FISH AND INVERTEBRATE COMMUNITY RESPONSE TO FLOW MAGNITUDE IN THE KANSAS RIVER

by

JOSEPH EDWARD GERKEN

B.S., Miami University, 2005
M.S., University of Central Arkansas, 2007

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2015

Abstract

River discharge influences fish and invertebrate communities and understanding how hydrologic variables contribute to fish and invertebrate composition can provide information for restoration and management. This study examines the relationship between several flow regime metrics that may influence fish and invertebrate community structure in large river systems such as the Kansas River. First, I examined how hydrology influences macroinvertebrate (drifting and benthic) density and fish communities before, during, and after flooding in both main and secondary channels. I found that drifting invertebrate density increased during flooding potentially providing increased prey opportunities for fishes. I also found that fluvial dependent and generalist fish species use inundated habitats more than fluvial specialists. My results suggest that the flux of water into inundated habitats supports a unique subset of invertebrate and fish communities of the main channel. Next, I examined the importance of lateral connectivity on fish and invertebrate composition by examining differences in seasonally and permanently inundated secondary channels in relation to main channel reaches. I found that drifting and benthic invertebrate assemblages and fish assemblages differed between seasonally inundated and permanently connected secondary channels. These results suggest that maintenance of diverse secondary channel connections is useful in preserving native biota in the Kansas River. Finally, I tested if hydrologic variables influenced recruitment of four native Kansas River fishes. I found that recruitment for two of the four fish species (flathead catfish, *Pylodictis olivaris*, and shovelnose sturgeon, *Scaphirhynchus platorynchus*) increased in high flow years. These results indicate that a natural and variable flow regime may be important for maintaining fish community structure in the Kansas River. The results of this study have implications for management strategies that include the use of high flows to provide a pulse of insect prey to the

main channel for fishes, restoration of natural high and low flow variability as important to fish recruitment, and diversity in secondary channel connectivity (seasonal and permanently connected) that promotes unique fish and invertebrate communities.

FISH AND INVERTEBRATE COMMUNITY RESPONSE TO FLOW MAGNITUDE IN THE KANSAS RIVER

by

JOSEPH EDWARD GERKEN

B.S., Miami University, 2005
M.S., University of Central Arkansas, 2007

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2015

Approved by:

Major Professor
Dr. Craig Paukert

Copyright

Abstract

River discharge influences fish and invertebrate communities and understanding how hydrologic variables contribute to fish and invertebrate composition can provide information for restoration and management. This study examines the relationship between several flow regime metrics that may influence fish and invertebrate community structure in large river systems such as the Kansas River. First, I examined how hydrology influences macroinvertebrate (drifting and benthic) density and fish communities before, during, and after flooding in both main and secondary channels. I found that drifting invertebrate density increased during flooding potentially providing increased prey opportunities for fishes. I also found that fluvial dependent and generalist fish species use inundated habitats more than fluvial specialists. My results suggest that the flux of water into inundated habitats supports a unique subset of invertebrate and fish communities of the main channel. Next, I examined the importance of lateral connectivity on fish and invertebrate composition by examining differences in seasonally and permanently inundated secondary channels in relation to main channel reaches. I found that drifting and benthic invertebrate assemblages and fish assemblages differed between seasonally inundated and permanently connected secondary channels. These results suggest that maintenance of diverse secondary channel connections is useful in preserving native biota in the Kansas River. Finally, I tested if hydrologic variables influenced recruitment of four native Kansas River fishes. I found that recruitment for two of the four fish species (flathead catfish, *Pylodictis olivaris*, and shovelnose sturgeon, *Scaphirhynchus platorynchus*) increased in high flow years. These results indicate that a natural and variable flow regime may be important for maintaining fish community structure in the Kansas River. The results of this study have implications for management strategies that include the use of high flows to provide a pulse of insect prey to the

main channel for fishes, restoration of natural high and low flow variability as important to fish recruitment, and diversity in secondary channel connectivity (seasonal and permanently connected) that promotes unique fish and invertebrate communities.

Table of Contents

List of Figures

List of Tables

Acknowledgements

I am tremendously grateful to my advisor, Craig Paukert, for providing me the guidance, mentoring, and support to be successful and for sticking with me to the end. I am thankful for all of the help you have given me and all of the opportunities that you have provided along the way. I thank Keith Gido for serving on my committee and for stepping in to help me reach the finish line. Your advice has been invaluable and I am gracious for all of your help. I am thankful to Walter Dodds for serving on my committee, for providing me with great advice, and for showing me that a harmonica can be more than a kids toy when put into the right hands. I thank Melinda Daniels for serving on my committee and helping me realize the important link between river geomorphology and riverine ecology. I thank Mike Quist for serving on my committee, for helping me learn fish aging skills, and for encouraging me to get involved with the American Fisheries Society. I thank Jason Ellis for his help and for serving as my outside committee chair on short notice.

I am thankful to numerous graduate and undergraduate students that helped me along the way both with field work and with helping me keep my sanity throughout the process. I am extremely thankful to Josh Perkin for always being a fantastic collaborator and even better friend. I am grateful for all of the time spent dissecting figures over a beverage or two. I thank Jason Fischer and Andrea Severson for keeping me company and helping me laugh in Leisure Hall. I am grateful to the assistance of Kirk Mammoliti, Kyle Steinert, Joe Rezek, and Andrew Dellett – this project would not have been possible without countless long hot summer days on the river. I would also like to thank Robert Clark for constantly reminding me of the important things in life and for always being a great friend regardless of the circumstances. I thank Billie

Deam, Stan Cook, and Pat Callaghan for being great role models and fantastic friends and for spending countless nights with me solving all of the world's problems.

I would like to thank my parents Gary and Judy Gerken for their continued support throughout my life and academic career. Dad, thank you for always taking time out of your busy schedule when I was growing up to teach me the importance of playing outside and enjoying nature and for providing me with a role-model that I always have and always will look up to. The memories of our days digging up worms and nights fishing until dark (or later) are constant reminders of how fun and exciting biology and nature can be. Mom, thank you for always supporting me and for inspiring me to explore nature and always embrace my curiosity. You have always been there for me and have always been proud of me even when my endeavors were crazy or seemingly impossible. None of this would have been possible without your support.

I would like to thank my sister Christina for instilling my love for science at an early age by playing outside with me for hours growing up. I would like to thank my brother Todd for including me in many outdoor adventures including reaching for the "gaff hook" and almost feeding me to an alligator. I am thankful to Jeff Gerken for teaching me to love fish by taking me fishing and letting me catch that giant catfish in Tennessee. I would also like to thank my uncle Dale for his steadfast support and for suffering through numerous rounds of golf to help me keep my sanity.

I am so incredibly thankful to my wife Alison for her constant support, encouragement, and help along the way. She has helped in me in so many ways and this would not have been possible without her constant help and unwavering love. Thank you for always being by my side and for keeping me sane and happy. I would also like to thank our 10-year old puppy Max for all of the happiness and companionship he has provided me over the past 10 years.

This project was funded by the Kansas Department of Wildlife, Parks, and Transportation and additional support was provided from the U.S. Fish and Wildlife Service. I am extremely grateful for the support of these agencies and many employees that supported this project.

Chapter 1 - Flooding and Lateral Connectivity: An Ecosystem Perspective

Flowing water is a defining characteristic of all riverine ecosystems but flow regimes within and among rivers are naturally dynamic and vary both spatially and temporally (Poff et al. 1997; Landres et al. 1999). Hydrology of lotic systems commonly includes periods of high and low flows but the duration, frequency, timing, and magnitude of these events varies among rivers and river alterations (Poff et al. 1997). Hydrology can alter many aspects of riverine systems including habitat structure, nutrient flow, and biodiversity (Power et al. 1995, Doyle et al. 2005, Konar et al. 2013). Therefore, understanding how river flows regulate ecological processes and influence riverine organisms is important for conservation and management of these dynamic systems.

