7 ± 0.61	17.6 ± 0.73	16.5 ± 0.66
DS	30.3 ± 0.55	30.2 ± 0.63	30.0 ± 0.64	29.5 ± 0.56	28.6 ± 0.61	28.4 ± 0.57	28.4 ± 0.66	28.1 ± 0.68	26.6 ± 0.67	16.6 ± 0.71	15.7 ± 0.83	15.0 ± 0.85
TR	30.4 ± 0.58	30.5 ± 0.69	30.3 ± 0.69	29.9 ± 0.53	29.3 ± 0.63	28.7 ± 0.57	25.5 ± 0.60	25.9 ± 0.73	25.1 ± 0.64	16.3 ± 0.61	16.2 ± 0.77	15.6 ± 0.77
Turbidity	sqrt (NTU)											
HR	7.58 ± 1.13	6.97 ± 1.27	6.09 ± 1.13	11.5 ± 1.03	11.8 ± 1.13	12.9 ± 1.05	8.13 ± 0.95	8.68 ± 0.95	8.94 ± 0.99	9.51 ± 1.01	9.36 ± 1.11	10.4 ± 1.12
	57.52	48.59	37.10	131.74	140.01	166.21	66.06	75.38	79.97	90.47	87.66	107.50
UP			7.18 ± 0.99			11.7 ± 1.11				8.93 ± 1.00		
	38.05	49.18	51.57	121.10	139.36	137.88	73.82	66.21	73.61	79.80	86.54	83.99
US		6.17 ± 1.59				12.1 ± 1.07			8.87 ± 1.02			
22	36.24	38.10	26.71	143.27	130.77	145.61	61.28	72.87	78.62	95.93	131.22	93.43
DP	7.11 ± 1.05 50.56	7.61 ± 1.18 57.98	6.24 ± 1.14 38.88	10.8 ± 0.93 116.30	11.4 ± 1.09 129.92	10.7 ± 0.98 114.74	7.18 ± 1.00 51.57	7.98 ± 1.23 63.70	8.08 ± 1.07 65.31	9.15 ± 1.03 83.65	8.86 ± 1.19 78.49	8.88 ± 1.10 78.93
DS			8.97 ± 1.06									
DS	66.66	83.81	80.46	136.84	10.4 - 1.03	10.4 - 0.38	92.04	94.27	110.12	133.07	100.19	124.15
TR		7.62 ± 1.13				12.3 ± 0.98				9.69 ± 1.03		
	55.45	58.08	52.12	123.50	104.67	152.39	70.38	52.24	79.11	93.98	88.61	101.21
Substrat	$e(G_s)$											
HR	3.31 ± 5.48	7.06 ± 6.46	11.0 ± 5.48	2.72 ± 4.68	0.94 ± 5.48	0.78 ± 4.87	2.48 ± 4.08	27.1 ± 4.08	22.8 ± 4.37	4.97 ± 4.54	1.24 ± 5.32	4.05 ± 5.41
UP	0.67 ± 4.33	0.01 ± 5.75	0.93 ± 4.33	2.72 ± 4.45	1.69 ± 5.88	1.65 ± 5.30	7.28 ± 3.64	11.5 ± 6.03	1.86 ± 4.03	1.16 ± 4.43	0.61 ± 5.32	1.75 ± 4.43
US	0.56 ± 6.74	0.28 ± 8.53	0.75 ± 6.74	0.69 ± 5.02	2.76 ± 7.03	0.31 ± 5.02	1.43 ± 4.75	0.78 ± 5.88	1.40 ± 4.56	0.76 ± 5.90	0.25 ± 6.97	0.62 ± 6.63
DP	2.66 ± 4.89	0.69 ± 5.86	1.57 ± 5.59	1.84 ± 3.87	2.87 ± 5.17	0.99 ± 4.33	1.43 ± 4.50	0.62 ± 6.19	1.27 ± 4.98	0.67 ± 4.70	0.77 ± 5.87	0.79 ± 5.20
DS	0.71 ± 4.07	0.89 ± 4.89	0.75 ± 4.91	1.36 ± 4.21	1.00 ± 4.70	2.49 ± 4.33	0.90 ± 5.13	0.93 ± 5.24	0.76 ± 5.17	1.14 ± 5.63	1.68 ± 6.68	1.32 ± 6.96
TR	0.55 ± 4.36	1.19 ± 5.45	2.31 ± 5.45	0.58 ± 3.91	0.72 ± 4.95	1.35 ± 4.33	1.22 ± 4.54	1.09 ± 5.86	1.77 ± 4.95	1.04 ± 4.69	1.18 ± 6.20	1.27 ± 6.20

Velocity-

Velocity differed by region, sample unit category and month (Table 2.2), but not by diel period (Table 2.4). Upstream and downstream secondary-channel regions had slower velocity than upstream and downstream primary-channel regions (5.5<|t|<8.1, P<0.01). Velocity was slower in July (0.23 \pm 0.02, 0.054 m/s) than August (0.29 \pm 0.02, 0.084 m/s; |t| = 2.9, P < 0.01), September (0.33 \pm 0.02, 0.106 m/s; |t| = 4.8, P < 0.01) or October (0.31 \pm 0.02, 0.094 m/s; |t| = 3.5, P < 0.01) (Table 2.11). Water velocity nearshore (0.19 \pm 0.02, 0.035 m/s) was slower than moderate (0.30 \pm 0.02, 0.091 m/s; |t| = 6.9, P < 0.01) or offshore (0.37 \pm 0.02, 0.138 m/s; |t| = 12.1, P < 0.01) velocity across all months (Table 2.12).

Water Temperature-

Water temperature differed by sample unit category, month (Table 2.2), and by diel period (Table 2.4). Shallower waters near-shore (26.19 \pm 0.28 C°) were warmer than deeper offshore (25.30 \pm 0.28 C°; |t| = 1.8, P < 0.05) waters (Table 2.12). Water was cooler at night than during the day (|t| = 3.8, P < 0.01; Table 2.5). Near-shore sample units (30.00 \pm 0.28 C°) were warmer than moderate (28.90 \pm 0.28 C°; |t| = 2.8, P < 0.01) or offshore sample units (28.66 \pm 0.29 C°; |t| = 3.4, P < 0.01) during the day (Table 2.12). Temperature decreased from July (30.4 \pm 0.3 C°) to August (29.4 \pm 0.3 C°) through September (26.5 \pm 0.3 C°) and October (16.5 \pm 0.3 C°); mean temperature at point bars was lower than at wing-dike bars during July and August but higher during October (Table 2.11).

Turbidity, substrate, slope, shoreline sinuosity-

Mean turbidity had an increasing pattern from July through October, but was significantly higher (5.4 < |t| < 14.0, P < 0.01) in August than any other month (Table 2.11). Substrate particle sizes were not different between point and wing-dike sandbars (|F| = 0.4, P = 0.53) or among months (Table 2.2; |F| = 1.9, P = 0.13). However, mean substrate particle size was larger at the head of point bars during September (P < 0.05)than other regions during other months (Table 2.11; see Appendix C for discussion of this result). Mean slopes were shallower in upstream regions (head, upstream primary and secondary regions) at point sandbars than at wing-dike sandbars, but were similar in downstream regions (tail, downstream primary and downstream secondary regions) between point and wing-dike sandbars. They followed an opposite pattern from head to tail region where point bars had shallower mean slope toward the head region and generally steepened downstream toward the tail, and wing-dike bars were steepest at the head and slope decreased toward the tail (Figure 2.13). Shorelines were less sinuous in October (P < 0.01) than the previous three months. Shorelines at point bars (24.89 ± 3.49) were more sinuous than at wing-dike bars (11.56 \pm 3.54; |t| = 7.1, P < 0.01) with month and region (upstream primary and secondary, downstream primary and secondary) pooled by sandbar type (Table 2.11).

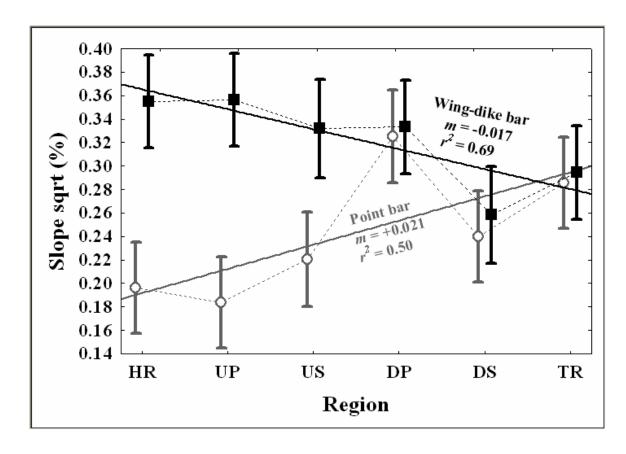


Figure 2.13. Sandbar slope mean \pm standard error (SE, pooled variance) among regions between point (open circles) and wing-dike (closed squares) sandbars. Sandbar slopes were tested with split-split plot ANOVA and reported here with square-root transformed data; see table 2.10 for back-transformed means. Solid lines with slope (m) and r^2 statistics represent regressions through regions by sandbar type. Region codes: HR = head, UP = upstream primary, US = upstream secondary, DP = downstream primary, DS = downstream secondary, TR = tail region.

Small-bodied fish assemblage structure

Structure of the small-bodied fish assemblage was tested in DCA from 20,690 individuals (85% of all individuals ≤105-mm TL) by species, length class, and macrohabitat use guild; unidentified carpsuckers, n = 3,358 and fishes <10 mm TL were excluded from the analysis. Length class 5 (5-9 mm TL) was composed of only 11 individuals (0.05% of total catch) from 4 species and 6 sample units, failed to meet the minimum number of samples inclusion criteria, and were excluded from further analysis (Table 2.13). Total inertia was highest by species and lowest by macrohabitat use guild (Table 2.14). However, the habitat use guild group was not used in comparison of total inertia to determine how the assemblage was structured because it had disproportionately fewer units (n = 3) relative to species (n = 25) and length class (n = 19). Fish body length best explained how the small-bodied fish assemblage at sandbar ATTZ was structured as it exhibited the lowest total inertia. Total inertia of the species group was more than twice that of the length class group (Table 2.14). Species occupied a larger ordination space and visually appeared more scattered than length classes (Figure 2.14). Therefore, the body length dataset was selected for further analysis with spatial statistics to test for clustering among fishes relative to length class.

Fishes were grouped relative to body length in sample space as indicated by mean nearest neighbor distance test and Moran's I test for spatial autocorrelation. Each test independently detected significant (P < 0.01) clustering among length class units in ordination space. Getis-Ord general G test indicated that larger fishes may occur exclusively grouped (i.e., without smaller fishes) more than smaller fishes because clustering was significant among larger length classes. Unfortunately, Getis-Ord does

Table 2.13. Counts of fishes used in detrended correspondence analysis (DCA) analyses to test assemblage structure relative to species, body length class (5-mm class width), and macrohabitat use guild. Length classes are 5-mm and labeled by the shortest length within each class (e.g., '10' is 10-14 mm TL). Matrix to determine number of individuals is interpretable by species, length class, macrohabitat use guild, species by length class, or macrohabitat use guild by length class. Length class sums (bold by column) apply to species (above) and macrohabitat use guild (below). See Table 2.1 for species code definitions. Macrohabitat use guild codes: FS = fluvial specialist, FD = fluvial dependent, MG = macrohabitat generalist. Length class '5' occurred in less than 1% of samples; therefore, those individuals were excluded from DCA analyses

									Len	gth Cl	ass (5	mm)									
Fish	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Sum
Species																					
GDEY	0	0	0	0	0	2	0	0	4	2	1	0	0	1	0	0	0	0	0	0	10
GZSD	0	0	0	1	1	4	12	16	45	64	44	27	9	27	89	223	229	120	39	22	972
SFCB	0	1	1	9	5	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	20
SGCB	0	1	6	12	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25
SKCB	1	19	83	130	128	121	107	54	9	3	2	0	1	0	1	1	0	0	0	0	660
SVCB	0	0	7	18	14	12	12	10	5	4	2	3	7	6	4	6	4	0	0	0	114
PNMW	0	4	7	30	23	9	8	14	14	4	2	2	0	0	0	0	0	0	0	0	117
BNMW	0	1	6	2	4	2	5	5	1	2	0	1	0	0	0	0	0	0	0	0	29
BHMW	0	2	20	53	44	44	40	15	6	3	0	1	0	0	0	0	0	0	0	0	228
BMSN	0	1	3	0	1	2	5	5	4	0	0	0	0	0	0	0	0	0	0	0	21
SNSN	0	16	28	21	18	13	20	3	4	5	1	0	0	0	0	0	0	0	0	0	129
RVSN	0	6	12	57	62	39	17	8	6	3	2	0	0	0	0	0	0	0	0	0	212
RDSN	2	97	285			909	456	276	145	70	25	13	3	0	1	1	0	0	0	0	3969
ERSN	7	228	109	50	81	230	174	159	106	119	98	75	51	20	9	3	0	0	0	0	1519
QLBK	0	9	53	15	9	23	6	5	3	1	1	0	0	0	0	0	0	0	0	0	125
RVCS	1	673	4516	2987	742	322	133	70	39	30	13	19	10	8	8	3	1	1	0	0	9576
BMBF	0	0	7	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	10
CNCF	0	1	3	11	27	84	127	184	268	361	368	296	202	144	78	42	19	25	13	5	2258
BLCF	0	0	0	0	0	0	1	1	0	0	3	2	1	4	1	1	0	0	1	0	15
MQTF	0	14	57	80	37	16	8	18	1	0	0	0	0	0	0	0	0	0	0	0	231
SDBS	0	0	0	0	0	1	0	0	1	0	1	5	1	1	0	1	1	0	0	0	12
WTPH	0	0	0	0	0	2	1	2	3	2	2	0	0	0	0	0	0	0	0	0	12
GNSF	0	0	2	2	3	3	1	2	1	5	0	1	0	0	0	0	0	0	0	0	20
BLGL	0	0	9	18	22	6	12	8	3	0	0	0	0	0	0	0	0	0	0	0	78
FWDM	0	8	24	33	16	4	6	19	20	38	51	36	29	16	6	5	11	7	4	6	339
Sum	11	1081	5238	4138	2321	1851	1154	874	688	716	616	481	314	227	197	286	265	153	57	33	20701
Guild														·					-		
FS	1	44	133	229	219	178	152	71	23	11	8	2	2	4	2	2	0	0	1	0	1082
FD	0	4	7	30	23	14	9	16	22	8	6	7	1	2	0	1	1	0	0	0	151
MG	10	1033	5098	3879	2079	1659	993	787	643	697	602	472	311	221	195	283	264	153	56	33	19468

Table 2.14. Results of detrended correspondence analysis (DCA) ordinations by species, length class, and macrohabitat use guild. Guild assemblage group was not included in comparison of total inertia (lower is better) among groups to determine which best explained small-bodied fish assemblage structure due to low n.

	Assemblage group										
Statistic	Species	Length	Guild								
Number (n)	25	19	3								
Cumulative % variance explained											
Axis 1	9.60	21.70	56.90								
Axis 2	16.40	27.20	67.30								
Axis 3	22.10	31.30	0.00								
Total inertia (λ)	7.86	3.48	0.97								

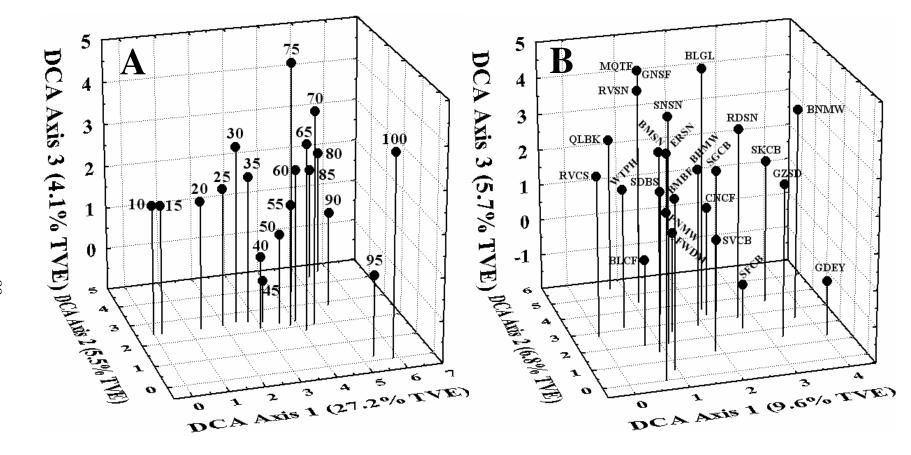


Figure 2.14. Detrended correspondence analysis scores plotted along the first three ordination axes with percent of total variation explained (%TVE) for fishes organized by (A) length class and (B) species. Dots represent DCA score for all fishes analyzed within their length class or species units.

not identify exactly which length classes were involved in clustering, and only identifies where clustering is most significant. Therefore it is possible that smaller length classes were clustered as well, but to a lesser degree than larger ones. To address this problem I partition length classes into three groups, small (length class 10-35), medium (40-70), and large (75-100), and tested for clustering within each group. Both mean nearest neighbor test and Moran's I failed to detect a cluster pattern within small and medium groups length classes; both confirmed clustering in the large group length classes. Getis-Ord indicated that clustering was significant $(0.05 > P \ge 0.01)$ among larger length classes within the 75-105 mm TL range.

Standard distance among fishes by length class indicated that larger fishes were distributed in a pattern more consistent with clustering than smaller fishes; regression of standard distance by length class indicate this distribution pattern relative to body length is significant ($r^2 = 0.71$, P < 0.001; Figure 2.15A). As with Getis-Ord test above, no quantitative method was available to determine at exactly which length class clustering became significant. Therefore, I assigned a division between clustering and non-clustering at 150 where a clear break occurred at the > 90 mm length class to indicate clustering at a standard distance below 150 (Figure 2.15A). The > 90 mm length class composed the larger half of the 75-105 mm TL range where clustering occurred based on Getis-Ord test. Although total inertia was highest in the species dataset, standard distance among unique species was plotted for visual comparison with length class standard distance. Channel catfish, western mosquitofish (*Gambusia affinis*), and bluegill (*Lepomis macrochirus*) had standard distances below 150 (Figure 2.15B).

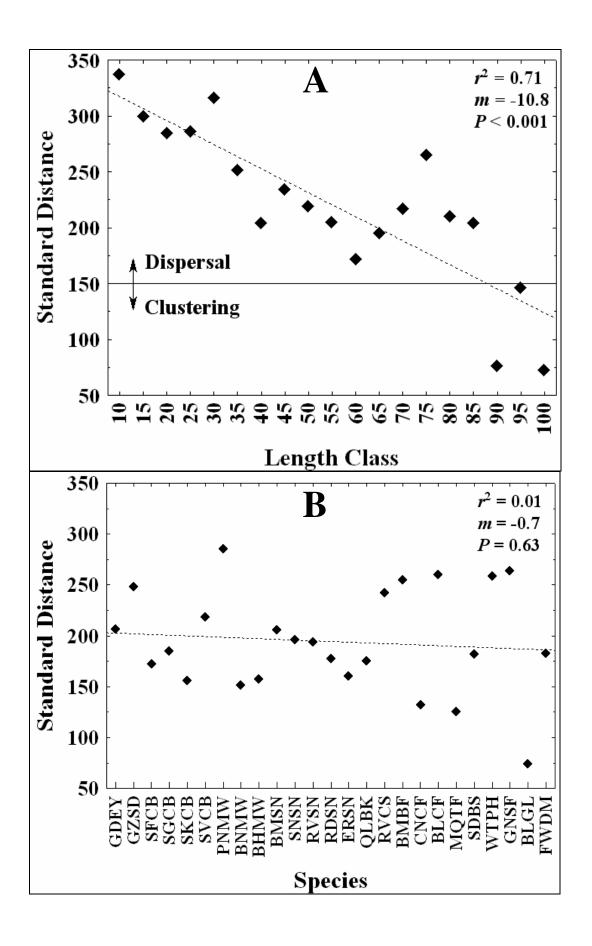


Figure 2.15. Standard distance among lower Missouri River small-bodied fishes collected at sandbar ATTZ and grouped into (A) 5-mm length classes and (B) species. Standard distance above 150 in window 'A' indicates that fishes within a length class have a distribution pattern not consistent with clustering in DCA ordination space; standard distance below 150 indicates they have a distribution pattern consistent with clustering in DCA ordination space. Length classes that occur close together in DCA ordination space (i.e., clustering) are interpreted to co-occur more frequently than length classes that are space further apart (i.e., dispersal). Dashed line with associated statistics is the regression through points where r^2 is fit of the line, m is slope of the line, and P is probability that the slope is different from zero.

Discussion

Shallow, slow velocity habitat at sandbar ATTZ on lower Missouri River was used by many small-bodied fishes. The ecological significance of sandbar ATTZ is reflected by the remarkably species rich fauna found there, constituting 44% of the 110 species reported present in LMOR main-channel and floodplain habitats by Galat et al. (2005). This implies that sandbar ATTZ is an important habitat type contributing to biodiversity in LMOR, particularly since sandbar surface area was reduced by 98% after river channelization (Funk and Robinson 1974).

Fishes collected from sandbar ATTZ were more abundant and on average shorter during July and August than September and October. Small-bodied fishes differentially used ATTZ depth zones between 0.0 and 0.5 m relative to body length. Near-shore ATTZ with shallowest depths (0.12m) had higher abundance and lower mean fish length than deeper habitats further away from shore during the day. At night, fishes were still most abundant near-shore, even more so than during the day, but mean body length increased. I hypothesize this is because larger fishes that were further offshore during the day moved nearer to shore at night in response to reduced terrestrial predation risk or cooler water temperature (see *Diel patterns of fishes at sandbar ATTZ* below for further discussion).

Many species in LMOR grow to a length >105 mm TL (Pflieger 1997; Pierce et al. 2003). Non-native common carp (*Cyprinus carpio*) was the largest Cyprinid collected in this study followed by silver chub (*Macrhybopsis storeriana*). Silver chub is a common "small" fish of LMOR and often can achieve lengths >100 mm (Pflieger 1997). I collected many specimens ≤ 105 mm TL from species that grow to both small and large

adult size (e.g., river carpsucker and red shiner) indicating that the 105-mm maximum length criterion was appropriate to quantify the term "small-bodied" fish.

The period of high abundance for the smallest fishes (<35 mm TL) corresponds well with timing of spawning (April-June) for many fluvial fishes (Galat et al. 1998) and expected subsequent high age-0 abundance following multiple rises in river discharge on LMOR (Figure 2.6). Possible explanations for the reduction of small-bodied fishes after August include: 1) sampling effectiveness of PAEDs decreased after August, 2) fishes experienced sudden mass mortality after August or, 3) fishes survived, grew during July and August, and underwent ontogenetic habitat shifts away from sandbar ATTZ after August.

Dominance of smaller size small-bodied fishes (<35 mm TL) suggests that either (1) PAEDs may have been size selective, or (2) these sized fishes dominate the size composition in sandbar ATTZ. Electrofishing gear is known to be size selective because immobilization, and thus sampling efficiency, is largely a function of energy transfer between water and fish (Reynolds 1996, 2000). Less power is required to immobilize larger fish because total body voltage, thus electrical shock to fish, increases with body size (Dolan and Miranda 2003). Therefore, electrofishing size selectivity tends to bias samples towards larger fish (Scholten 2003). It is unlikely that PAEDs were size selective because results from size frequency analysis were not consistent with electrofishing size selectivity. The right skewness in Figure 2.5 is consistent with particle size theory that small organisms are more abundant than large organisms (Hutchinson and MacArthur 1959; Sheldon et al. 1972; Brown and Maurer 1986; Kozłowski and Gawelczyk 2002) suggesting that PAEDs effectively sampled sandbar ATTZ to

accurately represent the size structure of the small-bodied fish assemblage. By comparison, the number of species collected by PAEDs (49) appears consistent with previous surveys from seine hauls at sandbars (46 species, Grace 1985) or channel-border-sandbar habitat types (31 species, Grady and Milligan 1998) on LMOR. Since voltage gradients produced by PAEDs were above the minimum effective immobilization threshold, and since I did not observe any evidence in the field pointing to a mass fish kill, I support the option that fishes experienced ontogeny and will discuss below habitat use in light of results from analyses.

Use of sandbar ATTZ by small-bodied fishes

Body size plays a fundamental role in interactions among fishes and between a fish and its environment (Hutchinson and MacArthur 1959; Roff 1981; Brown and Maurer 1986; Kerr 1989; Blanckenhorn 2000). Results of DCA ordinations show that the small-bodied fish assemblage collected in sandbar ATTZ was more structured by body length than species associations. The relative degree of dispersal and high abundance in all near-shore samples of smaller size small-bodied fishes (<35 mm TL) suggests that they were widely distributed throughout the nearest-shore sandbar ATTZ sampled in this study.

Lack of statistical significance in CPUE by region, but significant differences in CPUE by depth, indicates that small-bodied fishes use most of the ATTZ present around sandbars, and instead partition sandbar ATTZ by depth. However, the upstream secondary region was composed of shorter length fishes than other regions during July and August. Many native LMOR species (e.g., river carpsucker, gizzard shad, channel

catfish, speckled chub, sicklefin chub, sturgeon chub, plains minnow, and sand shiner) clearly used sandbar ATTZ as nursery. Results conclusively show that shallow, near-shore habitat is used by more, and smaller (<35 mm TL), small-bodied fishes than adjacent deeper habitats. The near-shore zone provided warmer water temperature and lower flow velocity than deeper habitats further offshore. These observations are consistent with conditions associated with growth of age-0 fluvial fishes and nursery habitat in other large rivers (Copp et al. 1994; Pavlov 1994; Garner 1996, 1997; Poizat and Pont 1996; Jurajda 1999; Keckeis et al. 2001; Grift et al. 2003; Nunn et al. 2003; King 2004a).

Fish often occur in high densities in areas where food is abundant (Chará et al. 2006); particularly age-0 fishes because they must feed at a maximal rate to achieve rapid growth. Many benthic invertebrates use SSVH like the near-shore zone as flow refuge in lotic systems (Lancaster and Hildrew 1993; Rempel et al. 1999; Lancaster 1999, 2000); and recent work on food webs within the main channel of other large rivers shows that productivity of microfauna is sufficient to sustain growth and survival of age-0 fishes there (Robertson 1990; Dettmers et al. 2001; King 2004b). Algal production was the primary driver of trophic system dynamics within a braided, river-floodplain reach of upper Mississippi River (Delong and Thorp 2006); and low velocity areas around sandbars support high densities of rotifers in other turbid prairie-river tributaries to LMOR (Thorp and Mantovani 2005). Lee (2007) found that macroinvertebrates were nearly twice as abundant in the aquatic near-shore zone as on the emergent part of sandbars on LMOR; she sampled only out to 5.0-cm deep around sandbars, yet found invertebrates were present in particularly high abundances in waters where finest

substrates and lowest flow velocity occurred. Results clearly demonstrate that the near-shore zone at sandbar ATTZ on LMOR is dominated by 10-34 mm TL fishes. Therefore, if food resources are produced or maintained in the relative refuge of near-shore sandbar ATTZ as it is in the floodplain ATTZ (Junk et al. 1989; Boulton and Lloyd 1992; Tockner et al. 2000), it is reasonable to expect that the highly abundant small-bodied fishes <35 mm TL, most of which are shorter than length-at-age-1, forage in the near-shore zone providing further support that sandbars provide nursery for many riverine fishes.

The size-fitness hypothesis predicts that near-shore habitats of sandbar ATTZ should be dominated by larger (e.g., >35 mm TL) fishes if food resources are abundant there because fitness generally increases with body-size giving larger fishes a competitive foraging advantage over smaller fishes (Polis 1984; Griffiths 1992; Fore and Keckeis 1998; Jennings et al. 2001). However, the distribution of small-bodied fishes relative to body length at sandbar ATTZ does not support this prediction because CPUE decreased and fish mean length increased with increasing depth. Instead, other literature suggests that larger small-bodied fishes (e.g., >35 mm TL in this study) may avoid shallow nearshore areas because they experience higher risk from terrestrial predators (e.g., wading birds) (Angermeier and Karr 1983; Power 1984, 1987; Schlosser 1988, 1991, 1995), whereas smaller fishes (e.g., <35 mm TL in this study) generally do not experience such high terrestrial predation risk. Smaller fishes are less conspicuous (Blanckenhorn 2000), and require less time and distance to move their whole body outside of an approaching predator's gape during escape movements (Paglianti and Dornenici 2006). They may implement predator avoidance behavior such as dynamic shoaling where the structural

shape of the group changes (Kushlan 1981; Theodorakis 1989; Crowder et al. 1997; Landa 1998; Nøttestad and Axelsen 1999; Axelsen et al. 2001). The group may also disperse in response to threats (Eaton et al. 1977; Eaton and DiDomenico 1986; Pitcher and Turner 1986; Fuiman and Magurran 1994). The type and degree of behavioral reaction is relative to the immediate threat level (Helfman 1989; Brown et al. 2006). These adaptations to minimize predation risk among smaller fishes (<35 mm TL) may explain why they sustain high abundance relative to larger fishes in near-shore sandbar ATTZ.

Diel patterns of fishes at sandbar ATTZ

Distribution and abundance of small-bodied fishes relative to body length between light and dark diel periods appears to illustrate the trophic value of shallow near-shore habitat. Darkness may reduce predation risk from terrestrial piscivores to larger (e.g., >35 mm TL) fishes. Therefore, the increase in fish mean length observed during night suggests opportunistic habitat use to maximize the foraging rate-predation risk tradeoff (Werner et al. 1983; Mittelbach 1986; Jacobsen and Berg 1998; Werner and Hall 1988; Arrington and Winemiller 2003) where the motivation of larger fishes to move near-shore at night was to feed when predation risk was low. Juvenile Atlantic salmon (*Salmo salar*) switched to shallow foraging at night and retreated to refuge during the day in winter because escape speed from endothermic terrestrial predators was slower in cooler water temperature (Fraser et al. 1993). Lower nocturnal temperature at sandbar ATTZ may also partially explain the observed near-shore movement by larger fishes (70-105 mm TL) because metabolic costs of feeding and digestion may overcome energetic

gain of greater consumption if water temperature exceeds a critical threshold during the day (Diana 1995; Kestemont and Baras 2001). Nevertheless, an increase in fish abundance and length near-shore at night suggests higher competition and predation risk (from aquatic piscovores) for smaller fishes (<35 mm TL) that occupy this zone during the day.

The offshore zone may offer nocturnal benefits that mimic those experienced near-shore during the day; if so, fishes <35 mm TL should retreat offshore at night. First, smaller fishes should abandon the near-shore zone at night to escape predation or competition pressure from larger fishes. Second, predation risk should be relatively low offshore at night because: 1) many potential predators (i.e., larger fishes) have moved nearer to shore; 2) predator search time increases because prey body volume is small relative to greater water volume; and 3) its dark, which reduces efficiency of visual predators. However, the nocturnal near-shore increase in fish mean length does not provide strong evidence that diurnal near-shore fishes retreated to offshore habitats at night because the increase may be due to only the addition of longer fish, only the depletion of shorter fish, or a combination of both.

Results of length distribution in near-shore, moderate, and offshore habitat between diel period indicates that many fishes <35 mm TL did not perform a diel shift to the offshore habitat. Instead, it suggests that many fishes present in the near-shore zone during the day remained there at night. In addition, fish median body length decreased more dramatically in offshore habitat from light to dark period providing support for the conclusion that many larger fishes (>35 mm TL) moved in-shore and fewer smaller (<35 mm TL) diurnal near-shore fishes moved offshore at night. Therefore, the predation

buffer that apparently segregates smaller and larger fishes into near-shore and offshore habitats during the day (i.e., terrestrial predation risk) may be eliminated at night and may effectively reduce foraging, growth, and survival of diurnal near-shore age-0 fishes. However, results from DCA analysis show that smaller size fishes tend to disperse and larger fishes tend to group (i.e., with other large fishes) during the day. If this pattern holds true at night, the effective increase in competition and predation-risk to smaller fishes (<35 mm TL) may not follow a 1:1 ratio. That is, since smaller fishes (<35 mm TL) are much more abundant than larger fishes (>35 mm TL) (see also: Sheldon et al. 1972; Kozłowski and Gawelczyk 2002), and larger fishes tend to occur with similar sized individuals, the dispersal pattern shown by smaller fishes may mitigate increased competition and predation-risk if they occupy near-shore spaces not occupied by less abundant and more grouped larger fishes.

Schlosser (1988) experimentally confirmed Power's (1987) hypothesis that prey fishes select habitats to reduce predation risk from predatory fishes. However, he found that body size did not affect prey use of shallow vs. deep habitats between day and night in the presence of aquatic piscivores; likely because all prey-sized fish (hornyhead chub, *Nocomis bigutattus*, 60-110 mm TL) were vulnerable to the predator (smallmouth bass, *Micropterus dolomieui*, 282 ± 23 mm TL). Instead differential depth use occurred in the absence of bass (larger chubs used deeper water), and was attributed to terrestrial predation risk due to wading birds. Although Power (1987) and Schlosser (1988) drew their conclusions from small streams, results from sandbar ATTZ in the much larger LMOR agree well with their prediction of terrestrial-aquatic predator effect on the distribution and abundance of small-bodied fishes.