Lateral movement of water from the main channel into floodplains is an important component of river flow for biodiversity and ecosystem function (Heiller et al. 1995; Bunn and Arthington 2002). For example, inundation of floodplain habitats in the Mississippi River in 2011 corresponded with increased fish diversity and native fish growth rates compared to main channel habitats (Phelps et al. 2015). Floodplain habitats are some of the most biologically diverse habitats in the world and they provide many ecological benefits to aquatic organisms in large-river systems (Tockner and Stanford 2002) that rely on floodplain habitats for many important life history needs (Tockner and Stanford 2002; Winemiler 2005; Górski et al. 2011). The Flood Pulse Concept (Junk et al. 1989) theorizes that most of the energy (i.e. nutrients) in large rivers is derived from floodplain habitats and therefore high flows are necessary for many lotic organisms to persist. However, the timing, duration, and magnitude of floods can alter the benefits of flooding (Poff et al. 1997) and benefits of lateral connectivity and floodplain habitats

may change depending on the amount of lateral connectivity (i.e. seasonally or permanently connected habitats).

Lateral connectivity between main channel and floodplain habitats during flooding was historically a common natural process in many large rivers and provided important ecological benefits for riverine organisms (Poff et al. 1997; Galat et al. 1998), and also provides many benefits to humans (Zimmerman et al. 2008, Vörösmarty 2010, Dodds et al. 2013). The widespread regulation of stream flow and restriction of overbank flooding via levees has altered floodplain inundation regimes in most large river systems (Fahrig 2003; Carlisle et al. 2011) and thus lateral connectivity between main channel and true floodplain habitats is rare or absent in many rivers. Mitigation and other restoration activities to provide inundation of secondary channels and other riparian habitats may be important for fish and invertebrate communities in these systems (Poff et al. 1997; Besacier-Monbertrand et al. 2014). Many recent studies have examined the relationship between lateral connectivity and fish and invertebrate communities (e.g. McMullen and Lytle 2012; Besacier-Monbertrand et al. 2014; Górski et al. 2014). However, understanding the combined response of fish and invertebrate communities to lateral connectivity may help us better understand the overall importance of floodplain inundation on riverine ecosystems.

We tested three hypotheses to examine the importance of hydrologic variation and lateral connectivity for fish and invertebrates in the Kansas River, a seventh-order river in the Great Plains. Chapter 2 describes how fish and invertebrate assemblages were affected by flooding and increased lateral connectivity in a seasonally connected secondary channel only inundated during flooding. We examine invertebrate abundance trends in main channel habitats before, during, and after flooding and among main and secondary channel habitats during flooding over three

years of sampling. We then relate these trends to fishes and examine patterns in fish communities among habitats to identify the importance of lateral connectivity and inundation of seasonal floodplain habitats for biota in large river systems. Chapter 3 builds on these findings but expands them to a permanently connected secondary channel. We again examine trends in invertebrate and fish assemblages and compare the findings from the permanently connected secondary channel to the seasonally connected secondary channel studied in chapter two. In an effort to further understand the benefits of lateral connectivity, we examine the role of hydrology on fish recruitment patterns in the Kansas River in Chapter 4. Finally, in Chapter 5 we present the main findings of each chapter and summarize the importance of all the research presented in the previous chapters. These findings provide critical information regarding the importance of flooding and lateral connectivity for the biota of a temperate large-river ecosystem and may help guide restoration efforts focused on lateral connectivity and the natural flow regime.

Literature Cited

Besacier-Monbertrand, A.L., A. Paillex, and E. Castella. 2014. Short-term impacts of lateral hydrological connectivity restoration on aquatic macroinvertebrates. *River Research and Applications* 30:557-570.

Bunn, S.E. and A.H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492-507.

Carlisle, D.M., D.M. Wolock, and M.R. Meador. 2011. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264-270.

Dodds, W.K., J.S. Perkin, and J.E. Gerken. 2013. Human impact on freshwater ecosystem services: a global perspective. *Environmental Science and Technology* 47:9061-9068.

Doyle, M.W., E.H. Stanley, D.L. Strayer, R.B. Jacobson, and J.C. Schmidt. 2005. Effective discharge analysis of ecological processes in streams. *Water Resources Research* 41: W11411; doi:10.1029/2005WR004222.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

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. Semelitsch. 1998. Flooding to restore connectivity in regulated, large-river wetlands. *Bioscience* 48:721-733.

Górski, K., J.J. De Leeuw, H.V. Winter, D.A. Vekhov, A.E. Minin, A.D. Buijse, and L.A.J. Nagelkerke. 2011. Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. *Freshwater Biology* 56:210-2225.

Heiler, G., T. Hein, F. Schiemer, and G. Bornette. 1995. Hydrological connectivity and flood pulses as the central aspects for the integrity of a river-floodplain system. *Regulated Rivers- Research and Management* 11:351-361.

Junk, W.J., P.B. Bayley, and R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106:110-127.

Konar, M., M.J. Todd, R. Muneepeerakul, A. Rinaldo, I. Rodriguez-Iturbe. 2013. Hydrology as a driver of biodiversity. *Advances in Water Resources* 51:317-325.

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179-1188.

McMullen L.E. and D.A. Lytle. 2012. Quantifying invertebrate resistance to floods: a global-scale meta-analysis. *Ecological Applications* 22:2164-2175.

Phelps, Q.E., S.J. Tripp, D.P. Herzog, and J.E. Garvey. 2015. Temporary connectivity: the relative benefits of large river floodplain inundation in the lower Mississippi River. *Restoration Ecology* 23:53-56.

Poff, N.L., J.D. Allen, 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.

Power, M.E., A. Sun, G. Parker, W.E. Dietrich, and J.T. Wootton. 1995. Hydraulic food-chain models. *Bioscience* 45:159-167.

Tockner, K. and J.A. Stanford. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29:308-330.

Vörösmarty, C.J., P.B. McIntyre, M.O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S.E. Bunn, C.A. Sullivan, C.R. Liermann, and P.M. Davies. 2010. Global threats to human water security and river biodiversity. *Nature* 467:555-561.

Winemiller, K.O. 2005. Floodplain river food webs: generalizations and implications for fisheries management. Pages 285–312 in R. L. Welcomme and T. Petr, editors. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries. Volume 2. Mekong River Commission, Phnom Penh, Cambodia.

Zimmerman, J. B., J.R. Mihelcic, and J. Smith. 2008. Global Stressors on Water Quality and Quantity. *Environmental Science and Technology* 42:4247-4254.

Chapter 2 – Fish and Invertebrate Community Response to High Flows and Floodplain Inundation in the Kansas River

ABSTRACT

Flow regimes control many components of aquatic ecosystems and affect the distribution and abundance of aquatic organisms. Floods and floodplain connectivity are integral components of the natural flow regime of many lotic systems and are believed to regulate energy flow to macroinvertebrates and fishes. First, we examined how hydrology impacts invertebrate densities and presence and absence of fishes before, during, and after flooding over a three year period in main channel habitats in a Great Plains river. Next, we assayed invertebrate densities and fish communities response to hydrology among main channel and inundated secondary channel habitats during flooding. Drifting invertebrate densities increased by an average of 471% in all habitats during flooding demonstrating that floods proved a pulse of invertebrates to the river system potentially resulting in an increase in prey availability to fish. In contrast, highest benthic invertebrate densities were consistently observed before or after, but never during, flooding. Models with year and flood stage had the strongest support for differences in benthic and drifting invertebrate communities among sampling periods indicating that benthic and drifting invertebrate communities respond to hydrology but that these hydrologic effects are confounded by annual variation. During flooding, inundated habitats supported a unique invertebrate community with higher densities of Chaoboridae (32.6% of catch) whereas Chironomidae were dominant in main channel habitats (47 – 50%). We found that fluvial dependent and generalist fish species used inundated habitats more than fluvial specialist. Although there are many potential mechanisms by which fish and invertebrates may benefit (e.g. spawning, feeding, and

refugia habitats) from secondary channels, our results indicate that the secondary channel habitats are important for these organisms, both directly and indirectly.