Depth-velocity profile of small-bodied fishes at sandbar ATTZ

I previously discussed the hypothesized role of terrestrial predation risk in the distribution of small-bodied fishes relative to water depth and body length at sandbar ATTZ. A similar body length pattern was observed relative to mean velocity used by species. Smaller size fishes may use slower velocity habitat (i.e., nearest to shore ATTZ) as flow refuge (Flore and Keckeis 1998). It is likely that depth and velocity interact to influence habitat use by fishes. Results from this analysis were inconclusive for whether depth or velocity was more important in structuring habitat use by fishes, but will be further discussed in Chapter 3.

The relative short mean length (<35 mm TL) in sandbar ATTZ of the five native minnows (sicklefin chub, sturgeon chub, speckled chub, plains minnow, sand shiner) concurrently monitored by USFWS supports the hypothesis that the main-channel provides function beyond a transportation highway for adults (Galat and Zweimüller 2001; Dettmers et al. 2001; King 2004b; Hirzinger et al. 2004). Reeves (2006) found that larvae of native *Macrhybopsis* spp. were more abundant at sandbar ATTZ than in deeper main channel habitats. Short mean body length for post larval sicklefin chub, sturgeon chub, speckled chub, plains minnow, and sand shiner in this study indicates that sandbars may be important habitat for early life stages of these fluvial species, and supports similar speculations by previous researchers who have worked on LMOR sandbar fishes (Jennings 1979; Grace 1985; Grace and Pflieger 1985; Gelwicks et al. 1996; Grady and Milligan 1998). These five species were all similar in body length yet differed in depth and velocity use. The differences may be directly related to habitat used by adults of

each species and ecomorphological pressure to rapidly develop adult morphologies to cope with unpredictable, short-term, wide fluctuations in flows characteristic of the preregulated LMOR. Small-bodied native minnows (e.g., Cyprinidae) with more streamlined body profiles, like sicklefin chub and sturgeon chub, use higher water velocity habitats than other species that are deeper bodied and poorly streamlined like common carp (*Cyprinus carpio*) and gizzard shad (*Dorosoma cepedianum*) (Welker 2000).

Adult sicklefin chub are known to use deeper, faster flowing waters in or near the navigation channel of LMOR (Starostka et al. 2005; Welker and Scaranecchia 2006) whereas adult plains minnow use shallower, slower habitats (Yu and Peters 2003; Starostka et al. 2005). Results from this study similarly show differential depth and velocity use by smaller sized (mean TL <35 mm) members of these two species. This suggests that native fluvial species evolved intraspecific ontogenetic niche separation to avoid conspecific competition between adults and age-0; and interspecies separation among similarly sized (e.g., <35 mm TL, age-0) fishes in areas where many species co-occur and compete for similar resources, such as in nursery habitat (Pease et al. 2006). Copp and Peňáz (1988) and Copp (1992) similarly reported that age-0 rheophilic species used swifter waters than age-0 limnophilic species.

Summary and conclusion

Evidence presented strongly suggests that many small-bodied fishes in LMOR use sandbar ATTZ as nursery during early life history. The reduction in abundance and increase in body length after August suggests that the age-0 fishes present before

September underwent ontogenetic habitat shifts to water deeper than 0.5 m or to other habitats away from sandbar ATTZ after August. Shallow near-shore areas provide environmental conditions that promote growth and survival of age-0 fishes in other large rivers and strongly suggest a similar nursery function on LMOR. This research shows that the concept of ATTZ is important and applicable within main-channel borders of large rivers. Fisheries management at sandbar ATTZ, and probably other ATTZ habitats in the main channel of large rivers, should consider the role of body length and include it in habitat restoration and native fish conservation planning processes. Sandbar ATTZ is a source of shallow, slow velocity main-channel habitat, analogous to off-channel nursery areas like tributary mouths, connected scour basins, and floodplains. Consequently, the sandbar ATTZ should be targeted for the conservation of native fluvial species that may not use floodplain ATTZ during early life history.

These results support extrapolation of the mechanism (i.e., predator-prey and competitive dynamics) that appears to drive the distribution of fishes relative to size from small streams to large-river ecosystems. Although others (e.g., Copp and Jurjada 1993; Baras and Nindaba 1999b; Wolter and Freyhof 2004) have reported similar distribution and abundance of fishes between light and dark diel periods, I did not find accounts in the literature on the effect of terrestrial-aquatic predator-prey interactions on the distribution and abundance of small-bodied fishes in larger rivers. Therefore, this research represents the first known documentation of a distributional pattern by fishes in an ATTZ nursery habitat within the main channel of a large floodplain river that is consistent with a distribution pattern known to be influenced by an aquatic-terrestrial predator-prey interaction. Future study is needed to quantify the effect of terrestrial predators on depth

distributions of sandbar ATTZ fishes and determine if other nocturnal predators (e.g., mammals, night herons) hunt the near-shore zone. In addition, work is needed to quantify the effect of higher nocturnal near-shore abundance of larger fishes (>35 mm TL), to determine their role as predators or competitors, and their effects on growth and survival of smaller (<35 mm TL) small-bodied fishes.

Literature Cited

- Angermeier, P. L. and J. R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. Environmental Biology of Fishes 9: 117-135.
- ArcGIS 9.1. 2005. ESRI. Redlands, CA.
- Arrington, D. A. and K. O. Winemiller. 2003. Diel changeover in sandbank fish assemblages in a neotropical floodplain river. Journal of Fish Biology 63: 442-459.
- Axelsen, B. E., T. Anker-Nilssen, P. Fossu, C. Kvamme, and L. Nøttestad. 2001. Pretty patterns but a simple strategy: predator-prey interactions between juvenile herring and Atlantic puffins observed with multibeam sonar. Canadian Journal of Zoology 79: 1586-1596.
- Bain, M. B. and J. T. Finn. 1991. Analysis of microhabitat use by fish: investigator effect and investigator bias. Rivers 2(1): 57-65.
- Bain, M. B., J. T. Finn and H. E. Booke. 1985. A quantitative method for sampling riverine microhabitats by electrofishing. North American Journal of Fisheries Management 5: 489-493.
- Baras, E. 1995. An improved electrofishing methodology for assessment of habitat use by young-of-the-year fishes. Archiv für Hydrobiologie 134: 403-415.
- Baras, E. and J. Nindaba. 1999a. Seasonal and diel utilization of inshore microhabitats by larvae and juvenile of *Leuciscus cephalus* and *Leuciscus leuciscus*. Environmental Biology of Fishes 56: 183-197.
- Baras, E. and J. Nindaba. 1999b. Diel dynamics of habitat use by riverine young-of-the year *Barbus baubus* and *Chondrostoma nasus* (Cyprinidae). Archiv für Hydrobiologie 146: 431-448.
- Bischoff, A. and J. Freyhof. 1999. Seasonal shifts in day-time resource use of 0+ barbel, *Barbus barbus*. Environmental Biology of Fishes 56: 199-212.
- Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? The Quarterly Review of Biology 75: 385-407.
- Bonner, T. H. and G. R. Wilde. 2002. Effects of turbidity of prey consumption by prairie stream fishes. Transactions of the American Fisheries Society 131: 1203-1208.
- Boulton, A. J. and L. N. Lloyd. 1992. Flooding frequency and invertebrate emergence

- from dry floodplain sediments of River Murray, Australia. Regulated Rivers Research and Management 7: 137-151.
- Bowen, Z. H., K. D. Bovee, and T. J. Waddle. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. Transactions of the American Fisheries Society 132: 809-823.
- Brewer, S. K., C. F. Rabeni, and D. C. Heimann. 2005. The importance of day versus night fish sampling for instream flow determinations. Proc. Annu. Conference. SEAFWA 59: 336-347.
- Brown, D. J. and T. G. Coon. 1994. Abundance and assemblage structure of fish larvae in the lower Missouri River and its tributaries. Transactions of the American Fisheries Society 123: 718-732.
- Brown, J. H. and B. A. Maurer. 1986. Body size, ecological dominance and Cope's rule. Nature 324(2): 248-250.
- Brown, G. E., A. C. Rive, M. C. O. Ferrari, and D. P. Chivers. 2006. The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. Behavioral Ecology and Sociobiology 61: 9-16.
- Dettmers, J. M., D. H. Wahl, D. A. Soluk and S. Gutreuter. 2001. Life in the fast lane: fish and foodweb structure in the main channel of large rivers. Journal of the North American Benthological Society 20: 255-265.
- Chará, J. D., D. J. Baird, T. C. Telfer, and E. A. Rubio. 2006. Feeding ecology and habitat preferences of the catfish genus *Trichomycterus* in low-order streams of the Colombian Andes. Journal of Fish Biology 68: 1026-1040.
- Childs, M. R., R. W. Clarkson and A. T. Robinson. 1998. Resource use by larval and early juvenile native fishes in the Little Colorado River, Grand Canyon, Arizona. Transactions of the American Fisheries Society 127: 620-629.
- Copp, G. H. 1992. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. Environmental Biology of Fishes 33: 181-193.
- Copp, G. H., G. Guti, B. Rovny and J. Cerny. 1994. Hierarchical analysis of habitat use by 0+ juvenile fish in Hungarian/Slovak floodplain of the Danube River. Environmental Biology of Fishes 40: 329-348.
- Copp, G. H. and P. Jurajda. 1993. Do small riverine fish more inshore at night? Journal of Fish Biology 43(Suppl. A): 229-241.

- Copp, G. H. and M. Peňáz. 1988. Ecology of fish spawning and nursery zones in the floodplain, using a new sampling approach. Hydrobiologia 169: 209-224.
- Cowx, I. G., A. D. Nunn, and J. P. Harvey. 2001. Quantitative sampling of 0-group fish populations in large lowland rivers: point abundance sampling by electric fishing versus micromesh seine netting. Archiv für Hydrobiologie 151: 369-382.
- Crowder, L. B., D. D. Squires, and J. A. Rice. 1997. Nonadditive effects of terrestrial and aquatic predators on juvenile estuarine fish. Ecology 78: 1796-1804.
- Culp, J. M. 1989. Nocturnally constrained foraging of a lotic minnow (*Rhinichthys cataractae*). Canadian Journal of Zoology 67: 2008-2012.
- Delong, M. D. and J. H. Thorp. 2006. Significance of instream autotrophs in trophic dynamics of the Upper Mississippi River. Oecologia 147: 76-85.
- Dettmers, J. M., D. H. Wahl, D. A. Soluk and S. Gutreuter. 2001. Life in the fast lane: fish and foodweb structure in the main channel of large rivers. Journal of the North American Benthological Society 20(2): 255-265.
- Diana, J. S. 1995. Biology and ecology of fishes. Cooper Publishing Group LLC, USA.
- Dolan, C. R. and L. E. Miranda. 2003. Immobilization thresholds of electrofishing relative to fish size. Transactions of the American Fisheries Society 132: 969-976.
- Dolloff, C. A., P. A. Flebbe, and M. D. Owen. 1994. Fish habitat and fish populations in a southern Appalachian watershed before and after Hurricane Hugo. Transactions of the American Fisheries Society 123: 668-678.
- Eaton, R. C. and R. DiDomenico. 1986. Role of teleost escape response during development. Transactions of the American Fisheries Society 115: 128-142.
- Eaton, R. C., R. A. Bombardieri, and D. L. Meyer. 1977. The Mauthner-initiated startle response in Teleost fish. Journal of Experimental Biology 66: 65-81.
- Ellis, J. M., G. B. Farabee and J. B. Reynolds. 1979. Fish communities in three successional stages of side channels in the upper Mississippi River. Transactions of the Missouri Academy of Sciences 13: 5-20.
- Fisher, W. L. and M. E. Brown. 1993. A prepositioned areal electrofishing apparatus for sampling stream habitats. North American Journal of Fisheries Management 13: 807-816.
- Flore, L. and H. Keckeis. 1998. The effect of water current on foraging behaviour of the rheophilic cyprinid *Chondrostoma nasus* (L.) during ontogeny: evidence of a

- trade-off between energetic gain and swimming costs. Regulated Rivers: Research and Management 14: 141-154.
- Fraser, N. H. C., N. B. Metcalfe, and J. E. Thorpe. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Proceedings of the Royal Society of London Series B 252: 135-139.
- Freeman, M. C., Z. H. Bowen, K. D. Bovee, and E. R. Irwin. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. Ecological Applications 11: 179-190.
- Fuiman, L. A. and A. E. Magurran. 1994. Development of predator defenses in fishes. Reviews in Fish Biology and Fisheries 4: 145-183.
- Funk, J. L. and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series Report 11. Jefferson City.
- Galat, D.L., C.R. Berry, W.M. Gardner, J.C. Hendrickson, G.E. Mestl, G.J. Power, C. Stone, and M.R. Winston. 2005. Spatiotemporal patterns and changes in Missouri River fishes. American Fisheries Society Symposium 45: 249-291.
- Galat, D. L., L. H. Fredrickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, G. T. Gelwicks, J. E. Havel, D. L. Helmers, J. B. Hooker, J. R. Jones, M. F. Knowlton, J. Kubisiak, J. Mazourek, A. C. McColpin, R. B. Renken and R. D. Semlitsch. 1998. Flooding to restore connectivity of regulated, largeriver wetlands. Bioscience 48: 721-733.
- Galat, D. L., G. W. Whitledge, L. D. Patton, and J. Hooker. 2004. Larval fish use of lower Missouri River scour basins in relation to connectivity. Final Report to Missouri Department of Conservation, Columbia, MO.
- Galat, D. L., M. L. Wildhaber, and D. J. Dieterman. 2001. Spatial patterns of physical habitat. Volume 2. Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U.S. Geological Survey, Cooperative Research units, University of Missouri, 302 ABNR Bldg, Columbia, Missouri 65251-7240.
- Galat, D. L. and I. Zweimüller. 2001. Conserving large-river fishes: is the highway analogy an appropriate paradigm? Journal of the North American Benthological Society 20: 266-279.
- Garner, P. 1996. Microhabitat use and diet of 0+ cyprinid fishes in a lentic, regulated reach of the river Great Ouse, England. Journal of Fish Biology 48: 367-382.

- Garner, P. 1997. Seasonal variation in the habitat available for 0+ *Rutilus rutilus* (L.) in a regulated river. Aquatic Conservation: Marine and Freshwater Ecosystems 7: 199-210.
- Gelwicks, G. T., K. Graham and D. L. Galat. 1996. Status survey for sicklefin chub, sturgeon chub, and flathead chub in the Missouri River, Missouri. Final Report. Missouri Department of Conservation, Columbia, MO. 23p.
- Grace, T. B. 1985. The status and distribution of commercial and forage fish in the Missouri river and their utilization of selected habitats: Evaluation of sand island habitat in the Missouri River. Final Report. Missouri Department of Conservation, Columbia, MO. National Marine Fisheries Service Program 2-363-R, Project IV, Job II. 34p.
- Grace, T. B. and W. L. Pflieger. 1985. Fish survey of the Missouri and Mississippi rivers. Missouri Department of Conservation, Columbia, Missouri. National Marine Fisheries Service Program 2-363-R, Project IV, Job I. 56pp.
- Grady, J. M. and J. Milligan. 1998. Status of Selected cyprinid species at historic lower Missouri River sampling sites. U.S. Fish and Wildlife Service Report, Columbia Fisheries Resource Office, Columbia, MO.
- Gries, G., K. G. Whalen, F. Juanes, and D. L. Parrish. Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of a diel activity partitioning. Canadian Journal of Fisheries and Aquatic Sciences 54: 1408-1413.
- Griffiths, D. 1992. Size, abundance, and energy use in communities. Journal of Animal Ecology 61: 307-315.
- Grift, R. E., A. D. Buijse, W. L. T. Van Densen, M. A. M. Machiels, J. Dranenbarg, J. G. P. Klein Breteler and J. J. G. M. Backx. 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. River Research and Applications 19: 353-374.
- Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116: 851-855.
- Hay, C. H. 2006. Fish and invertebrate abundance in relation to abiotic factors in the Missouri River. Doctoral dissertation. University of Nebraska, Lincoln, Nebraska.
- Helfman, G. S. 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. Behavioral Ecology and Sociobiology 24: 47-58.
- Hesse, L. W. 2004. Length at age for selected fish species of the middle Missouri River:

- performance report to facilitate the use of non-aged fish data in the MRHD for modeling year-class indices. Prepared for The Missouri River Natural Resources Committee Biomonitoring and Assessment Program. Rivers Corporation, Inc. Crofton, NE. 21p.
- Hirzinger, V., H. Keckeis, H. L. Nemeschkal, and F. Schiemer. 2004. The importance of inshore areas for adult fish distribution along a free-flowing section of the Danube, Austria. River Research and Applications 20: 137-149.
- Hutchinson, G.E. and R.H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. The American Naturalist 93: 117-125.
- Jacobsen, L. and S. Berg. 1998. Diel variation in habitat use by planktivores in field enclosure experiments: the effect of submerged macrophytes and predation. Journal of Fish Biology 53: 1207-1219.
- Janáč, M., and P. Jurajda. 2005. Inter-calibration of three electric fishing techniques to estimate 0+ juvenile fish densities on sandy river beaches. Fisheries Management and Ecology 12: 161-167.
- Jennings, D. K. 1979. An evaluation of aquatic habitat associated with notched dikes on the Missouri River, Missouri. Master's Thesis. University of Missouri, Columbia, Missouri.
- Jennings, S., J.K. Pinnegar, N.V.C. Polunin, and T.W. Boon. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. Journal of Animal Ecology 70: 934-944.
- Johnson, S. L. and A. P. Covich. 2000. The importance of night-time observations for determining habitat preferences of stream biota. Regulated Rivers: Research and Management 16: 91-99.
- Junk, W. J., P. B. Bayley and R. E. Sparks. 1989. The flood pulse concept in riverfloodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences Ottawa 106: 110-127.
- Jurajda, P. 1999. Comparative nursery habitat use by 0+ fish in a modified lowland river. Regulated Rivers: Research and Management 15: 113-124.
- Keckeis, H., E. Kamler, E. Bauer-Nemeschkal and K. Schneeweiss. 2001. Survival, development and food energy partitioning of nase larvae and early juveniles at different temperatures. Journal of Fish Biology 59: 45-61.
- Kerr, S.R. 1989. The switch to size. Environmental Biology of Fishes 24: 157-159.
- Kestemont, P. and E. Baras. 2001. Environmental factors and feed intake: mechanisms

- and interactions. Pages 131-156 *in* D. Houlihan, T. Boujard, and M. Jobling, editors. Food intake in fish. Blackwell Science Ltd., London.
- King, A. J. 2004a. Ontogenetic patterns of habitat use by fishes within the main channel of an Australian floodplain river. Journal of Fish Biology 65: 1582-1603.
- King, A. J. 2004b. Density and distribution of potential prey for larval fishes in the main channel of a floodplain river: pelagic versus epibenthic meiofauna. River Research and Applications 20: 883-897.
- Kneib, R. T. 1987. Predation risk and use of intertidal habitats by young fishes and shrimp. Ecology 68: 379-386.
- Kozłowski, J. and A.T. Gawelczyk. 2002. Why are species' body size distributions usually skewed to the right? Functional Ecology 16: 419-432.
- Kushlan, J. A. 1981. Resource us strategies of wading birds. Wilson Bulletin 93: 145-163.
- Lancaster, J. 1999. Small-scale movements of lotic macroinvertebrates with variations in flow. Freshwater Biology 41: 605-619.
- Lancaster, J. 2000. Geometric scaling of microhabitat patches and their efficacy as refugia during disturbance. Journal of Animal Ecology 69: 442-547.
- Lancaster, J. L. and A. G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. Journal of the North American Benthological Society 12: 385-393.
- Landa, J. T. 1998. Bioeconomics of schooling fishes: selfish fish, quasi-free riders, and other fishy tales. Environmental Biology of Fishes 53: 353-364.
- Lee, J. F. 2007. Community composition and microhabitats of macroinvertebrates on sandbars within the lower Missouri River as a food source for foraging migratory shorebirds. Masters Thesis. South Dakota State University, Brookings, SD.
- McMahon, T. E., A. V. Zale, and D. J. Orth. 1996. Aquatic Habitat Measurements. Pages 83-120 *in* B. R. Murphy and D. W. Willis, editors. Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Mittelbach, G. 1986. Predator-mediated habitat use: some consequences for species interactions. Environmental Biology of Fishes 16: 159-169.
- Nøttestad, L. and B. E. Axelsen. 1999. Herring schooling manoeuvres in response to killer whale attacks. Canadian Journal of Zoology 77: 1540-1546.

- Nunn, A. D., I. G. Cowx, P. A. Frear, and J. P. Harvey. 2003. Is water temperature an accurate predictor of recruitment success in cyprinid fish populations in lowland rivers? Freshwater Biology 48: 579-588.
- Nunn, A. D., J. P. Harvey, and I. G. Cowx. 2007. Benefits to 0+ fishes of connecting man-made waterbodies to the lower River Trent, England. River Research and Applications 23: 361-376.
- Paglianti, A. and P. Domenici. 2006. The effect of size o the timing of visually mediated escape behavior in staghorn scuplin *Leptocottus armatus*. Journal of Fish Biology 68: 1177-1191.
- Pavlov, D. S. 1994. The downstream migration of young fishes in rivers: mechanisms and distribution. Folia Zoologica 46: 193-208.
- Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Transactions of the American Fisheries Society 121: 427-436.
- Pease, A. A., J. J. Davis, M. s. Edwards, and T. F. Turner. 2006. Habitat and resource use by larval and juvenile fishes in an arid-land river (Rio Grande, New Mexico). Freshwater Biology 51: 475-486.
- Peters, E. J., R. S. Holland, M. A. Callam and D. L. Bunnell. 1989. Platte River suitability criteria: habitat utilization, preference and suitability index criteria for fish and aquatic invertebrates in the Platte River. Federal Aid in Fish Restoration Project No. F-78-R Study III: Job III-2. University of Nebraska, Lincoln.
- Pflieger, W. L. 1997. The fishes of Missouri, revised edition. Missouri Department of Conservation, Jefferson City.
- Pierce, C. L., C. S. Guy, P. J. Braaten and M. A. Pegg. 2003. Fish growth, mortality, recruitment, condition, and size structure. Volume 4. Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U.S. Geological Survey, Cooperative Research Units, Iowa State University, Science Hall II, Ames, Iowa 50011.
- Pitcher, T. J. and J. R. Turner. 1986. Danger at dawn: experimental support for the twilight hypothesis in shoaling minnows. Journal of Fish Biology 29 (Suppl. A): 59-70.
- Poizat, G. and D. Pont. 1996. Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. Freshwater Biology 36: 611-622.
- Polis, G.A. 1984. Age structure component of niche width and intraspecific resource

- partitioning: can age groups function as ecological species? The American Naturalist 123: 541-564.
- Power, M. E. 1984. Depth distributions of armored catfish: predator-induced resource avoidance? Ecology 65: 523-528.
- Power, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pages 333-351 *in* W.C. Kerfoot and A. Sih, editors. Predation. Direct and indirect effects on aquatic communities. University Press of New England, Hanover, NH.
- Pratt, T. C. and M. G. Fox. 2001. Biotic influences on habitat selection by young-of-year walleye (*Stizostedion vitreum*) in the demersal stage. Canadian Journal of Fisheries and Aquatic Sciences 58: 1058-1069.
- Propst, D. L. and K. B. Gido. 2004. Responses of native and nonnative fishes to natural flow regime mimicry in the San Juan River. Transactions of the American Fisheries Society 133: 922-931.
- Quist, M. C., W. A. Hubert and F. J. Rahel. 2004. Relations among habitat characteristics, exotic species, and turbid-river cyprinids in the Missouri River drainage of Wyoming. Transactions of the American Fisheries Society 133: 727-742.
- Reeves, K. 2006. Use of main channel and shallow-water habitats by larval fishes in the lower Missouri River. Doctoral dissertation. University of Missouri, Columbia, Missouri.
- Rempel, L. L., J. S. Richardson, and M. C. Healey. 1999. Flow refugia for benthic macroinvertebrates during flooding of a large river. Journal of the North American Benthological Society 18: 34-48.
- Reynolds, J. B. 1996. Electrofishing. Pages 221-253 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Reynolds, J. B. 2000. Electrofishing Theory. Pages 3-23 *in* S.M. Allen-Gil, editor. New Perspectives in Electrofishing. U.S. Environmental Protection Agency.
- Rodríguez, M. A. and W. M. Lewis. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. Ecological Monographs 67: 109-128.
- Roussel, J-M. and A. Bardonnet. 1999. Ontogeny of diel pattern of stream-margin habitat use by emerging brown trout, *Salmo trutta*, in experimental channels: influence of food and predator presence. Environmental Biology of Fishes 56:

253-262.

- Robertson, A. L. 1990. The population dynamics of Chydoridae and Macrothricidae (Cladocera: Crustacea) from the River Thames, U.K. Freshwater Biology 33: 469-484.
- Roff, D. 1981. On being the right size. The American Naturalist 118: 405-422.
- Sappington, L., D. Dieterman, and D. Galat. Editors. 1998. 1998 Standard operating procedures to evaluate population structure and habitat use of benthic fishes along the Missouri and Lower Yellowstone Rivers. Missouri River Benthic Fish Consortium, USGS-BRD, Columbia Environmental Research Center, 4200 New Haven Rd., Columbia, Missouri 65201.
- SAS. 2004. SAS/STAT 9.1 users guide. SAS Institute. Cary, NC.
- Scholten, M. 2003. Efficiency of point abundance sampling by electro-fishing modified for short fishes. Journal of Applied Ichthyology 19: 265-277.
- Schlosser, I. J. 1988. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. Oikos 52: 36-40.
- Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience 41: 704-713.
- Schlosser, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303: 71-81.
- Schwartz, J. S. and E. E. Herricks. 2004. Use of prepositioned areal electrofishing devices with rod electrodes in small streams. North American Journal of Fisheries Management 24: 1330-1340.
- Sheldon, R.W., A. Prakash, and W.H. Sutcliffe, Jr. 1972. The size distribution of particles in the ocean. Limnology and Oceanography 17: 327-340.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129-1157.
- Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. Regulate Rivers: Research and Management 12: 391-413.
- Starostka, A., N. Frohnauer, W. Doyle, and T. Hill. 2005. Habitat assessment and monitoring program: initial year of biological monitoring. 2005 Annual Report. U.S. Fish and Wildlife Service-Columbia Fisheries Resource Office, Columbia, MO.

- Steel, R. G. D., J. H. Torrie, and D. A. Dickey. 1996. Principles and procedures of statistics: a biometrical approach, 3rd edition. McGraw-Hill, New York.
- Strange, E. M., P. B. Moyle, and T. C. Foin. 1993. Interactions between stochastic and deterministic processes in stream fish community assembly. Environmental Biology of Fishes 36: 1-15.
- ter Braak, C. J. F. and P. Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination, version 4.5. Microcomputer Power, Ithaca, New York.
- Tibbs, J. E. and D. L. Galat. 1997. Larval, juvenile, and adult small fish use of scour basins connected to the lower Missouri River. Final Report to Missouri Department of Conservation, Columbia, MO.
- Theodorakis, C. W. 1989. Size segregation and the effects of oddity on predation risk in minnow schools. Animal Behaviour 38: 496-502.
- Thorp, J. H. and S. Mantovani. 2005. Zooplankton of turbid and hydrologically dynamic prairie rivers. Freshwater Biology 50: 1474-1491.
- Tockner, K., F. Malard, and J.V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes 14: 2861-2883.
- Tracy-Smith, E. 2006. Relation of Missouri River flows to sandbar morphology with implications for selected biota. Master's Thesis. University of Missouri, Columbia, Missouri.
- Webb, P. W. and D. Weihs. 1986. Functional locomotor morphology of early life history stages of fishes. Transactions of the American Fisheries Society 115: 115-127.
- Welker, T. L. 2000. Ecology and structure of fish communities in the Missouri and lower Yellowstone rivers. Ph.D. Dissertation, University of Idaho. Volume 12 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. Available: https://www.nwo.usace.army.mil//html/pd-e/benthic_fish/volume12.pdf.
- Welker, T. L. and D. L. Scarnecchia. 2006. River alteration and niche overlap among three native minnows (Cyprinidae) in the Missouri River hydrosystem. Journal of Fish Biology 68: 1530-1550.
- Werner, E. E. and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352-1366.

- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittlebach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.
- Whitledge, G. W., D. L. Galat, and G. T. Gelwicks. 2005. Habitat use by fishes in periodically and continuously connected lower Missouri River floodplain water bodies. Final Report to Missouri Department of Conservation, Columbia, MO.
- Wolter, C. and J. Bischoff. 2001. Seasonal changes of fish diversity in the main channel of the large lowland river Oder. Regulated Rivers: Research and Management 17: 595-608.
- Wolter, C. and J. Freyhof. 2004. Diel distribution patterns of fishes in a temperate large lowland river. Journal of Fish Biology 64:632-642.
- Yu, S-L. and E. J. Peters. 2003. Diel and seasonal abundance of fishes in the Platte River, Nebraska, USA. Fisheries Science 69: 154-160.

CHAPTER III

Effect of Spatiotemporal and Environmental Factors on Small-bodied Fish
Assemblage Composition at Sandbar ATTZ on Lower Missouri River

Introduction

Ecologists quantitatively describe how organisms interact with each other and with their environment. Biotic and abiotic ecosystem components interact to create a large and complex pool of factors that affect fish assemblage dynamics (Hansen and Leggett 1985; Frissell et al. 1986; Wiens 1989; Tonn 1990; Tilman 1994; Aday et al. 2003). An objective of many studies on multi-species assemblages is to determine what factors are primarily responsible for observed variation in assemblage composition by quantifying the contribution of measured environmental factors (Rodríguez and Magnan 1995; ter Braak and Verdonschot 1995; Barko et al. 2004; Arrington and Winemiller 2006). Results of such studies provide managers with information to improve design and implementation of fish and habitat restoration programs.

Studies of organism-environment interactions were popularized with taxon-based approaches (Kerr 1989). However, Hutchinson and MacArthur (1959) were among early pioneers to realize the value of including more ecologically relevant criteria to describe the ecology of organisms. Today, fishes are known to group relative to a number of factors including species, body length, sex, parasite infection status, and recognition of familiar individuals (Hoare and Krause 2003). The role of body size has increasingly become a focus of studies on ecosystem (Sheldon et al. 1972), community (Griffiths 1992; Jennings et al. 2001; Woodward and Hildrew 2002), assemblage (Meffe and

Sheldon 1988; Krause et al. 1996; Chapter 2), and species level (Wilson 1975; Polis 1984; Allan and Pitcher 1986; Arendt and Wilson 1997) ecology.

Larger-sized fishes acquire more resources than smaller fishes, are less affected by extreme environmental conditions, and are less vulnerable to predators (Brown and Maurer 1986; Sogard 1997). In contrast, evolutionarily successful species tend towards smaller body size because they require fewer resources, have higher population densities, and shorter generation times (Pettersson et al. 1996; Blanckenhorn 2000; Kozłowski and Gawelczyk 2002). These life-history features allow small-bodied populations or species to survive periods of low resource availability, survive catastrophic events that may lead to extinction of lower density populations, produce more generations over the same time period and therefore adapt faster to changing environments (Brown and Maurer 1986; Kozlowski and Gawelczyk 2002).

Natural system processes conform to a hierarchical framework in which lower level factors operate within the constraints of higher level filters (Frissell et al. 1986; Tonn 1990; Wiens 1989; Wu and Loucks 1995; Poff 1997). Species and fish assemblages often reflect the influences of higher level filters through adaptation of traits in the former, or variation in composition in the latter (Lord and Norton 1990; Tonn 1990; Townsend and Hildrew 1994). Spoljaric and Reimchen (2007) found that body shape differed among isolated, but adjacent, populations of three-spined stickleback (*Gasterosteus aculeatus* L.). Populations in large, deep, clear lakes had more streamlined bodies (less derived, ancestral form) reducing drag during steady swimming and improved open-water foraging. In contrast, populations confined to small, shallow, stained ponds with greater habitat heterogeneity and shorter distance to travel while

foraging had a deeper, less streamlined, body shape. There, each population operated within the constraints imposed by the lake-type level filter, effecting habitat heterogeneity, which modified foraging strategy, and thus body shape.

A hierarchical paradigm applied to the role of body size in ecology provides support to the size-based evolutionary model discussed previously. Larger species have progressively slower phenotypic plasticity, slower adaptive capability, and are atop the size hierarchy; smaller species respond faster to environmental change and are lower in the hierarchy. Consistent with hierarchy theory, large species (i.e., high level filters) impose constraints on smaller species (i.e., low level factors; e.g., predation), and smaller species persist to provide the building blocks (e.g., forage base) for higher levels of organization.