INTRODUCTION

The flow regime controls many abiotic components of lotic ecosystems including habitat structure, water chemistry, and nutrient cycling (Poff and Ward 1989; Poff et al. 1997; Bunn and Arthington 2002). Hydrology also has a profound impact on the distribution and abundance of aquatic organisms and has been considered the "master variable" of lotic ecosystem structure and function (Power et al. 1995; Doyle et al. 2005). Natural hydrology varies both spatially and temporally and often includes periods of low-flows and flooding in addition to baseflow conditions (Poff et al. 1997; Landres et al. 1999) and this variation in the flow regime is essential in maintaining the structure and function of freshwater ecosystems (Poff et al. 1997; Bunn and Arthington 2002; Poff 2009).

Many theories have been developed to explain the role of varying flow conditions on lotic ecosystem structure and function and the biotic communities they support. The River Continuum Concept (RCC; Vannote et al. 1980) was among the first of these theories and developed a framework to understand the transfer of nutrients and energy in a longitudinal manner from headwaters downstream to large rivers. However, the RCC failed to consider the role of floodplain inundation. The Flood Pulse Concept (FPC; Junk et al. 1989) added to the RCC framework to incorporate the importance of the exchange of nutrients or energy between the floodplain and main channel of large rivers. Specifically, the FPC purports that connectivity between floodplains and main channel habitats is critical for productivity and biodiversity in large river systems (Junk et al. 1989; Tockner et al. 2002). Although both the RCC and FPC attempt to explain energy flow in lotic ecosystems, the two concepts are not mutually exclusive.

It is possible that a combination of these patterns occur in many lotic systems; however, the importance of each is unclear in temperate large river systems (Tockner et al. 2000; Thorp et al. 2006; Junk and Bayley 2007). More recently, the river wave model, which proposes that energy production and inputs are largely dependent on riverine flows, was developed to better synthesize energy flow in riverine ecosystems (Humphries et al. 2014). The river wave model suggests that local autochthonous production and allochthonous inputs are primary energy sources during low flows (i.e. wave troughs), upstream allochthonous inputs and downstream movement of material regulate energy when flows are increasing and decreasing (i.e. wave rising and falling limbs), and during peak flows (i.e. wave crests) production is primarily derived from floodplain habitats (Humphries et al. 2014). The shape of the wave (and corresponding changes in primary energy sources) is strongly linked to riverine hydrology and these patterns can be impacted by many factors including anthropogenic regulation, climate, and geomorphology (Humphries et al. 2014).

In many lotic systems, floods are natural disturbance events that include a period of high flow that connects main channel and floodplain habitats (Poff et al. 1997; Galat et al. 1998). Organisms, including fishes, in large river systems are dependent on these flooding events to initiate spawning, and provide nursery, feeding, and refugia habitats (Welcomme 1985; Zeug and Winemiller 2007). The natural flow regime, including flooding, varies spatially and temporally and many native fishes have adapted to survive and often thrive during extremes in their natural flow regime (Freeman et al. 2001; Koel and Sparks 2002).

Anthropogenic activities have altered the natural flow regime and impacted many large rivers (Vörösmarty et al. 2010; Dodds et al. 2013). For example, the construction of dams, levees, and the channelization of main channels have altered the timing, magnitude, and duration

of high flows, and reduced or eliminated floodplain connectivity in many large rivers (Poff et al. 1997; Puckridge et al. 1998, Carlisle et al. 2011) and led to declines in native species (Bunn and Arthington 2002; Poff and Zimmerman 2010). Altered flow regimes and accompanying water quality declines may also impact macroinvertebrate communities and disrupt the prey base for fishes (Lind et al. 2006). Because anthropogenic impacts are so pervasive in freshwater ecosystems, many contemporary management and restoration activities focused on maintaining biodiversity and ecosystem structure and function in large river systems incorporate protocols to mimic the natural flow regime (e.g. Propst and Gido 2004; Arthington et al. 2006; Kiernan et al. 2012).

Restoring natural floodplain connectivity may benefit large river fishes, invertebrates, and ecosystems through several pathways including increasing access to food sources and transferring nutrients and energy from inundated floodplain habitats to the main channel (Poff et al. 1997; Besacier-Monbertrand et al. 2014). Floods may increase the number of invertebrate prey available to fishes in the main channel either by increasing longitudinal connectivity (i.e., RCC), by increasing lateral connectivity (i.e., FPC), or a combination of both. Although autochthonous productivity and terrestrial carbon sources provide the foundation for large river food webs (Thorpe et al. 1998; Herwig et al. 2004; Winemiller 2005), macroinvertebrates can transfer these basal sources throughout the food web via "bottom-up" processes (Polis et al. 1997). Therefore, macroinvertebrates are a good surrogate for tracking when and where the energy is used in the system as they are a primary food source for many large river system fishes (Wipfli et al. 2010). High flows can lead to an increase in shear stress on benthic environments potentially leading to "catastrophic drift", causing an increase in the density of benthic invertebrates in the drift and decreased densities in benthic habitats (Callisto and Goulart 2005;

Lauridsen and Fribert 2005; Gibbins et al. 2007). Tracking invertebrate abundance before, during and after a flood may help us understand the role of flooding on prey availability and increase our understanding of the importance of high flows and floodplain connectivity and provide support for the river wave concept (Humphries et al. 2014). The influence of lateral connectivity between main channel and secondary channel habitats on macroinvertebrate communities may be regulated by physical or habitat effects of high flows on these taxa (Tockner et al. 2000; Starr et al. 2014). By examining invertebrate densities in main channel and floodplain habitats we may also increase our understanding of how invertebrate communities use secondary channel habitats in large rivers.

Despite the variable connectivity and corresponding intermittent flows in secondary channels, invertebrates may become established in these habitats under certain hydrologic conditions (Figure 2.1). If secondary channels contain standing water before flooding, they may support breeding and colonizing invertebrates that may then drift into the main channel during flooding (Boulton and Lloyd 2006). Otherwise, secondary channels may serve as a sink for invertebrates as invertebrates found in the secondary channel must be derived from drift from upstream reaches during floods (Figure 2.1). Macroinvertebrate colonization rates are highly variable and are influenced by a number of factors (e.g. temperature, dispersal rate, time since last inundation) in the inundated habitat (Mackay 1992; Boulton and Lloyd 2006). Macroinvertebrate populations can establish quickly (1-3 days) in recently inundated areas especially in areas with high densities of invertebrate resting stages or with high abundances of "explosive breeders" that can quickly become established in new aquatic environments (De Stasio 1989; Boulton and Lloyd 1992, Corti et al. 1997). Tracking the source (e.g. upstream or

floodplain reaches) of invertebrates during flooding can increase our understanding of potential invertebrate prey and consumption by fishes.

Many recent studies have examined the role of flooding and lateral connectivity on invertebrates (Cross et al 2011; McMullen and Lytle 2012; Besacier-Monbertrand et al. 2014) and movement of fishes between main channel and inundated habitats (Lyon et al. 2009; Conallin et al. 2011; Gorski et al. 2014). However, understanding the simultaneous changes in invertebrate abundance and fish movement as an interacting community will help us better understand the overall aquatic community response to lateral connectivity. We seek to advance our understanding of the importance of flooding and floodplain connectivity in temperate rivers by testing three hypotheses to identify the role of flooding on invertebrates and utilization of invertebrate prey resources for large river fishes. First, we examined how floods impact invertebrate abundance and density by testing the hypothesis that main channel macroinvertebrate community composition will change with flow conditions (before, during, after flooding) and density will increase in main channel habitats during flooding. Next, we examined invertebrate density and community composition among main channel and inundated habitats during flooding to identify the importance of these habitats as potential feeding habitats for fishes. Finally, we tested the hypothesis that fish prey on invertebrates from inundated habitats directly (by moving into inundated habitats) and indirectly (staying in main channel and feeding on prey carried into the main channel, sensu: Junk et al. 1989; Galat and Zweimuller 2001) resulting in different fish communities in main channel habitats where we expect more generalist species and secondary channel habitats where we expect more fluvial specialist fish species. Although our hypothesis was developed to examine differences in fish communities related to prey availability, fishes often use these habitats for other reasons such as spawning or

refugia from high flows (Welcomme 1985; Zeug and Winemiller 2007) and differences in community structure may be influences by other factors.