A growing number of studies have examined small-bodied fish habitat use in off-channel areas of large river-floodplain systems, and many look for habitat associations of species to drive fisheries restoration. Depth, flow velocity, and temperature are generally cited as factors influencing the distribution and abundance of age-0 fishes in river floodplains (Copp and Peňáz 1988; Copp 1992; Copp et al. 1994; Poizat and Pont 1996; Jurajda 1999; Langler and Smith 2001; Grift et al. 2003). Only recently have researchers recognized the importance of main-channel habitats for fluvial specialists species that do not use floodplains in their life history (Dettmers et al. 2001; Galat and Zweimüller 2001; King 2004). Barko et al. (2004) found that some young-of-the-year fishes were associated with main channel borders on the unimpounded upper Mississippi River. Understanding how main-channel habitats are used as building blocks of river ecology is important for large river fisheries restoration.

I reported in the previous chapter that lower Missouri River (LMOR) sandbar ATTZ was used by many small-bodied fishes and that the assemblage was organized along a body length gradient. Here I determine what external factors were most influential in structuring the small-bodied fish assemblage at sandbar ATTZ. Since fisheries managers generally operate under a species-based paradigm, it is useful to report how the small-bodied fish assemblage was structured relative to external factors for both species composition and body length organized assemblages. I partitioned external factors into two categories: 1) spatial and temporal, hereafter collectively called spatiotemporal, and 2) discrete environmental factors. Spatiotemporal categories included sandbar type (point, wing-dike sandbar), region (head, upstream primary, downstream primary, upstream secondary, downstream secondary, tail), sample unit (near-shore, moderate, offshore), month (July, August, September, October), and diel period (light, dark). Discrete environmental factors included those considered in Chapter 2: depth, velocity, temperature, turbidity, substrate particle size, slope, and, shoreline sinuosity, plus weather. Local weather conditions may affect proximate distribution of small-bodied fishes. Direct sunshine (i.e., no clouds) on shallow areas warms water at a faster rate, gives potential for greater primary productivity, and may support a greater density of foraging small-bodied fishes. High winds may increase wave amplitude, increase turbidity thereby decreasing predation risk, and re-suspend coarse organic materials as forage for small-bodied fishes, or transform a calm, benign environment into a turbulent unfavorable habitat for age-0 fishes. Rain may introduce new coarse organic material into shallow areas as forage to small-bodied fishes.

My objective was to quantify the interactions between small-bodied fishes and their environment and determine the relative contributions of spatiotemporal and environmental factors explaining the observed variation in the small-bodied fish assemblage composition organized by (1) species and (2) body length. This objective addresses three questions: (1) Do spatiotemporal and environmental factors equally explain the variation in species and body length assemblages? (2) What factor, or suite of factors, explains the most variation in composition for each assemblage type? (3) Are assemblage structure and habitat use more completely explained by the species or body length dataset?

Study Area

This study occurred along a 128-km reach of LMOR in central Missouri between the confluences of Moniteau Creek (rkm 254) and Chariton Creek (rkm 381) with Missouri River (river kilometers begin at zero and increase upstream from the confluence with Mississippi River; Figure 2.1). I selected eight sandbars, four point bars and four wing-dike bars, within this reach. These two sandbar types were selected because they compose 98% of LMOR sandbars in the study area (Reeves 2006) and were likely to have connected secondary channels during the period July-October (Reeves 2006; Tracy-Smith 2006). Mean distance between sandbars was 15.9 km; the furthest distance between adjacent sandbars was 35.4 km from Petite Saline sandbar (rkm 285) to Boonville sandbar (rkm 320), shortest distance was 3.2 km from Marion sandbar (rkm 253) to Hartsburg sandbar (rkm 256).

Methods

Fishes were collected within a hierarchical spatial sampling design using a prepositioned aerial electrofishing device (PAED) from July to October 2005 in sandbar ATTZ (water depth 0.0-0.5 m) on LMOR. The hierarchical spatial design was composed of three levels: 1) entire sandbars represented the largest spatial extent, 2) next, sandbars were decomposed into regions representing an intermediate level, and 3) the finest resolution was represented by three sample unit categories (near-shore, moderate, and offshore). Environmental factors were measured at each PAED after fishes were sampled, these included: depth, velocity, water temperature, turbidity, slope, shoreline sinuosity, substrate composition, and weather. See Chapter 2 for details on sampling design, PAEDs and fish sampling technique, and environmental data collection (except weather, see next paragraph).

Weather was classified into at least one, and up to three, of five binary categories based on my observation at the time each sample was collected as follows: sunny, partly cloudy, cloudy, raining, windy. I used the Beaufort wind speed scale (Table 3.1; NOAA 2007) to estimate wind speeds as being greater than (true = 1) or less than or equal to (false = 0) force 4 (13-18 mph). Clearly it is possible for rain and or wind to be combined with sunny, partly cloudy, or cloudy; however, not possible for sunny, partly cloudy, or cloudy to be combined with each other.

Table 3.1. Beaufort scale used to visually estimate wind speed.

	7	Wind	Appearance of wind effects		
Force	(mph)	Class	on water	on land	
0	<1	Calm	Surface smooth and mirror-like	Calm, smoke rises vertically	
1	1-3	Light Air	Scaly ripples, no foam crests	Smoke drift indicates wind direction, still wind vanes	
2	4-7	Light Breeze	Small wavelets, crests glassy, no breaking	Wind felt on face, leaves rustle, vanes begin to move	
3	8-12	Gentle Breeze	Large wavelets, crests begin to break, scattered whitecaps	Leaves and small twigs constantly moving, light flags extended	
4	13-18	Moderate Breeze	Small waves 1-4 ft. becoming longer, numerous whitecaps	Dust, leaves, and loose paper lifted, small tree branches move	
5	19-24	Fresh Breeze	Moderate waves 4-8 ft taking longer form, many whitecaps, some spray	Small trees in leaf begin to sway	
6	25-31	Strong Breeze	Larger waves 8-13 ft, whitecaps common, more spray	Larger tree branches moving, whistling in wires	
7	32-38	Near Gale	Sea heaps up, waves 13-20 ft, white foam streaks off breakers	Whole trees moving, resistance felt walking against wind	

Dataset Selection

Two datasets were created to compare the effects of spatiotemporal and environmental factors between species and body length assemblages: 1) a taxonomic dataset wherein fish were identified to species (Pflieger 1997) and the unit of measure was number of fish per cubic meter of water, hereafter called catch-per-unit-effort (CPUE, #/m³) per species; and 2) a body-length dataset in which fishes were measured (mm TL). Individuals within the body length dataset were categorized into 5-mm length

classes and labeled with respect to the low value from each length class range. Fishes with body length in the range 5-9 mm were labeled as length class '5', 10-14 mm were labeled as length class '10', and so on. Unit of measure for the body-length dataset was CPUE (#/m³) per 5-mm length class.

Both datasets here were the same as those used to test assemblage organization in Chapter 2. These included number of fish per cubic meter of water only from species or length classes collected in 2005 from emergent sandbars that were not collected in a tertiary channel, were ≤ 105 mm TL, and that occurred in at least 1% (n > 9) of the samples. Each dataset was constrained by a common set of factors (spatiotemporal and environmental) to compare their responses to ordination.

Data Processing

All spatiotemporal and five of the twelve environmental factors (e.g., weather) were categorical and therefore dummy coded according to ter Braak and Šmilauer (2002) for multivariate analysis. Temporal factors were coded by month (i.e., July, August, September, October) and diel period (i.e., light, dark); spatial factors by sandbar (i.e., point bar *PB*, wing-dike bar *WD*), region (i.e., head *HR*, upstream primary *UP*, upstream secondary *US*, downstream primary *DP*, downstream secondary *DS*, tail *TR*), and sample unit category (i.e., near-shore, moderate, offshore). Categorical environmental factors (i.e., sunny, partly cloudy, cloudy, raining, windy) were binary and coded as 1 (true) or 0 (false). Among continuous environmental factors, depth, velocity, turbidity, and slope were square root transformed to satisfy assumptions of normality (ter Braak and Šmilauer 2002).

Analyses

It was necessary to run a preliminary gradient analysis (detrended correspondence analysis, *DCA*) on each dataset (i.e., species, body length) to determine whether redundancy analysis (RA) or canonical correspondence techniques were appropriate to address my research questions (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). Gradient analysis with DCA produced gradient lengths greater than 4.0 SD on both datasets indicating that units (i.e., species, length classes) show strong unimodal response to gradients and that linear methods (e.g., RA) were not appropriate (ter Braak and Šmilauer 2002). Therefore, canonical correspondence analysis techniques were selected to address my research objective. CANOCO 4.5 (ter Braak and Šmilauer 2002) was used to perform analyses.

Explainable variation in assemblage composition was partitioned among spatiotemporal and environmental factors to identify the most parsimonious suite of factors accounting for assemblage composition variation. Total variation in the assemblage and the proportion of that total attributed to all factors (spatiotemporal and environmental) as one unit was first quantified for each dataset with canonical correspond analysis (CCA). Correlation coefficients were calculated among factors and the first two canonical axes to identify important factor-axis correlations, the three factors with the highest correlation for each axis was highlighted. Second, the proportional contribution of each factor to explain total assemblage variation was partitioned and quantified with partial canonical correspondence analysis (pCCA). Variation was partitioned

independently for each spatiotemporal (spatial = sandbar, region, sample unit; temporal = month, diel) and environmental factor.

I tested mean variance of continuous environmental factors against mean variance of spatiotemporal and binary environmental factors with the Student's t-test to determine if a possible bias of large variances among continuous relative to categorical factors influenced interpretation of CCA and pCCA results. If mean variance among continuous environmental factors was larger than among spatiotemporal factors, the true explanatory power of environmental factors may be underrepresented relative to that of spatiotemporal factors.

I report two measures for how variation in assemblage composition is partitioned by factor(s) or canonical ordination axes. (1) *Percent of total variation explained* (TVE) is the proportion of total assemblage variation attributable to a factor, suite of factors, or axis relative to the variation explainable by all factors; it can be summed over all factors (e.g., overall TVE) or axes and partitioned by specific factors or axes (e.g., axis-1 TVE). (2) *Partial percent of total variation explained* (pTVE) is the variation attributable to a factor, suite of factors, or axis relative to that explained by a larger subset of factors from which it is a member. Here the subset of factors will be all spatiotemporal and environmental factors combined where CCA is used, and spatiotemporal, environmental, or a group comprised of select factors from each subset where pCCA is used, and will be specified where each result is presented. Interactions terms are calculated by difference; small negative values result from calculation by difference and should be interpreted as approximately zero (Magnan et at. 1994; Rodríguez and Magnan 1995).

For example, if all factors (i.e., CCA) explained 18.8% of the assemblage variation (i.e., overall TVE), I would report what proportion of this 18.8% was attributable to axis-1 as follows: axis-1 TVE = 8.6%, axis-1 pTVE = 46.1%. That is, axis-1 TVE accounts for 8.6% of total assemblage composition variation leaving 10.1% to be explained by other axes; axis-1 pTVE accounts for slightly less than half (46.1%) of the TVE (i.e., 8.6%/18.8%) in assemblage composition.

Interpreting multivariate analysis bi-plots

The power of canonical ordination techniques is that they simultaneously consider many factors to represent their effects on a response variable (i.e., fish CPUE); a single plot of the data shows the relationships among factors, among fishes, and among factors and fishes. Factors are represented by arrows that point in the direction of increasing value and arrow length indicates its importance in ordination of fishes. Arrows also extend in the opposite direction (decreasing value) however they were not drawn to facilitate interpretation of plots. Arrows perpendicular to other arrows are not correlated; those pointing in similar direction are related. Species or length classes are represented by triangles and are positioned relative to factors (arrows) and other species or length classes (other triangles). The relationship between a species or length class and a factor is inferred by extending the factor arrow in the decreasing direction and drawing a perpendicular from the factor to a species or length class. Position of the intersect between the perpendicular and the factor arrow indicates whether the species or length class is associated with high or low values of the factor and is directly comparable to other species or length classes for that factor. Distance among triangles indicates their

similarity in distribution; those nearer each other tend to occur together in samples more often.

Results

The species organized dataset was composed of 25 species from 968 samples with 120 of the samples containing no fish meeting the inclusion criteria. The length organized dataset was composed of 19 length-classes from 968 samples with 129 of the samples containing no fish meeting the inclusion criteria. Species classes river carpsucker (*Carpiodes carpio*) and red shiner (*Cyprinella lutrensis*), and length classes 15 and 20, were numerically dominate in collections (Chapter 2, Table 2.13). See Chapter 2 for summaries of spatiotemporal and continuous environmental factors by month (Table 2.11; 2.12) and diel period (Table 2.5). Weather was sunny during fish collections for 65%, cloudy for 28%, and partly cloudy for 7% of sample units; rain occurred during 3% and it was windy during 10% of sample unit collections. Only bigmouth shiner, 31-mm (Hesse 2004), and sand shiner, 32-mm (Pierce et al. 2003) had estimates of length-at-age-1 <35 mm (Table 2.9).

Compared results of ordinations (CCA) show variability of the fish assemblage composition by species (λ = 7.861) was higher than variability by body length (λ = 3.482). The proportion of assemblage composition variation explained by spatiotemporal and environmental factors was higher in the body length (overall TVE = 30.1%) than in the species (overall TVE = 18.6%) dataset. Student's t-test showed mean variance of spatiotemporal factors (σ^2 = 0.13) was lower than mean variance of continuous environmental factors (σ^2 = 77.1, P = 0.006) but not different from the five binary (i.e.,

weather) environmental factors ($\sigma^2 = 0.10$, P = 0.308). Variances between spatiotemporal and environmental factors (continuous and binary pooled) were significant at P = 0.053. In the two sections that follow I report how variation was partitioned among spatiotemporal and environmental factors for datasets organized by species and bodylength. The percentages reported below are how the total explainable variation (TVE) is distributed among factors and ordination axes; they represent a cumulative decomposition of the total percentages listed above for each dataset.

Species

All spatiotemporal factors combined contributed 7.9% and environmental factors 4.3% of TVE in assemblage composition by species; the interaction between spatiotemporal and environmental factors accounted for 6.4% (Figure 3.1A). Months were more important in explaining the species assemblage than diel period. Spatial variation in species assemblage was best explained at the region scale. Depth, velocity, turbidity, and water temperature accounted for more than half (pTVE = 54.4%) of the variation in species composition explained by environmental factors (Figure 3.1A).

The first CCA axis constrained by all factors explained 8.6% TVE and 46.1% pTVE (Figure 3.2A). Sicklefin chub (*Macrhybopsis meeki*) and goldeye (*Hiodon alosoides*) were associated with the deepest depth and fastest flow velocity. River carpsucker (*C. carpio*), quillback (*C. cyprinus*), bigmouth buffalo (*Ictiobus cyprinellus*), and plains minnow (*Hybognathus placitus*) were associated with shallow water, slow velocity, and the months July and August (Figure 3.2A). Water temperature and the months September and October were most correlated with the first canonical axis; depth,

near-shore, and offshore sample units were most highly correlated with the second axis (Table 3.2). The first canonical axis constrained only by spatiotemporal factors, controlling for the effect of environmental factors (pCCA), explained 3.5% TVE and pTVE was 44.9%. Constraining only by environmental factors explained 1.1% TVE and pTVE was 25.6% along the first canonical axis (Figure 3.3).

Body length

All spatiotemporal factors combined explained 12.5% and environmental factors 5.8% TVE in assemblage composition by body length; the interaction between spatiotemporal and environmental factors accounted for 11.8% (Figure 3.1B). Months were more important in explaining temporal variation in body length assemblage than diel period; spatial variation in fishes by body length was best explained at the sample unit category scale. Depth, velocity, water temperature, turbidity, and wind account for more than half (pTVE = 56.5%) of the variation explained by environmental factors.

The first CCA axis, constrained by all factors, explained 17.3% TVE and 57.0% pTVE (Figure 3.2b). Small-bodied fishes were ordinated by body length along a depth and velocity gradient where smaller fishes (10-34 mm TL) were associated with shallower, slower velocity water (Figure 3.2B). Intermediate length fishes (35-49 mm TL) were associated with intermediate depth and velocity. Larger fishes (50-105 mm TL) were associated with deeper, faster water. Depth, water temperature, and near-shore sample units were most correlated with the first canonical axis; near-shore sample units, depth, and offshore sample units were most correlated with the second axis (Table 3.2). The first canonical axis constrained only by spatiotemporal factors, controlling for the

effect of environmental factors (pCCA), explained 3.5% TVE and pTVE was 44.9%. Constraining only by environmental factors explained 2.3% TVE and pTVE was 37.3% along the first canonical axis (Figure 3.4).