METHODS

Study site

The Kansas River is a 7th order sand bed river located in northeast Kansas and flows 274 km from its source near Junction City, KS to the Missouri River in Kansas City, KS. The Kansas River has a gradient of 0.5 – 1.2m/km resulting in a wide ($\bar{x}$ = 164 m) and shallow ($\bar{x}$ = 1.5m) channel throughout most of the river (Makinster and Paukert 2008; Eitzmann and Paukert 2010). With a watershed of approximately 155,000 km^2 (Colby et al. 1956), the Kansas River accounts for about 12% of the Missouri River watershed (Metcalf et al. 1966). The Kansas River mainstem is relatively free of impoundments with the exception of one lowhead dam, Bowersock Dam, located near Lawrence, Kansas (river kilometer 83) and one weir, Johnson County Weir, located near rkm 27. However, flood control dams on major tributaries including the Smokey Hill and Republican Rivers, have altered the flooding regime dramatically since the early 1960s (Costigan and Daniels 2012). As a result, extensive floodplain inundation along the Kansas River is now rare.

Our study design included three reaches in the main channel of the Kansas River near Manhattan, Kansas (39°11’24”N, 96°30’53”W) and an adjacent inundated secondary channel reach (Figure 2.2). Macroinvertebrates were collected from two main channel reaches of the Kansas River near Manhattan, Kansas (rkm 232) before, during, and after flooding (April – September) in 2009 – 2011 (Figure 2.3). Each reach was approximately 1km long and was divided into four equidistant transects. Samples were collected from the left, middle, and right of each transect for a total of twelve sampling sites in each reach. We defined flooding as

inundation of the sampled secondary channel, which occurred when flows were 137% higher than the 20 year mean annual flow. These floods were constrained to the river channel and never extended over-bank to true floodplain habitats but they inundated some riparian terrestrial (i.e. bank) habitats. Total flood duration was much longer in 2010 (76 days) than in 2009 (14 days) and 2011 (28 days). Secondary channel samples were only collected during periods of flooding in 2009 – 2011 because it did not have sufficient flows for sampling before and after flooding. Samples were collected starting on the first day of flooding in 2011 but we were unable to accurate calculate when flooding would occur in 2009 and 2010 and as a result samples were collected starting on the third day of flooding in these years.

Main channel macroinvertebrate response during flooding

Drifting Invertebrates

Drifting invertebrates were sampled during daylight hours at each site before, during, and after flooding in the upstream and downstream habitats using a 150 cm long paired bongo net with 50 cm diameter openings and 202 µm mesh attached to the bow of the boat with a 10 m tow rope and deployed downstream. The net was held in place using the outboard motor and floats were attached to the top of the bongo net to ensure the nets remained suspended near the top of the water column during sampling. For each sample, nets were deployed for 150 seconds and velocity was recorded for each net using a mechanical flow meter attached to the net opening.

Benthic Invertebrates

Benthic invertebrates were sampled at each site before, during, and after flooding in the upstream and downstream habitats before, during, and after flooding using a mini-ponar dredge (15.24 cm × 15.24 cm opening). Samples were emptied into a wash bucket and elutriated through

a 250 µm sieve in the field. After elutriation, all remaining substrate was washed through three sieves (63 – 250 µm) and into a catch pan. All sieves and the catch pan were visually examined for invertebrates to ensure that all invertebrates were collected before discarding the elutriated substrate. Invertebrate density was calculated from invertebrate abundance data as catch per unit volume (number per m^{-3}) for drifting invertebrates and catch per unit area (number per m^{-2}) for benthic invertebrates. Because invertebrate density was standardized for volume (drifting) and area (benthic), these groups were analyzed separately.

Invertebrate Laboratory Methods

All invertebrate samples were preserved in 10% buffered neutral formalin in the field, stained with Rose Bengal, and returned to the laboratory, sorted, identified to order, and enumerated. Common aquatic invertebrates were identified to family when possible. As a result, some taxa of the order diptera were identified to family (i.e. ceratopogonidae, chaoboridae, and chironomidae) whereas other dipterans, including terrestrial and adult dipterans, were classified as "grouped diptera". When necessary, large samples were split using a Folsom Plankton Splitter and one half of the sample was randomly selected for processing.

Data Analysis

Seven candidate models were created to identify how main channel macroinvertebrate densities varied with respect to sampling year, reach (upstream main channel, downstream main channel, inundated secondary channel), and flood stage (before, during, or after flooding; Table 2.1) for drifting and benthic invertebrates separately. We also included a null model with just the intercept to provide a reference for model performance. We used an information theoretic approach based on Akaike's information criterion (AIC; Akaike 1974, Burnham and Anderson 2002) to identify best fit models. Akaike information criterion corrected for small sample size

(AICc) to decrease the probability of selecting overfit models (Burnham and Anderson 2002). We calculated ΔAIC_c ($\Delta AIC_c = AIC_c - AIC_{c(minimum)}$) to identify best fit models, and candidate models with $\Delta AIC_c < 2$ were considered competing models with similar performance (Burnham and Anderson 2002). In such cases, we calculated Akaike weights (w_i), which indicates the probability that model *i* is the best fit model among competing candidate models (Burnham and Anderson 2002).

To evaluate differences in community structure among samples, a Bray-Curtis distance metric was used followed by an analysis of similarity (ANOSIM) to test for effects of sampling years and flood stages in the main channel reaches. Non-metric multidimensional scaling (NMDS) was used to visually examine variation in macroinvertebrate structure among flood stages in the main channel. Scree plots were constructed and we visually examined the relationship between stress and number of retained axes to determine the optimal number of axes to retain. The Similarity Percentage (SIMPER) function was used to identify the contribution of each taxa to the overall dissimilarity among groups for the NMDS plot. All statistical analyses were conducted using R version 2.13.1 (The R Foundation for Statistical Computing 2011).

Main channel and inundated habitat macroinvertebrate response during flooding

Drifting and benthic macroinvertebrates were collected in upstream and downstream main channel reaches and an inundated secondary reach during floods when all habitats were connected using the methods outlined in the previous section. Three candidate models were created to examine how macroinvertebrate density varied in relation to sampling year and reach during flooding conditions (Table 2.1). Akaike information criterion and ΔAIC_c scores were used to examine relative model performance and identify best fit models.

We tested the hypothesis that macroinvertebrate communities were similar among reaches during flooding using a Bray-Curtis distance metric followed by an analysis of similarity (ANOSIM). Non-metric multidimensional scaling (NMDS) was used to visually examine variation in macroinvertebrate structure among reaches during flooding. We identified the optimal number of axes to retain by visually examining Scree plots. Similarity percentage (SIMPER) was calculated for each plot to identify the contribution of each species to the overall dissimilarity among reach groups.

Fish community response to flooding

We tested the hypothesis that fish consume invertebrate prey originating from inundated habitats during flooding by collecting fish from the two main channel reaches and one inundated secondary channel reach of the Kansas River near Manhattan, Kansas (rkm 232). Fishes were collected from each reach using a combination of pulsed-DC boat electrofishing, experimental gill nets, and seines. Pulsed-DC electrofishing was conducted following the standardized protocols presented by Guy et al. (2009) and Miranda (2009). At each transect, one 300-second sample was collected from a randomly selected bank with the boat moving downstream for a total of four samples per habitat (main channel upstream, downstream, and secondary channel). Captured fish from each transect were enumerated, measured (mm), and identified to species or returned to the laboratory when necessary for identification.

Monofilament experimental gill nets (1.8 m tall and 30.5 m long with four total 7.6 m long panels of 1.90, 3.81, 5.08, and 7.62 cm bar measure mesh) were used to further examine the fish assemblage at each transect. One gill net was set in the evening at a randomly selected location (left, middle, right) of each transect following standardized protocols defined by Lester

et al. (2009) and Curry et al. (2009) and retrieved the following morning for a total of four nets per habitat. Nets were set parallel to the flow to reduce drag during periods of high flow and maintain consistency among all sampling periods.

Small bodied fishes were collected with seines from one bank of each of the four transects in each reach. Three to five seine hauls were conducted at each site using a 6.0 m long and 1.2 m deep straight seine with 0.64 cm mesh following standardized methodology outlined by Curry et al. (2009). High flows during flooding limited habitats suitable for seining; as a result, seining sites were determined based on availability. If multiple habitats suitable for seining were identified for a particular transect one was randomly selected for sampling. Seine samples were preserved in 10% formalin and returned to the laboratory for identification and enumeration.

Data Analysis

Fish Community

Catch rates for fishes were highly variable during flooding, primarily as a result of gear inefficiency during this high-water period. Therefore, fish abundance data were converted to presence or absence for all analyses. Binary data are less sensitive than quantitative data but should be used in place of abundance data when such data are unreliable (Kwak and Peterson 2007). We used non-metric multidimensional scaling of a Jaccard distance matrix to test the hypothesis that fish assemblages (using species presence/absence) were consistent among all reaches during flooding. Scree plots were used to identify how many axes to retain by comparing the number of retained axes to overall stress. SIMPER values were calculated to identify the contribution of each species to overall dissimilarity among groups. Additionally, fishes were classified into habitat-use guilds as generalist, fluvial specialists or fluvial dependent based on

life history characteristics to facilitate generalized comparisons among fish communities in different reaches (Travnichek et al. 1995, Galat and Zweimüller 2001). Briefly, generalists use many habitats (lotic and lentic) and are able to complete their entire life cycle without flowing water, fluvial dependents require lotic habitats to successfully complete some portion of their life history, and fluvial specialists require lotic habitats for the majority of their life history and are almost always found in lotic systems (Travnichek et al. 1995, Galat and Zweimüller 2001).

All statistical analyses were conducted using R version 2.13.1 (The R Foundation for Statistical Computing 2011).

RESULTS

Macroinvertebrate response to main channel flooding

Drifting Invertebrates

We collected 347 drifting invertebrate samples from the upstream and downstream reaches of the Kansas River in 2009, 2010, and 2011. A total of 34,182 drifting invertebrates representing 6 orders and at least 14 families were captured over the course of the study. Chironomidae were the most abundant taxa in drift samples among all flood stages (Table 2.2a) accounting for 46.3% of the total catch. Grouped Diptera (i.e. terrestrial, adult, and rare dipterans), Chironomidae, and Ephemeroptera were the most abundant taxa before, during, and after flooding respectively (Table 2.2a). Among all samples, ten taxa accounted for at least 5% of the total catch and were retained for further analyses.

Two competing models that predicted drifting invertebrate densities in the main channel before, during and after flooding had deltaAICc < 2.0 (Table 2.1). Both the top model (year and flood stage; w_i=0.69) and the competing model (year, flood stage, and reach; w_i=0.31) included year and flood stage indicating that invertebrate density changed with flows but that this pattern

was not consistent among years. Drifting invertebrate density was higher during floods compared to before or after flooding in each of the three years of the study (Figure 2.4). Whereas drifting invertebrate densities in the main channel upstream and downstream reaches increased an average of 471% during flooding compared to pre-flood conditions 2009 and 2010 samples, average densities increased 7,775% in 2011 (Figure 2.4).Whereas increased densities may be related to peak flow magnitude which was about twice as high in 2011 than in 2009 and 2010, peak flows were not observed until after samples were collected and flows during collection were similar among all years (Figure 2.3).

Main channel drifting invertebrate assemblage structure was generally more similar before and after flooding compared to samples collected during flooding (stress = 0.17; Figure 2.5). Seven taxa (Ceratopogonidae, Chaoboridae, Chironomidae, grouped Diptera, Ephemeroptera, Oligochaeta, Trichoptera) accounted for a majority of dissimilarity among reaches. Grouped Diptera, Ceratopogonidae, and Chaoboridae were generally indicative of pre-flood conditions, whereas Oligochaeta, and Chironomidae were associated with flooding. Post flood drifting invertebrate assemblages were associated with Ephemeroptera and Trichoptera.

Benthic Invertebrates

We collected 143 benthic invertebrate samples from the upstream and downstream reaches of the Kansas River in 2009, 2010, and 2011. A total of 3,484 benthic invertebrates representing 8 orders and 15 families were captured. Among all reaches and sampling periods, benthic invertebrate assemblages were dominated by Chironomidae (Table 2.2a). Chironomidae was the most abundant benthic taxa before and during flooding whereas Oligochaeta were most abundant after flooding (Table 2.2a). Eight taxa each accounted for greater than 5% of the total catch and were retained for further analyses.

Only one model (year and flood stage; w_i=0.72); had strong support (ΔAIC <2) for benthic invertebrates densities (Table 2.1). However, a second model (year, flood stage, and reach; w_i=0.26) had marginal support (ΔAIC = 2.04) indicating that river reach may have some impact on benthic invertebrate abundances. No consistent patterns were discernible for benthic invertebrate density between main channel reaches or among years which shows lower densities prior to flooding in 2009 but higher densities in other years during the same period (Figure 2.4).

Benthic invertebrate assemblages before and after flooding showed more similarity to each other than to assemblages during flooding (NMDS, stress = 0.34; Figure 2.5). Benthic invertebrate assemblages tended to be similar among upstream and downstream reaches regardless of flood stage. However, the benthic invertebrate assemblage showed some unique characteristics, including high densities of Corixidae, during flooding in 2011 possibly indicating a shift in assemblage structure for these samples compared to other samples. Similarity percentage analysis indicated that Corixidae were most strongly associated with pre-flood conditions, grouped Diptera were most strongly associated with flooding conditions, and post-flood conditions were associated with an increase in Ceratopogonidae and Trichoptera.

Main channel and inundated habitat macroinvertebrate response during flooding

Drifting Invertebrates

A total of 184 drifting invertebrate samples were collected from the upstream, downstream, and inundated secondary channel in 2009, 2010, and 2011. Among all reaches, 28,239 drifting invertebrates were collected during flooding conditions including taxa from 6 orders and 16 families. Chironomidae was the most abundant taxa among all samples and were the most common taxa in upstream and downstream main channel reaches (Table 2.2b).

Chaoboridae was the most abundant taxa in the inundated secondary channel during flooding (Table 2.2b). Eight taxa accounted for at least 5% of the total catch and were retained for further analyses.

The model with sampling year and study reach (w_i=1.00) was the only supported model for drifting invertebrate assemblages during flooding (Table 2.1). Drifting invertebrate densities were similar among all reaches in 2009 and 2010, but densities were an order of magnitude higher in the upstream and downstream reaches compared to the inundated secondary channel in 2011 (Figure 2.6).

Dissimilarity among reaches was often high for the drifting invertebrate assemblages during flooding (NMDS, stress = 0.08; Figure 2.7). Drifting invertebrate assemblages were similar in the upstream and downstream main channel reaches but were dissimilar from the assemblage observed in the inundated secondary channel. Similarity percentage analysis indicated that upstream and downstream main channel reaches were most strongly associated with Chironomidae, Oligochaeta, and Trichoptera. Drifting invertebrate assemblages in flooded habitats were primarily associated with Corixidae and Chaoboridae.

Benthic Invertebrates

We collected 102 benthic invertebrate samples from upstream, downstream, and inundated secondary channels during flooding conditions in 2009, 2010, and 2011. Among benthic samples, 1,155 macroinvertebrates were collected including individuals from 9 orders and 19 families. Chironomidae were the most abundant benthic taxa in upstream main channel and inundated secondary channel reaches whereas Oligochaeta was most abundant in the downstream main channel reach (Table 2.2b). Among all samples, eight taxa represented at least 5% of the total catch and were retained for further analyses.