Table 3.2. Canonical correspondence analysis (CCA) correlation coefficients of spatiotemporal and environmental factors with the first two canonical axes of small-bodied fish assemblages organized by species and body length.

	Species		Body length	
Factor	Axis-1	Axis-2	Axis-1	Axis-2
Temporal				
July	-0.420	0.095	-0.411	0.230
August	-0.279	0.066	-0.152	0.021
September	0.597	-0.184	0.431	-0.284
October	0.498	-0.055	0.467	-0.091
Light	0.131	-0.137	0.058	-0.066
Dark	0.054	0.241	0.198	-0.007
Spatial				
Point bar	-0.168	0.033	-0.227	0.214
Wing-dike bar	0.168	-0.033	0.227	-0.214
HR	0.196	-0.070	0.187	-0.030
UP	0.099	0.079	0.104	0.049
US	0.160	-0.093	0.080	-0.131
DP	0.105	0.017	0.082	0.062
DS	-0.259	0.053	-0.205	0.112
TL	-0.072	-0.031	-0.071	-0.109
Near-shore	-0.407	-0.505	-0.610	-0.357
Moderate	0.291	0.313	0.451	0.203
Offshore	0.241	0.439	0.341	0.289
Continuous				
Depth	0.485	0.521	0.648	0.308
Velocity	0.390	0.253	0.463	0.208
Temperature	-0.679	0.038	-0.619	0.131
Turbidity	0.001	0.048	-0.012	0.067
Substrate	0.067	-0.043	0.055	-0.002
Slope	0.133	-0.066	0.025	-0.051
S.sinuosity	-0.093	0.007	-0.158	0.079
Binary				
Sunny	0.188	-0.045	0.106	-0.035
Cloudy	-0.059	-0.006	-0.025	-0.013
P. cloudy	-0.006	-0.005	0.050	-0.024
Rain	0.143	0.002	0.176	0.014
Wind	0.206	-0.017	0.198	-0.160

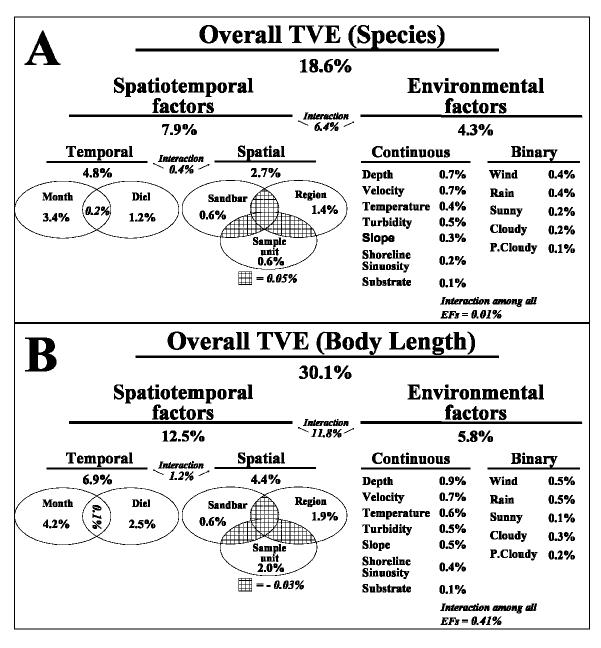


Figure 3.1. Explained variation in small-bodied fish assemblage composition partitioned by (A) species and (B) body length. Percentages listed are percent of total variation explained (%TVE) partitioned by spatiotemporal and environmental factor subgroups. Interaction TVEs were calculated by difference and are listed in *italics*. See text for explanation of negative interaction value.

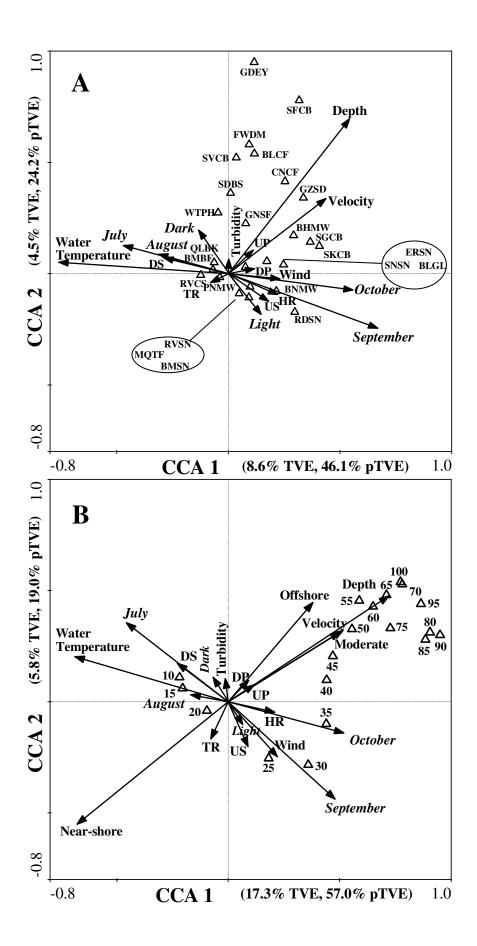


Figure 3.2. Canonical correspondence analysis (CCA) biplot depicting relationships among (A) species, (B) 5-mm length classes, and their environmental factors. Species and length classes are represented by open triangles and factor gradients are represented by arrows. For clarity, the eight environmental factors (A and B = slope, shoreline sinuosity, substrate particle size, ledge, sunny, cloudy, partly cloudy, rain) and one or two spatial CoVs (A = sandbar type, depth class; B = sandbar type) with lowest percent of total variation explained (%TVE) were omitted from the graph. Temporal CoVs (month and diel) always accounted for greater than 1.1% TVE and were therefore included in the graph (labeled with italics). Each axis is labeled with TVE and partial percent of total variation explained (pTVE). Length classes are labeled by shortest length within each class, e.g., 10 = fishes ranging from 10 to 14 mm TL. See Table 2.1 for species code definitions.

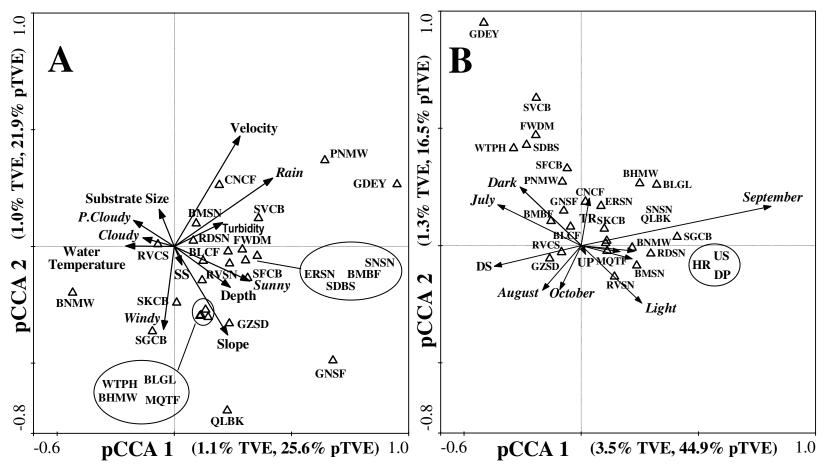


Figure 3.3. Partial canonical correspondence analysis (pCCA) showing relationships among (A) species (CPUE) and environmental factors (EFs) (controlling for effect of spatiotemporal factors), and (B) species (CPUE) and spatiotemporal factors (STs) (controlling for effect of EFs). Fishes are represented by open triangles and factors by arrows. Each axis is labeled with percent of total variation explained (%TVE) and partial percent of total variation explained (%pTVE) specific to each set of factors. Length classes are labeled by shortest length within each class, e.g., 10 = fishes ranging from 10 to 14 mm TL. See Table 2.1 for species code definitions.

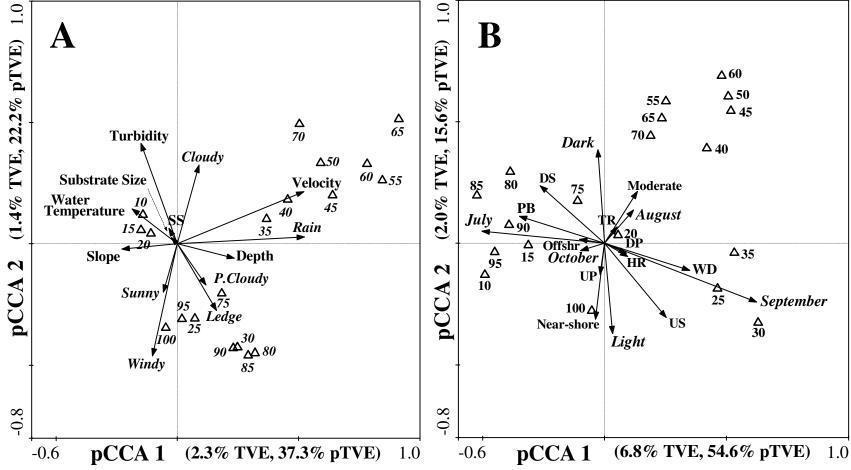


Figure 3.4. Partial canonical correspondence analysis (pCCA) showing relationships among (A) length classes (CPUE) and environmental factors (EFs) (controlling for effect of spatiotemporal factors), and (B) length classes (CPUE) and spatiotemporal factors (controlling for effect of EFs). Fishes are represented by open triangles and factors by arrows. Each axis is labeled with percent of total variation explained (%TVE) and partial percent of total variation explained (%pTVE) specific to each set of factors. Length classes are labeled by shortest length within each class, e.g., 10 = fishes ranging from 10 to 14 mm TL.

Discussion

Results show that small-bodied fishes differentially use sandbar ATTZ in LMOR. First (1), spatiotemporal and environmental factors did not equally explain the variation in composition of species and body length assemblages. Instead, spatiotemporal factors explained a greater proportion of the variation in fish assemblage structure than environmental factors for both the species and body length datasets. Second (2), depth, velocity, and temperature were the most important factors in ordination, but decomposition of the variation showed that month explained the greatest proportion of variability in assemblage composition in both the species and body length datasets. Composition of LMOR sandbar ATTZ fish assemblage changed most by month, but depth, velocity, and temperature were important local factors structuring assemblages during months in this study. Lower variability from the body length dataset supports the conclusion in Chapter 2 that small-bodied fishes were spatially distributed in shallowwater sandbar habitat more by body length than by species. Additionally, higher TVE from the body length CCA than species CCA is evidence that the small-bodied fish assemblage is more aligned along a body-length gradient relative to spatiotemporal and environmental factors. Therefore, (3) body length was the more parsimonious and ecologically appropriate way to describe the organization of small-bodied fishes relative to spatiotemporal and environmental factors. Specifically, fishes used depths, velocities, and temperatures relative to body length with smaller, small-bodied fishes using shallower, slower, and warmer water.

Species- vs. body-length-environment relationships

The proportion of the body length assemblage structure explained by constraining factors (i.e., spatiotemporal and environmental factors) for each dataset is near or within a range (20-50%) typically reported by other researchers for organism-environment relationships (Borcard et al. 1992; Magnan and Rodríguez 1994; Rodríguez and Magnan 1995; Marchetti and Moyle 2001; Økland 2003; Barko et al. 2004; Hulse 2005; Reeves 2006). The remaining unexplained proportion in this study may be due to (1) unmonitored or imprecisely monitored factors or (2), the proximate stochasticity of an extremely large and complex hierarchically structured ecological system (Townsend 1989; Tonn 1990; Poff 1997).

Comparison of composition variability between assemblage types was inherently biased towards better explanation of the length organized assemblage because there were more species (n = 25) than length classes (n = 19). Since there were more units in the species dataset to be ordered, there were more possible sub-assemblage group combinations, and total inertia in assemblage composition should be higher. However, total variability of the species assemblage was more than twice that of the length-based assemblage and overall TVE was higher indicating that ecological mechanisms contribute to structuring the fish assemblage by body length. Therefore, body length was a more ecologically relevant structuring factor influencing small-bodied fishes' habitat use than was conspecific association.

Spatiotemporal vs. environmental factors

Decomposition of assemblage structure variation shows that spatiotemporal factors explained a greater proportion of the variability in assemblage composition than did environmental factors. However, CCA results show that local environmental factors depth, velocity, and temperature were important (e.g., Figure 3.2) in structuring the assemblage in both datasets. This is more logically interpreted within the context of a hierarchical framework.

Temporal factors represent the highest level filters in this study. Water temperature operates within the constraints of month (i.e., warmer in July to cooler in October) and diel period (i.e., cooler at night). Spatial factors serve as the next lower level filter. I found in Chapter 2 that: 1) depth was shallower nearer to shore than further offshore; 2) upstream and downstream secondary channel regions provided slower water velocity than upstream and downstream primary channel regions, and was slower in the near-shore zone than the offshore zone; 3) water temperatures differed near-shore between diel periods, but not in the offshore zone. Finally, these three environmental factors represent the lowest level filter influencing microhabitat use and small-bodied fish assemblage composition at sandbar ATTZ in this study. Juvenile (i.e., age-0) riverine fishes often use shallow, slow velocity, warm water areas as nursery because risk of mortality is relatively low and the environment is benign, supporting growth and survival (Copp and Peňáz 1988; Copp 1992; Jurajda 1999; Keckeis et al. 2001; King 2004). Other local biotic factors that were not directly measured such as predation and competition likely influence microhabitat use and assemblage structure (e.g., Power 1987; Chapter 2). Since lower level factors form the building blocks of higher level

filters, there are relatively few high level filters that constrain low level factors.

Therefore, one possible explanation for high TVE of temporal factors is that a more complete subset of the available time related factors were measured.

Another explanation for the high TVE of spatiotemporal factors is from the result of Student's t-test showing that variance among spatiotemporal and environmental factors was different at P = 0.053. This is because categorical factors, like region, were constant (a sandbar's head region is always a head region) whereas continuous factors, like temperature, were highly variable. If environmental factors were more homoscedastic (e.g., water temperature was always very near 22.0° C), they may have accounted for a greater proportion of the variation in fish assemblage composition (Gurevitch and Hedges 1999; Zar 1999). Instead, results of pCCA indicate that the interaction among spatial, temporal, and environmental factors are nearly as, or more important than, spatial, temporal, or environmental factors alone. This high interaction term indicates how complex the ecology of sandbar ATTZ is and that spatiotemporal and environmental factors should not be decoupled, but synchronized in LMOR fishery recovery plans.

Since small-bodied fishes and the local environments they use operate within a framework constrained by higher level temporal and spatial factors, their distribution reflects the influence of diverse variables from multiple levels simultaneously (Frissell et al. 1986; Tonn 1990; Wu and Loucks 1995; Hoeinghaus et al. 2007). Microhabitats selected by fishes may provide a balance among pressures to occupy spaces that maximize foraging and growth opportunity (Werner and Hall 1974; Werner et al. 1983; Rosenfeld et al. 2005), and minimize mortality risk from predation (Power 1987; Werner and Hall 1988; Byström et al. 2003) and harsh environmental conditions (Harvey 1987;

Matthews 1987; Gillette et al. 2006). Results from canonical ordination clearly show that 10-34 mm TL fishes used microhabitats with low velocity and shallow depth. Results from Chapter 2 quantitatively showed that the near-shore zone was shallow with low velocity. There, I discussed the implications of this zone to age-0 fishes in the context of a predation refuge. Next, I discuss habitat use relative to body length at LMOR sandbar ATTZ.

Body size and habitat use

Literature on fish shoals and the role of body length in structuring their assembly indicates that benefits of grouping by body length are reduced predation mortality and increased foraging efficiency (Calder 1984; Pitcher et al. 1986; Krause et al. 1996; Krause et al. 1998; Blanckenhorn 2000; Krause et al. 2000; Hoare and Krause 2003). Fishes within shoals have a greater probability of encountering food resources than do solitary individuals (Pitcher et al. 1982). Shoals with low variability in body length have lower per capita predation risk, likely due to a predator confusion effect (Landeau and Terborgh 1986; Krause and Godin 1994) and exhibit greater per capita energy gain because no individuals have a consumptive advantage due to large body size (Brown and Maurer 1986; Griffiths 1992; Krause 1994; Krause et al. 1998). The small-bodied fish assemblage at LMOR sandbar ATTZ may have been structured relative to body length for similar reasons to minimize predation risk and maximize foraging efficiency.

Shallow depth, slow velocity, and warm water temperature are well documented as local environmental conditions associated with nursery use by age-0 fluvial fishes (Copp 1992; King 2004; Grift et al. 2003; Wolter and Arlinghaus 2003; Barko et al.