The model with year and reach (w_i=1.00) was the only supported model for benthic invertebrate assemblages during flooding (Table 2.1). No consistent patterns were observed for benthic invertebrate densities among reaches during flooding (Figure 2.6). However, in 2009 benthic invertebrate densities were much higher in the inundated secondary channel compared to upstream and downstream main channel reaches. In 2011, relatively high benthic invertebrate densities were observed in the downstream and inundated secondary channel reaches compared to the upstream reach. Large spikes in average benthic invertebrate densities were not observed in any reaches in 2010.

Benthic invertebrate communities were similar between the upstream and downstream main channel reaches but less similar to the inundated secondary channel (NMDS; stress = 0.11; Figure 2.8). Similarity percentage analyses indicated Corixidae and Coleoptera were generally positively associated with the inundated secondary channel whereas Ephemeroptera and Oligochaeta were generally positively associated with main channel reaches.

Fish community response to flooding

Among all reaches from 2009 – 2011 we collected 257 fish samples including 84 electrofishing samples, 21 gill net samples, and 152 seine hauls. From all samples, a total of 23,686 fishes were collected including 498 fishes collected during electrofishing, 116 collected with gill nets, and 23,072 fishes collected with seines. Individuals were collected from 31 species representing 6 families and 19 species accounted for at least 5% of the total catch and were retained for further analyses.

A total of 37.3% of the variation among fish communities in upstream, downstream, and inundated secondary channel habitats during flooding was explained by two axes that were

retained for the non-metric multidimensional scaling plots examining variation in fish community structure (Figure 2.9). Variation along the first axis was most strongly positively correlated with species found in the main channel habitats (shovelnose sturgeon, *Scaphirhynchus platorynchus;* blue sucker, *Cycleptus elongates*; and red shiner, *Cyprinella lutrensis*) and most strongly negatively correlated with species found in the inundated secondary channel (longnose gar, *Lepisosteus osseus;* river carpsucker, *Carpiodes carpio*; and freshwater drum, *Aplodinotus grunniens*; Figure 2.9). In general, fish communities from the main channel (shortnose gar, *Lepisosteus platostomus;* goldeye, *Hiodon alosoides*; and smallmouth buffalo, *Ictiobus bubalus*) were associated with positive axis 2 scores whereas fishes found in the inundated secondary channel (gizzard shad, *Dorosoma cepedianum*; white bass, *Morone chrysops*; and sauger, *Sander canadensis*; Figure 2.9).

DISCUSSION

Floods can impact many aspects of lotic ecosystems including increasing energy sources (prey) for fishes. Our results indicate that floods result in a pulse of higher macroinvertebrate densities that may be used as prey for fishes in secondary channel and main channel habitats. Specifically, flooding increased the density of drifting macroinvertebrates in main channel habitats of the Kansas River compared to base flow conditions before and after flooding in all three years of this study. Additionally, highest total (sum of upstream and downstream) benthic invertebrate densities were observed either before or after, but never during, flooding in each of the years of this study. These findings are consistent with other studies that found that increased discharges during flooding can increase shear stress near the benthos and cause “catastrophic drift” where a majority of benthic invertebrates enter the drift thereby lowering the density of benthic invertebrates and subsequently increasing the density of invertebrates in the drift

(Callisto and Goulart 2005; Lauridsen and Fribert 2005; Gibbins et al. 2007). Although invertebrates can enter the drift voluntarily, most voluntary drift occurs overnight with peaks often observed just after sunset and just before sunrise (Elliott 1969; Brittain and Eikeland 1988; Sagar and Glova 1992). Because all of our samples were collected during daylight hours we surmise that invertebrate drift in our study was primarily involuntary drift as a result of entrainment disturbance to the benthos. Involuntary drift related to increasing flows is especially pervasive in sandbed rivers where relatively small increases in velocity can lead to entrainment of substrate and benthic invertebrates (Beisel et al. 1998; Allan 2007; Gibbins et al. 2010). As such, it is likely that invertebrates captured in drift samples were dislodged from upstream main channel habitats as well as brought into the main channel from inundated terrestrial habitats.

The highest densities of benthic and drifting invertebrates were observed in 2011. Additionally, drifting invertebrate densities were similar in 2009 and 2010 but were an order of magnitude higher in main channel habitats in 2011. The spikes observed in 2011 may likely be explained by the timing of sampling in 2011 relative to the timing of flooding. In 2011 we sampled on the first day of flooding immediately after flooding conditions began (i.e. hydrograph rising limb). The strong spike that we observed indicated that floods may instigate an initial period of high energy influx followed by sustained increased, though less extreme, invertebrate densities in the drift compared to baseflow conditions (Junk et al. 1989). However, because the spike was not observed in 2009 or 2010 it is possible that this pulse quickly subsides to a level where macroinvertebrate density is relatively equal among all habitats and similar to baseflow.

Year and flood stage were important predictors of both drifting and benthic macroinvertebrate densities suggesting that floods impact macroinvertebrate densities. Although

many metrics of the flood (e.g. magnitude, timing, duration) may alter the impact of a particular flood on macroinvertebrates densities, our results are confounded by not sampling on the same day of a flooding event among years (e.g. first day of rising limb). Therefore, we do not fully understand the impact of our flood sampling timing on macroinvertebrate densities. However, aquatic macroinvertebrate emergence rates are highly correlated with water temperature (Thorp et al. 1997; Boulton and Lloyd 2006). As a result, aquatic macroinvertebrate densities may be lower during early season floods and these floods may transport fewer inverts downstream than a comparable flood later in the season (Boulton and Lloyd 2006). Water temperatures collected from USGS Station 06887500 near Wamego, Kansas were on average 12-14°C lower for early season (i.e. April) floods compared to later season (i.e. July) floods so it is likely that more invertebrates would have emerged during later season floods and could further explain how flood timing could alter the benefits of flooding. Main channel drifting invertebrate samples during flooding were dominated by Chironomidae and Oligochaete, which were predominantly found in benthic samples prior to flooding suggesting that scouring is at least partially responsible for the increase in drifting invertebrate density during flooding. Chironomidae are among the most susceptible benthic taxa to enter the drift (Rader 1997; Cross et al. 2011).

Fish feed on drifting invertebrates (e.g. Cadwallader 1975; Flecker 1992) and fishes benefit from increased drift resulting from floods (Valdez et al. 2001; Lagarrigue et al. 2002). Drifting invertebrate concentrations increased during flooding in every year of our study suggesting that floods may benefit fishes by increasing drift rates and moving invertebrate prey from inundated habitats to the main channel. Invertebrates can colonize and breed in inundated habitats, such as the secondary channel in this study, during baseflow conditions if the habitat has previously been inundated or there is sufficient precipitation to create standing pools of water

(Paillex et al. 2007, Starr et al. 2014). As such, some main channel fishes may benefit from inundations of terrestrial habitats without directly moving into inundated habitats by feeding on invertebrates that enter the drift and are carried to the main channel. Invertebrate densities were higher in main channel habitats during flooding indicating that high flow events may enhance feeding habitats for many fish (e.g. Galat and Zweimuller 2001; Jardine et al. 2012).

Habitat variation among sites likely accounted for many of the differences observed for drifting and benthic invertebrate communities in the main channel and secondary channel habitats. Main channel sites were dominated by sandy benthic substrates whereas the benthic substrate of the inundated secondary channel was predominantly mud (J. Gerken personal observation). Sand and mud benthic zones often support different invertebrate communities (Ward 1992) and may account for many of the differences observed between main channel and secondary channel habitats.

The higher benthic invertebrate densities generally found in the inundated secondary channel may benefit some fishes by increasing prey availability in main channel habitats during flooding. This supports the idea that inundated habitats provide energy for main channel fishes (e.g. Galat and Zweimuller 2001). However, we cannot definitively show how energy varied among main channel and inundated habitats because we examined invertebrates densities instead of biomass. For example, although chironomids were found in the highest densities in many of our samples, these species may not be as valuable energetically as invertebrates that were found in lower densities but likely had greater biomass (e.g. ephemeroptera). Our results suggest that the contribution of macroinvertebrates from one inundated habitat to the main channel may be negligible compared to the number of invertebrates in the main channel, but the cumulative influx from a combination of inundated riparian and floodplain terrestrial habitats may provide a

considerable influx of macroinvertebrates into the main channel (Tockner et al. 2000; Baxter et al. 2005; Thorp et al. 2006).

The contribution of inundated floodplain habitats may also depend on flow rates into and through inundated habitats. Flows through the secondary channel of our study were always less than 5% of the flows observed in the main channel (K. Costigan, Kansas State University, unpublished data). In inundated habitats with minimal flows, invertebrates may drift into inundated habitats from the main channel and settle out in areas of lower flow making them a sink of invertebrate energy. Conversely, if higher flows are present in inundated habitats invertebrates may not be able to settle out and instead we may see invertebrates derived from the floodplain washed into the main channel and therefore the inundated habitat would serve as an energy source to main channel habitats. Drifting invertebrate concentrations were always higher during flooding compared to before or after flooding indicating that higher flows may carry invertebrates from inundated floodplain habitats to main channel habitats. Our results contrast Smock (1994) who observed in two headwater streams in Virginia where a net loss of invertebrate abundance was observed from the floodplain to the main channel but a net gain of invertebrate biomass occurred from the main channel to the floodplain. However, the distance between main channels and floodplains was relatively small because the study was conducted in headwater streams and invertebrate crawling accounted for much of the movement of invertebrates among reaches (Smock 1994). It is unlikely that large quantities of invertebrates would be able to traverse the high flows and relatively large spatial distance between main channel and floodplain habitats in our study, and drift into or out of inundated habitats likely accounts for a large proportion of invertebrate movement during flooding in our system (e.g. Brittain and Eikeland 1988; Gibbins et al. 2007). Understanding how flow dynamics of

inundated habitats may impact transfer of invertebrates into or out of flooded habitats may provide more resolution on the importance of inundated habitats as potential energy sources.

The majority of the fishes captured during this study were captured in the inundated secondary channel at least once suggesting these habitats are used by most fishes. Many generalist (e.g. river carpsucker, freshwater drum) and fluvial dependent fish species (e.g. longnose gar) were commonly found in the inundated secondary channel indicating that these habitats may serve as a refugia habitat for fishes to escape high flows in the main channel. In contrast, some fluvial specialist species, such as shovelnose sturgeon and blue sucker, were rarely captured in inundated habitats. Whereas many fluvial specialists were captured in secondary channel habitats at least once, fluvial specialists were not consistently observed in these reaches highlighting the importance of main channel habitats for some fish species (Galat and Zweimüller 2001). Our results are consistent with the findings of Galat and Zweimüller (2001) for large river fishes in the United States and Europe and indicate that fluvial dependents and fluvial generalists are likely using inundated habitats but that most fluvial specialists tend to remain in main channel habitats during flooding.

Fishes may serve an important role in the transport of energy among inundated and main channel habitats by feeding in inundated habitats and moving to the main channel (Jardine et al. 2012). Though we could not conclusively identify a link of invertebrate prey from the inundated secondary habitat to the main channel, fishes likely move energy from inundated habitats to main channel habitats by feeding directly in the inundated habitats before returning to the main channel. This may be especially important during periods of high flow when increased turbidity may constrain feeding processes of fishes in main channel habitats (Abrahams and Kattenfeld 1997). Whereas there are higher densities of invertebrates in the main channel, fishes may be

more efficient feeders in inundated habitats and therefore exhibit a net gain by feeding in inundated habitats where invertebrate densities are lower (but still increased compared to baseflow) compared to staying in the main channel where invertebrate densities are higher but more energy may be required to remain in higher flows and faster currents for fish to use the increase in prey availability (Balcombe et al. 2012, Jardine et al. 2012). Future studies should examine feeding efficiency of fishes in inundated and main channel habitats especially during periods of flooding when differences in turbidity may be exacerbated.

CONCLUSIONS

This study provides empirical evidence on the impacts of high flows on fish and invertebrate communities during flooding. We found that high flows result in higher drifting invertebrate densities likely from upstream reaches and inundated secondary channels which may benefit fishes in a variety of ways. We did not observe definitive movement of invertebrates from inundated to main channel habitats but we observed patterns of fish utilizing inundated habitats. As such, the importance of floodplain habitats may vary based on size and shape of the habitat and characteristics of high flows (e.g. duration, magnitude, and timing). Although the energy input provided by one inundated habitat may be negligible in itself, the total influx of energy provided by all inundated terrestrial habitats is likely to provide benefits to the riverine ecosystem. Maintaining lateral connectivity in large rivers may benefit many native fishes found in these systems and management and restoration efforts focused on large river fishes may benefit by increasing or maintaining lateral connectivity between main channel and inundated terrestrial habitats. Future studies should quantify invertebrate biomass and use a bioenergetics approach to gain further insight into how floods and lateral connectivity impact fish and invertebrate communities in large rivers.

Our study provides a framework for the benefits of floods and shows that the duration and magnitude of flooding may considerably alter invertebrate communities and related benefits to fishes. However, we were not able to provide the resolution necessary to identify specific factors linking floodplain energy to main channel productivity. Future studies should examine how changes to the timing, duration, and magnitude (i.e. specific parts of the natural flow regime) impact temperate river ecosystems and the applicability of the FPC.

LITERATURE CITED

Abrahams, M. and M. Kattenfeld. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology* 40:169-174.

Allan, J.D. 2007. Stream ecology: structure and function of running waters. *Springer, New York, New York*.

Arthington, A.H., S.E. Bunn, N.L. Poff, and R.J. Naiman. 2006. The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications* 16:1311-1318.

Balcombe, S.R., J.S. Lobegeiger, S.M. Marshall, J.C. Marshall, D. Ly, and D.N. Jones. 2012. Fish body condition and recruitment success reflect antecedent flows in an Australian dry land river. *Fisheries Science* 78:841-847.

Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201-220.

Beisel, J.N., P. Usseglio-Polatera, S. Thomas, and J.C. Moreteau. 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia* 389:73-88.

Besacier-Monbertrand, A.L., A. Paillex, and E. Castella. 2014. Short-term impacts of lateral hydrological connectivity restoration on aquatic macroinvertebrates. *River Research and Applications* 30:557-570.

Boulton, A.J. and L.N. Lloyd. 2006. Flooding frequency and invertebrate emergence from dry floodplain sediments of the river Murray, Australia. *Regulated Rivers: Research and Management* 7:137-151.

Brittain, J. and T.J. Eikeland. 1988. Invertebrate drift – a review. *Hydrobiologia* 166:77-93.

Bunn, S.E. and A.H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492-507.

Callisto, M. and M. Goulart. 2005. Invertebrate drift along a longitudinal gradient in a Neotropical stream in Serra do Cipó National Park, Brazil. *Hydrobiologia* 539:47-56.

Carlisle, D.M., D.M. Wolock, and M.R. Meador. 2011. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264-270.

Colby, C.C., H.L. Dillingham, E.G. Erikson, G.F. Jenks, J.O. Jones, and R. Sinclair. 1956. The Kansas River basin, pilot study of a watershed. *Univeristy of Kansas Press*, Lawrence, Kansas, USA.

Conallin, A.J., K.A. Hillyard, K.F. Walker, B.M. Gillanders, and B.B. Smith. 2011. Offstream movements of fish during drought in a regulated lowland river. *River Research and Applications* 27:1237-1252.

Cross, W.F., C.V. Baxter, K.C. Donner, E.J. Rosi-Marshall, T.A. Kennedy, R.O. Hall Jr., H.A. Wellard Kelly, and R.S. Rogers. 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. *Ecological Applications* 21:2016-2033.