2004; Hirzinger et al. 2004). The shallow, slow velocity water near-shore was used predominately by 10-34 mm TL fishes from July through October indicating that it may provide refuge. Energetic cost to maintain position in current is inversely related to size (Flore and Keckeis 1998) in small-bodied fishes, and early life-stage fishes may be displaced (wash-out) if a critical current velocity threshold is exceeded (Harvey 1987; Stahlberg and Peckmann 1987; Heggenes and Traaen 1988; Pavlov 1994). Even if velocities do not exceed the critical wash-out level, fitness may be reduced because food consumption rapidly decreases at a velocity below the critical threshold for many smallbodied fishes (Flore and Keckeis 1998; Asaeda et al. 2007). Warmer temperature nearshore at sandbar ATTZ was more favorable for growth and may have improved swimming ability, and thus predator avoidance behavior, of age-0 fishes (Kaufmann and Wieser 1992; Fuiman and Batty 1997; Mann and Bass 1997). However, growth is also highly dependent upon food availability, consumption (Mann 1997), and energetic cost to maintain position in current (Facey and Grossman 1992); current speed above a maximum consumption velocity may not support growth. Although I did not measure growth directly, results from sandbar ATTZ indicate that, within the 0.0-0.5 m depth study zone, 10-34 mm TL fishes that used the shallow, near-shore zone experienced conditions favorable for growth, relative to moderate and offshore zones, because it provided a refuge from fast velocity where water temperature was warmer than adjacent deeper, faster, and cooler off-shore zone.

The 10-34 mm TL fishes collected during this study were shorter than the minimum length-at-age-1 where data were available for most species (Chapter 2, Table 2.8). Results further support that fish from multiple species grew from July to October

because body length increased along this monthly gradient. This indicates the near-shore zone at sandbar ATTZ provided nursery to many age-0 fishes within the main channel of LMOR and that synchronizing availability of shallow water, slow velocity near-shore habitat with use by age-0 fishes is critical.

Management implications for LMOR sandbar ATTZ

Manipulation of river hydrology to mimic a more natural annual flow regime to restore native fish populations is gaining support from the literature since Junk et al. (1989) outlined the importance of an annual flood pulse in the life history of many riverine fishes of large regulated rivers (Sparks et al. 1990; Hesse and Metsel 1993; Hesse and Sheets 1993; Sparks 1995; Johnson and Richardson 1995; Poff and Allan 1995; Stanford et al. 1996). Notable is the formalization of the *natural flow paradigm* (Poff et al. 1997) and its utility in work to restore floodplain (Galat et al. 1998; Kemp et al. 1999; Agostinho et al. 2004) and main-channel habitats (Travnichek et al. 1995; Galat and Zweimüller 2001) for fishes in large regulated rivers.

Galat and Lipkin (2000) used mean monthly discharge (Q) to characterize what a more natural flow regime looked like before upstream dams were operational for a 20 year period (1929-1948) on LMOR, at Boonville, MO. The annual hydrograph was predominantly unimodal with large spring rise (maximum Q ~ 3000 m³/s, June), followed by a period of low flow that begun in July (Q ~ 1700 m³/s) and extended from August (Q ~ 1000 m³/s) to February (Q August - February period ~ 1000 \pm 500 m³/s); a second smaller rise occurred during November (Q ~ 1300 m³/s). In contrast, mean monthly discharge was higher (except maximum Q ~ 2600 m³/s, May) during a 30 year period

(1967-1996) after dams became operational (July Q ~ 2300, August Q ~ 1750 m 3 /s). Tracy-Smith (2006) developed detailed maps and predictive models to estimate the quantity of sandbar ATTZ (0.0-0.5 m) available at multiple discharge levels; she showed that area of sandbar ATTZ in the depth range 0.0-0.5 m was greatest when discharge was near 1500 m 3 /s. Results from this study imply that, since July-August is the period when the smallest fishes (10-25 mm TL) use the shallowest part of sandbar ATTZ, discharge near 1500 m 3 /s under the current channel configuration is critical during these months because it provides nursery habitat for age-0 of many native species that use sandbar ATTZ on LMOR.

Conclusion

Factors did not equally explain the variation in species and body length organized assemblages. Instead, a hierarchical order of factors appears to have structured the small-bodied fish assemblage and their habitat use relative to body length during the study period. Among higher order factors, month was most important for explaining the body length assemblage composition because fish body length increased with month. A logical explanation for this pattern is that fishes grew during months when water was warm. Lower order factors were important in describing the distribution of small-bodied fishes at finer resolutions. This indicates that the proximate distribution of small-bodied fishes relative to body length within regions was controlled by the important local environmental factors depth, velocity, and temperature. Therefore among the factors considered in this study, and in the context of a hierarchical system, month acted as a

filter to constrain body-length assemblage composition at lower levels in sandbar ATTZ on LMOR.

Efforts to improve sandbar ATTZ as nursery for small-bodied fishes should consider the interactive effects of hierarchical factors and their implications for fishes. Regulating water releases from upstream reservoirs to provide river discharge near 1500 m³/s in central Missouri during July and August may be an effective method within the contemporary constricted main channel to increase the 0.0-0.5 m depth zone adjacent to existing sandbars. Efforts to create new sandbar habitat should consider its role as main-channel nursery because 10-34 mm TL fishes, thus probably age-0, were most associated with the near shore zone where depth was shallow, velocity was slow, and temperature was warm. Increasing availability of sandbars with the near-shore nursery attributes discussed here may improve recruitment of many native species on LMOR.

Literature Cited

- Aday, D. D., R. J. H. Hoxmeier, and D. H. Wahl. 2003. Direct and indirect effects of gizzard shad on bluegill growth and population size structure. Transactions of the American Fisheries Society 132: 47-56.
- Agostinho, A. A., L. C. Gomes, S. Veríssimo, and E. K. Okada. 2004. Flood regime, dam regulation and fish in the upper Paraná River: effects on assemblage attributes, reproduction and recruitment. Reviews in Fish Biology and Fisheries 14: 11-19.
- Allan, J. R. and T. J. Pitcher. 1986. Species segregation during predator evasion in cyprinid fish shoals. Freshwater Biology 16: 653-659.
- Arendt, J.D. and D.S. Wilson. 1997. Optimistic growth: competition and an ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). Evolution 5: 1946-1954.
- Arrington, D. A. and K. O. Winemiller. 2006. Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. Journal of the North American Bentological Society 25: 126-141.
- Asaeda, T., J. Manatunge, and T. Fujino. 2007. The effects of predation risk and current velocity stress on growth, condition and swimming energetics of Japanese minnow (*Pseudorasbora parva*). Ecological Research 22: 32-40.
- Barko, V. A., M. W. Palmer, D. P. Herzog, and B. S. Ickes. 2004. Influential environmental gradients and spatiotemporal patterns of fish assemblages in the unimpounded upper Mississippi River. The American Midland Naturalist 152: 369-385.
- Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? The Quarterly Review of Biology 75: 385-407.
- Borcard, D. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.
- Brown, J.H. and B.A. Maurer. 1986. Body size, ecological dominance and Cope's rule. Nature 324: 248-250.
- Byström, P., L. Persson, E. Wahlström and E. Westman. 2003. Size- and density dependent habitat use in predators: consequences for habitat shifts in young fish. Journal of Animal Ecology 72: 156-168.
- Calder, W.A. 1984. Size, function, and life history. Harvard University Press, USA.

- Copp, G. H. 1992. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. Environmental Biology of Fishes 33: 181-193.
- Copp, G. H., G. Guti, B. Rovny and J. Cerny. 1994. Hierarchical analysis of habitat use by 0+ juvenile fish in Hungarian/Slovak floodplain of the Danube River. Environmental Biology of Fishes 40: 329-348.
- Copp, G. H. and M. Peňáz. 1988. Ecology of fish spawning and nursery zones in the floodplain, using a new sampling approach. Hydrobiologia 169: 209-224.
- Facey, D. E. and G. D. Grossman. 1992. The relationship between water velocity, energetic costs, and microhabitat use in four North American stream fishes. Hydrobiologia 239: 1-6.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10: 199-214.
- Flore, L. and H. Keckeis. 1998. The effect of water current on foraging behaviour of the rheophilic cyprinid *Chondrostoma nasus* (L.) during ontogeny: evidence of a trade-off between energetic gain and swimming costs. Regulated Rivers: Research and Management 14: 141-154.
- Fuiman, L. A., and R. S. Batty. 1997. What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. The Journal of Experimental Biology 200: 1745-1755.
- Galat, D. L., L. H. Fredrickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, G. T. Gelwicks, J. E. Havel, D. L. Helmers, J. B. Hooker, J. R. Jones, M. F. Knowlton, J. Kubisiak, J. Mazourek, A. C. McColpin, R. B. Renken and R. D. Semlitsch. 1998. Flooding to restore connectivity of regulated, largeriver wetlands. Bioscience 48: 721-733.
- Galat, D. L. and R. Lipkin. 2000. Restoring ecological integrity of great rivers: historical hydrographs aid in defining reference conditions for the Missouri River. Hydrobiologia 422: 29-48.
- Galat, D. L. and I. Zweimüller. 2001. Conserving large-river fishes: is the highway analogy an appropriate paradigm? Journal of the North American Benthological Society 20: 266-279.
- Gelwicks, G. T., K. Graham and D. L. Galat. 1996. Status survey for sicklefin chub, sturgeon chub, and flathead chub in the Missouri River, Missouri. Final Report. Missouri Department of Conservation, Columbia, MO. 23p.
- Gillette, D. P., J. S. Tiemann, D. R. Edds and M. L. Wildhaber. 2006. Habitat use by a

- Midwestern U.S.A. riverine fish assemblage: effects of season, water temperature and river discharge. Journal of Fish Biology 68: 1494-1512.
- Grace, T. B. 1985. The status and distribution of commercial and forage fish in the Missouri river and their utilization of selected habitats: Evaluation of sand island habitat in the Missouri River. Final Report. Missouri Department of Conservation, Columbia, MO. National Marine Fisheries Service Program 2-363-R, Project IV, Job II. 34p.
- Griffiths, D. 1992. Size, abundance, and energy use in communities. Journal of Animal Ecology 61: 307-315.
- Grift, R. E., A. D. Buijse, W. L. T. Van Densen, M. A. M. Machiels, J. Dranenbarg, J. G. P. Klein Breteler and J. J. G. M. Backx. 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. River Research and Applications 19: 353-374.
- Gurevitch, J. and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology 80: 1142-1149.
- Hanson, J. M. and W. C. Leggett. 1985. Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes. Canadian Journal of Fisheries and Aquatic Sciences 42: 280-286.
- Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116: 851-855.
- Heggenes, J. and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. Journal of Fish Biology 32: 717-727.
- Hesse, L. W. and G. E. Metsel. 1993. An alternative hydrograph for the Missouri River based on the precontrol condition. North American Journal of Fisheries Management 13: 360-366.
- Hesse, L. W. and W. Sheets. 1993. The Missouri River hydrosystem. Fisheries 18(5): 5-14.
- Hirzinger, V., H. Keckeis, H. L. Nemeschkal, and F. Schiemer. 2004. The importance of inshore areas for adult fish distribution along a free-flowing section of the Danube, Austria. River Research and Applications 20: 137-149.
- Hoare, D. J. and J. Krause. 2003. Social organisation, shoal structure and information transfer. Fish and Fisheries 4: 269-279.

- Hoeinghaus, D. J., K. O. Winemiller, and J. S. Birnbaum. 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. Journal of Biogeography 34: 324-338.
- Hulse, S. N. 2005. Reach scale and sample design influences on middle Mississippi River fishes. Master's Thesis. University of Missouri, Columbia, Missouri.
- Hutchinson, G.E. and R.H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. The American Naturalist 93: 117-125.
- Jennings, S., J.K. Pinnegar, N.V.C. Polunin, and T.W. Boon. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. Journal of Animal Ecology 70: 934-944.
- Johnson, B. L. and W. B. Richardson. 1995. Past, present, and future concepts in large river ecology. Bioscience 45: 134-141.
- Junk, W. J., P. B. Bayley and R. E. Sparks. 1989. The flood pulse concept in riverfloodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences Ottawa 106: 110-127.
- Jurajda, P. 1999. Comparative nursery habitat use by 0+ fish in a modified lowland river. Regulated Rivers: Research and Management 15: 113-124.
- Kaufmann, R. and W. Wieser. 1992. Influence of temperature and ambient oxygen on the swimming energetics of cyprinid larvae and juveniles. Environmental Biology of Fishes 33: 87-95.
- Keckeis, H., E. Kamler, E. Bauer-Nemeschkal and K. Schneeweiss. 2001. Survival, development and food energy partitioning of nase larvae and early juveniles at different temperatures. Journal of Fish Biology 59: 45-61.
- Kemp, J. L., D. M. Harper and G. A. Crosa. 1999. Use of 'functional habitats' to link ecology with morphology and hydrology in river rehabilitation. Aquatic Conservation: Marine and Freshwater Ecosystems 9: 159-178.
- Kerr, S.R. 1989. The switch to size. Environmental Biology of Fishes 24: 157-159.
- King, A. J. 2004. Ontogenetic patterns of habitat use by fishes within the main channel of an Australian floodplain river. Journal of Fish Biology 65: 1582-1603.
- Kozłowski, J. and A.T. Gawelczyk. 2002. Why are species' body size distributions usually skewed to the right? Functional Ecology 16: 419-432.
- Krause, J. 1994. The influence of food competition and predation risk on size

- assortative shoaling in juvenile chub (*Leuciscus cephalus*). Ethology 96: 105-116.
- Krause, J. and J.-G. J. Godin. 1994. Shoal choice in the banded killifish (*Fundulus diaphanous*, Teleostei, Cyprinodontidae): effects of predation risk, fish size, species composition, and size of shoals. Ethology 98: 128-136.
- Krause, J., J.-G. J. Godin, and D. Brown. 1996. Size-assortativeness in multi-species fish shoals. Journal of Fish Biology 49: 221-225.
- Krause, J., J.-G. J. Godin, and D. Brown. 1998. Body length variation within multi species fish shoals: the effects of shoal size and number of species. Oecologia 114: 67-72.
- Krause, J., D. J. Hoare, D. Croft, J. Lawrence, A. Ward, G. D. Ruxton, J. –G. J. Godin, and R. James. 2000. Fish shoal composition: mechanisms and constraints. Proceedings of the Royal Society of London Series B 267: 2011-2017.
- Landeau, L. and J. Terborgh. 1986. Oddity and confusion effect in predation. Animal Behaviour 34: 1372-1380.
- Langler, G. J. and C. Smith. 2001. Effects of habitat enhancement on 0-group fishes in a lowland river. Regulated Rivers: Research and Management 17: 677-686.
- Lepš, J. and P. Šmilauer. 2003. Multivariate analysis of ecological data using CANOCO. Press Syndicate of The University of Cambridge, Cambridge, United Kingdom.
- Lord, J. M. and D. A. Norton. 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4: 197-202.
- Magnan, P., M. A. Rodríguez, P. Legendre, and S. Lacasse. 1994. Dietary variation in a freshwater fishe species: relative contributions of biotic interactions, abiotic factors, and spatial structure. Canadian Journal of Fisheries and Aquatic Sciences 51: 2856-2865.
- Mann, R. H. K. 1997. Temporal and spatial variations in the growth of 0 group roach (*Rutilus rutilus*) in the river Great Ouse, in relation to water temperature and food availability. Regulated Rivers: Research and Management 13: 277-285.
- Mann, R. H. K. and J. A. B. Bass. 1997. The critical water velocities of larval roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) and implications for river management. Regulated Rivers: Research and Management 13: 295-301.
- Marchetti, M. P. and P. B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications 11: 530-539.

- Matthews, W. J. 1987. Physiochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. Pages 111-120 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, OK.
- Meffe, G. K. and A. L. Sheldon. 1988. The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. The American Midland Naturalist 120: 225-240.
- NOAA. 2007. Beaufort wind scale. National Oceanic and Atmospheric Administration's National Weather Service. Available: www.spc.noaa.gov/index.html (April 2007).
- Økland, R. H. 2003. Partitioning the variation in a plot-by-species data matrix that is related to *n* sets of explanatory variables. Journal of Vegetation Science 14: 693-700.
- Pavlov, D. S. 1994. The downstream migration of young fishes in rivers: mechanisms and distribution. Folia Zoologica 46: 193-208.
- Pettersson, J., J. I. Johnson, and T. Bohlin. 1996. The competitive advantage of large body size declines with increasing group size in rainbow trout. Journal of Fish Biology 49: 370-372.
- Pierce, C. L., C. S. Guy, P. J. Braaten and M. A. Pegg. 2003. Fish growth, mortality, recruitment, condition, and size structure. Volume 4. Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U.S. Geological Survey, Cooperative Research Units, Iowa State University, Science Hall II, Ames, Iowa 50011.
- Pitcher, T. J., A. E. Magurran, and I. J. Winfield. 1982. Fish in larger shoals find food faster. Behavioral Ecology and Sociobiology 10: 149-151.
- Pitcher, T. J., A. E. Magurran, and J. R. Allan. 1986. Size-segregative behaviour in minnow shoals. Journal of Fish Biology 29: 83-95.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16: 391-409.
- Poff, N. L. and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76: 606-627.
- Poff, L. N., A. J. David, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. Bioscience 47:

- 769-784.
- Poizat, G. and D. Pont. 1996. Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. Freshwater Biology 36: 611-622.
- Polis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? The American Naturalist 123: 541-564.
- Power, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pages 333-351 *in* W.C. Kerfoot and A. Sih, editors. Predation. Direct and indirect effects on aquatic communities. University Press of New England, Hanover, NH.
- Reeves, K. 2006. Use of main channel and shallow-water habitats by larval fishes in the lower Missouri River. Doctoral dissertation. University of Missouri, Columbia, Missouri.
- Rodríguez, M. A. and P. Magnan. 1995. Application of multivariate analyses in studies of the organization and structure of fish and invertebrate communities. Aquatic Sciences 57: 199-216.
- Rosenfeld, J. S., T. Leiter, G. Linder and L. Rothman. 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 62: 1691-1701.
- Ryer, C. H. and B. L. Olla. 1991. Agonistic behavior in a schooling fish: form, function and ontogeny. Environmental Biology of Fishes 31: 355-363.
- Sheldon, R.W., A. Prakash, and W.H. Sutcliffe, Jr. 1972. The size distribution of particles in the ocean. Limnology and Oceanography 17: 327-340.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129-1157.
- Sparks, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. Bioscience 45: 168-182.
- Sparks, R. E., P. B. Bayley, S. L. Kohler and L. L. Osborne. 1990. Disturbance and recovery of large floodplain rivers. Environmental Management 14: 699-709.
- Spoljaric, M. A. and T. E. Reimchen. 2007. 10,000 years later: evolution of body shape in Haida Gwaii three-spined stickleback. Journal of Fish Biology 70: 1484-1503.
- Stahlberg, S. and P. Peckmann. 1987. The critical swimming speed of small Teleost fish

- species in a flume. Archiv für Hydrobiologie 110: 179-193.
- Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A Lichatowich and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. Regulated Rivers: Research and Management 12: 391-413.
- ter Braak, C. J. F. and P. Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination, version 4.5. Microcomputer Power, Ithaca, New York.
- ter Braak, C. J. F. and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57: 255-289.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75: 2-16.
- Tonn, W. M. 1990. Climate change and fish communities: a conceptual framework. Transactions of the American Fisheries Society 119: 337-352.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Bentological Society 8: 36-50.
- Townsend, C. R. and A. G. Hildrew. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31: 265–275.
- Tracy-Smith, E. 2006. Relation of Missouri River flows to sandbar morphology with implications for selected biota. Master's Thesis. University of Missouri, Columbia, Missouri.
- Travnichek, V. H., M. B. Bain, and M. J. Maceina. 1995. Recovery of a warmwater fish assemblage after the initiation of a minimum-flow release downstream from a hydroelectric dam. Transactions of the American Fisheries Society 124: 836-844.
- Werner, E.E. and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate –predation risk trade-off. Ecology 69: 1352-1366.
- Werner, E.E. and D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042-1052.
- Werner, E. E., G. Mittlebach, D. J. Hall and J. F. Gilliam. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64: 1525-1539.
- Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

- Wilson, D.S. 1975. The adequacy of body size as a niche difference. The American Naturalist 109: 769-784.
- Wolter, C. and R. Arlinghaus. 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. Reviews in Fish Biology and Fisheries 13: 63-89.
- Woodward, G. and A.G. Hildrew. Body-size determinants of niche overlap and intraguild predation within a complex food web. Journal of Animal Ecology 71: 1063-1074.
- Wu, J. and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. The Quarterly Review of Biology 70: 439-466.
- Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice-Hall, Upper Saddle River, New Jersey.

.

Summary, Conclusions and Implications

Major findings and recommendations from the research presented herein can be summarized as follows:

- 1. This study researched habitat use of fishes in the aquatic-terrestrial-transition-zone associated with sandbars (sandbar ATTZ) on lower Missouri River (LMOR) in central Missouri (rkm 254-381). Sandbar ATTZ was defined as water up to 0.5 m deep adjacent to sandbars. Spatial, temporal, and environmental factors influencing habitat use by fish were examined within the context of a hierarchy. There were three spatial levels: sandbars (coarse resolution), regions (intermediate resolution), and sample units (fine resolution, 3.75m²). There were two temporal levels, month and diel periods. Environmental factors operated within the constraints of spatial and temporal filters, these factors were: depth, velocity, water temperature, turbidity, substrate composition, sandbar slope, and sandbar shoreline sinuosity.
- 2. Fourty-eight (of 110) LMOR species were collected, reflecting the ecological significance of sandbar ATTZ in a large regulated river. Most fishes collected from the sandbar ATTZ were small (≤105 mm TL), and most were probably younger than age-1 (*ca.* <35 mm TL) based on available length-at-age data from 14 LMOR species. This indicates that sandbars serve as main-channel nursery habitat for many fish species. Conservation and rehabilitation of sandbars and other main-channel ATTZs may contribute to improved ontogenetic recruitment of imperiled small-bodied species such as sicklefin chub (*Macrhybopsis meeki*),

- sturgeon chub (*M. gelida*), and plains minnow (*Hybognathus placitus*) that use main-channel habitats.
- 3. The sandbar ATTZ small-bodied fish assemblage was primarily organized into subgroups of fishes with similar body length. This and supporting arguments from others advocate considering body length as a fundamental aspect of riverine fish ecology and applying it as an appropriate paradigm for fisheries management and restoration in channelized large rivers.
- 4. Most (10-34 mm TL) small-bodied fishes used the shallow near-shore zone (mean depth = 0.13 m) where velocity was slower and temperature was warmer than in deeper offshore ATTZ habitats (mean depths = 0.25 and 0.45 m). Small-bodied fishes were most abundant during July and August when the assemblage was dominated by 10-24 mm TL fishes. Although fish body length provided the most robust explanation for the overall structure of the small-bodied fish assemblage, there was some species specific differential habitat use along a depth-velocity gradient. Mangers interested in improving recruitment of native riverine fishes should consider the role of body size on habitat use and synchronize availability of sandbar ATTZ with the periods of greatest use by age-0 species.
- 5. The distribution and abundance of small-bodied fishes changed along a depth gradient between day and night periods. Many fishes that used offshore ATTZ areas during the day moved nearer to shore at night. An argument supporting an aquatic-terrestrial predator-prey interaction developed in small streams explains the observed diel movements of fishes relative to body length in the 0.0-0.5 m sandbar ATTZ of LMOR. Further research is needed to test the hypothesis of a

- aquatic-terrestrial predator influence on near-shore, diel movement patterns of small-bodied fishes at large-river sandbars.
- 6. The ecology of sandbar ATTZ is complex. Interactions between hierarchically ordered spatiotemporal and environmental factors accounted for a relatively large proportion of explainable variation in distribution and habitat use by small-bodied fishes. Stochastic processes, such as variable river discharge and predator-prey and competitive interactions among fishes, may account for much of the unexplainable variation in distribution and habitat use of small-bodied fishes.
 Native fisheries restoration should consider the complex hierarchical nature of spatial, temporal, and environmental factors in the distribution and habitat use of small-bodied fishes within the sandbar ATTZ.

Appendix A

Small and submerged sandbar sample design

Sampling effort was distributed using the following method on sandbars that were small (<40-m) or submerged if depth is \le 0.5 m. The highest elevation point on each sandbar was recorded with GPS to serve as a reference point to locate the sandbar and distribute sample units if it was submerged. Rebar was used to mark the upstream, downstream, and lateral extent of 0.5-m depth water around the point. Up to seven lateral transects spaced no less than 15-m apart were established, one at the highest elevation point and up to three on each the up and downstream side up to 0.5-m depth. Up to five samples were collected from each transect depending upon the depths available; one from the shallowest point, two on each side at 0.5-m depth, and two at intermediate depths among the first three. However, if any transects were sampled with fewer than five sample units, the unused units were distributed along other transects at un-sampled depths or in a way that best covered the range of available habitat. Additional samples were collected to included unique habitat features (e.g., large-woody debris, vegetation, etc.) not covered by transects. Only one sample was collected if only one point was ≤ 0.5 m deep.

Appendix B

SAS codes used for data analyses.

Month design:

```
*CPUE
option ps=70 ls=100;
data ;infile 'f:\anova_data\mo_cpue_ev.csv' dsd missover firstobs=2;
input MNTH$ SBTP$ SBID$ REGN$ DPCS$ CPUE SDPT SVEL TEMP STRB SUBS SSLP
SSSS;
proc print;
proc mixed; classes mnth sbtp sbid regn dpcs;
model cpue=sbtp|regn|dpcs|mnth;
random sbid(sbtp) sbid(sbtp regn) sbid(sbtp regn dpcs);
lsmeans sbtp|regn|dpcs|mnth/pdiff;
run;
*BODY LENGTH
option ps=70 ls=100;
data ;infile 'f:\anova_data\mo_bodylength.csv' dsd missover firstobs=2;
input MNTH$ SBTP$ SBID$ REGN$ DPCS$ BDLN;
*proc print;
proc mixed; classes mnth sbtp sbid regn dpcs;
model bdln=sbtp|regn|dpcs|mnth;
random sbid(sbtp) sbid(sbtp regn) sbid(sbtp regn dpcs);
lsmeans sbtp|reqn|dpcs|mnth/pdiff;
run;
Diel design:
*CPUE
option ps=70 ls=100;
data ;infile 'f:\anova_data\diel_cpue_ev.csv' dsd missover firstobs=2;
input DIEL$ SBID$ REGN$ DPCS$ CPUE SDPT SVEL TEMP;
proc print;
proc mixed; classes diel sbid regn dpcs;
model cpue=regn|dpcs|diel;
random sbid(regn) sbid(regn dpcs);
lsmeans regn|dpcs|diel/pdiff;
run;
*BODY LENGTH
option ps=70 ls=100;
data ;infile 'f:\anova_data\diel_bodylength.csv' dsd missover
firstobs=2;
input DIEL$ SBID$ REGN$ DPCS$ BDLN;
*proc print;
proc mixed; classes diel sbid regn dpcs;
model bdln=regn|dpcs|diel;
random sbid(regn) sbid(regn dpcs);
lsmeans regn|dpcs|diel/pdiff;
run;
```

Metadata for SAS code input classes:

MNTH = temporal factor month

DIEL = temporal factor diel period

SBTP = spatial factor sandbar type

SBID = unique identifier for each of the eight individual sandbars used in this study

REGN = spatial factor region

DPCS = spatial factor sample unit category

sDPT = environmental factor depth, square root transformed

sVEL = environmental factor velocity, square root transformed

TEMP = environmental factor water temperature

sTRB = environmental factor turbidity, square root transformed

SUBS = environmental factor substrate particle size index

sSLP = environmental factor slope, square root transformed

SSSS = environmental factor sandbar shoreline sinuosity

CPUE = catch-per-unit-effort

BDLN = body length

Appendix C

September substrates

I did not expect to see a significant difference in substrate particle size among months, especially as dramatically different as September was. The data showed this was due to a greater proportion of gravel and some cobble in samples at head region of point bars during September. Since the primary transportation mode of fluvial sediments is suspension or saltation in flowing water, I examined the hydrograph at Boonville, MO near the midpoint of the study reach and found a sharp rise and fall in discharge that occurred in late August and early September (Figure 2.6). If this discharge spike redistributed river sediments it may have deposited larger substrates in the head region of point bars; there, during high discharge, the effects of the sandbar would have slowed velocity and deposited larger substrates. Lower discharge following the receding limb, shallow slope in head regions of point bars, and digital model outputs of sandbar morphology in relation to discharge (particularly the head region of point bars, see Tracy-Smith (2006)) indicates that samples collected near the deeper end of the range 0.0-.05 m would have been an unusually long distance offshore. A discharge spike followed by a period lower discharge during September may have made habitats with larger deposited substrates in head region of point bars accessible to my 0.0-0.5 m depth sample design.

Literature Cited

Tracy-Smith, E. 2006. Relation of Missouri River flows to sandbar morphology with implications for selected biota. Master's Thesis. University of Missouri, Columbia, Missouri.

Appendix D

Table D1. Chart to convert substrate particle size index values to four particle size classes on the modified Wentworth scale. Index values representing equal proportions of adjacent particle size classes were extracted directly from the raw data.

Index when substrates					
	are 100% 50%		Particle size range (mm)		
Substrate					
Silt	0.03		< 0.0625		
		0.18			
Sand	1.03		0.0625 - 2		
		5.80			
Gravel	33.00		2 - 64		
		187.00			
Cobble	1056.00		> 64		

Table D2. Mean catch-per-unit-effort (CPUE $\#/m^3$) and body length (mm TL) \pm standard error (SE) between light and dark diel periods for species collected in shallow waters adjacent to sandbars on lower Missouri River. An asterisk preceding mean or SE value indicates the value is greater than 0.0 and less than 0.05.

	Light		Dark	
Family &	Body		Body	
Species	CPUE	length	CPUE	length
Hiodontidae				
goldeye	*0.1 ± *0.1	44.7 ± 0.0	$0.1 \pm *0.1$	47.5 ± 4.4
Clupeidae				
gizzard shad	0.5 ± 0.2	74.8 ± 4.2	0.4 ± 0.1	56.8 ± 2.6
Cyprinidae				
sicklefin chub	*0.1 ± *0.1	31.8 ± 2.8	*0.1 ± *0.1	24.9 ± 0.7
sturgeon chub	$0.1 \pm *0.1$	18.4 ± 0.6	*0.1 ± *0.1	24.5 ± 2.2
speckled chub	$0.1 \pm *0.1$	22.1 ± 1.1	0.6 ± 0.2	27.1 ± 0.7
silver chub	$0.1 \pm *0.1$	32.5 ± 2.3	0.8 ± 0.3	36.8 ± 1.9
plains minnow	0.1 ± 0.1	29.4 ± 5.6	*0.1 ± *0.1	25.4 ± 0.4
bluntnose minnow	*0.1 ± *0.1	17.5 ± 0.0		
bullhead minnow	$0.1 \pm *0.1$	22.4 ± 1.0	0.6 ± 0.2	27.2 ± 1.7
bigmouth shiner			*0.1 ± *0.1	30.5 ± 14.0
sand shiner	$0.1 \pm *0.1$	19.1 ± 3.9	*0.1 ± *0.1	19.8 ± 0.0
river shiner	0.1 ± 0.1	24.1 ± 2.5	0.1 ± 0.1	19.5 ± 2.2
red shiner	3.1 ± 1.1	27.5 ± 0.9	2.4 ± 0.9	28.7 ± 1.2
emerald shiner	0.6 ± 0.2	35.9 ± 2.7	4.6 ± 1.6	33.6 ± 1.0
Catostomidae				
quillback	$0.1 \pm *0.1$	26.3 ± 3.0	0.2 ± 0.2	28.0 ± 1.5
river carpsucker	42.4 ± 17	18.7 ± 0.1	61.3 ± 35	20.2 ± 0.1
bigmouth buffalo			$0.1 \pm *0.1$	15.0 ± 0.3
Ictaluridae				
channel catfish blue catfish	0.3 ± 0.1	48.3 ± 2.2	3.8 ± 1.3	57.1 ± 3.8

Table D2. Continued.

	Light		Dark	
Family &		Body		Body
Species	CPUE	length	CPUE	length
Poecilliidae				
western mosquitofish	0.4 ± 0.3	27.7 ± 1.8	0.3 ± 0.2	19.8 ± 1.2
Moronidae				
striped bass	*0.1 ± *0.1	30.6 ± 0.0	0.1 ± 0.1	61.1 ± 2.2
white perch			0.1 ± 0.1	42.9 ± 1.7
Centrarchidae				
green sunfish				
bluegill	$0.1 \pm *0.1$	21.4 ± 1.5	0.4 ± 0.2	23.6 ± 0.9
Sciaenidae				
freshwater drum	0.3 ± 0.1	33.6 ± 2.6	1.5 ± 0.3	39.7 ± 1.7