Curry, R.A., R.M. Hughes, M.E. McMaster, and D.J. Zafft. 2009. Coldwater fish in rivers. Pages 139-158 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

De Stasio, B.T., Jr. 1989. The seed bank of a freshwater crustacean: copepodology for the plant ecologist. *Ecology* 70:1377-1389.

Dodds, W.K., J.S. Perkin, and J.E. Gerken. 2013. Human impact on freshwater ecosystem services: a global perspective. *Environmental Science and Technology* 47:9061-9068.

Doyle, M.W., E.H. Stanley, D.L. Strayer, R.B. Jacobson, and J.C. Schmidt. 2005. Effective discharge analysis of ecological processes in streams. *Water Resources Research* 41: W11411; doi:10.1029/2005WR004222.

Eitzmann, J.L., and C.P. Paukert. 2010. Longitudinal differences in habitat complexity and fish assemblage structure of a Great Plains River. *American Midland Naturalist* 163: 14-32.

Elliott, J.M. 1969. Diel periodicity in invertebrate drift and the effect of different sampling periods. *Oikos* 20:523-528.

Flecker, A.S. 1992. Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. *Ecology* 73:438-448.

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.

Galat, D.L. and I. Zweimüller. 2001. Conserving large-river fishes: is the highway analogy and appropriate paradigm? *Journal of the North American Benthological Society* 20:266-279.

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. Semelitsch. 1998. Flooding to restore connectivity in regulated, large-river wetlands. *Bioscience* 48:721-733.

Gibbins, C.N., D. Vericat, R.J. Batalla. 2007. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. *Freshwater Biology* 52:2369-2384.

Gibbins, C.N., D. Vericat, R.J. Batalla. 2010. Relations between invertebrate drift and flow velocity in sand-bed and riffle habitats and the limits imposed by substrate stability and benthic density. *Journal of the North American Benthological Society* 29:945-958.

Guy, C.S., P.J. Braaten, D.P. Herzog, J. Pitlo, and R.S. Rogers. 2009. Warmwater fish in rivers. Pages 59-84 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Herwig, B.R., D.A. Soluk, J.M. Dettmers, and D.H. Wahl. 2004. Trophic structure and energy flow in backwater lakes of two large floodplain rivers assessed using stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 61:12-22.

Humphries, P., H.Keckeis, and B. Finlayson. 2014. The river wave concept: integrating river ecosystem models. *Bioscience* 64:870-882.

Jardine, T.D., B.J. Pusey, S.K. Hamilton, N.E. Pettit, P.M. Davies, M.M. Douglas, V. Sinnamon, I.A. Halliday, S.E. Bunn. 2012. Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. *Oecologia* 168:829-838.

Junk, W.J., P.B. Bayley, and R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106:110-127.

Junk, W.J. and P.B. Bayley. 2007. The scope of the flood pulse concept regarding riverine fish and fisheries, given geographic and man-made differences between systems. *American Fisheries Society Symposium 49*:587:603.

Kiernan, J.D., P.B. Moyle, and P.K. Crain. 2012. Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. *Ecological Applications* 22:1472-1482.

Koel, T.M. and R.E. Sparks 2002. Historical patterns of river stage and fish communities as criteria for operations of dams on the Illinois River. *River Research and Applications* 18:3-19.

Lagarrigue, T., R. Céréghino, P. Lim, P. Reyes-Marchant, R. Chppaz, P. Lavandier, and A. Belaud. 2002. Diel and seasonal variations in brown trout (*Salmo trutta*) feeding patterns and relationship with invertebrate drift under natural and hydropeaking conditions in a mountain stream. *Aquatic Living Resources* 15:129-137.

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179-1188.

Lauridsen, R.B. and N. Friberg. 2005. Stream macroinvertebrate drift response to pulsed exposure of the synthetic pyrethroid Lamda-Cyhalothrin. *Environmental Toxicology* 20:513-521.

Lester, N.P., P.E. Bailey, and W.A. Hubert. 2009. Coldwater fish in small standing waters. Pages 85-96 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Lind, P.R., B.J. Robson, and B.D. Mitchell. 2006. The influence of reduced flow during a drought on patterns of variation in macroinvertebrate assemblages across a spatial hierarchy in two lowland rivers. *Freshwater Biology* 51:2282-2295.

Mackay, R.J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 49:617-628.

Makinster, A.S. and C.P. Paukert. 2008. Effects and utility of minimum length limits and mortality caps for flathead catfish in discrete reaches of a large prairie river. *North American Journal of Fisheries Management* 28:97-108.

McMullen L.E. and D.A. Lytle. 2012. Quantifying invertebrate resistance to floods: a global-scale meta-analysis. *Ecological Applications* 22:2164-2175.

Metcalf, A.L. 1966. Fishes of the Kansas River system in relation to zoogeography of the Great Plains. University of Kansas, Lawrence, Kansas, USA.

Miranda, L.E. 2009. Standardizing electrofishing power for boat electrofishing. Pages 223-230 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Paillex, A., E. Castella, and G. Carron. 2007. Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. *Journal of the North American Benthological Society* 26:779-796.

Poff, N.L. and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805-1818.

Poff, N.L., J.D. Allen, 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.

Poff, N.L. and J.K.H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55:194-205.

Power, M.E., A. Sun, G. Parker, W.E. Dietrich, and J.T. Wootton. 1995. Hydraulic food-chain models. *Bioscience,* 45:159-167.

Propst, D.L. and K.B. Gido. 2004 Response of native and nonnative fishes to natural flow regime mimicry in the San Juan River. *Transactions of the American Fisheries Society* 133:922-931.

Puckridge, J.T., F. Sheldon, K.F. Walker, and A.J. Boulton. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* 49:55-72.

Rader, R.B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1211-1234.

Sagar, P.M. and G.J. Glova. 1992. Diel changes in the abundance and size composition of invertebrate drift in 5 rivers in South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 26:103-114.

Smock, L.A. 1994. Movement of invertebrates between stream channels and forested floodplains. *Journal of the North American Benthological Society* 13:524-531.

Starr, S.M., J.P. Benstead, and R.A. Sponseller. 2014. Spatial and temporal organization of macroinvertebrate assemblages in a lowland floodplain ecosystem. *Landscape Ecology* 29:1017-1031.

Thorp, J.H., M.D. Delong, K.S. Greenwood, and A.F. Casper. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia* 117:551–563.

Thorp, J.H., M.C. Thoms, and M.D. Delong. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* 22:123-147.

Tockner, K., F. Malard, and J.V. Ward. 2000. An extension of the flood pulse concept. *Hydrological Processes* 14:2861-2883.

Tockner, K. and J.A. Stanford. 2002. Riverine flood plains: present state and future trends. *Environmental conservation* 29:308-330.

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.

Valdez, R.A., T.L. Hoffnagle, C.C. McIvor, T. McKinney, and W.C. Leibfried. 2001. Effects of a test flood on fishes of the Colorado River in Grand Canyon, Arizona. *Ecological Applications* 11:686-700.

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.

Vörösmarty, C.J., P.B. McIntyre, M.O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S.E. Bunn, C.A. Sullivan, C.R. Liermann, and P.M. Davies. 2010. Global threats to human water security and river biodiversity. *Nature*, 467:555-561.

Ward, J.V. 1992. Aquatic Insect Ecology, Part 1, Biology and Habitat. Wiley: New York, New York. 438pp.

Welcomme, R.L. 1985. River fisheries. Food and Agriculture Organization – fisheries technical paper 262. United Nations, Publication Division, Rome, Italy. 330 pages.

Winemiller, K.O. 2005. Floodplain river food webs: generalizations and implications for fisheries management. Pages 285–312 in R. L. Welcomme and T. Petr, editors. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries. Volume 2. Mekong River Commission, Phnom Penh, Cambodia.

Winemiller, K.O. and D.B. Jepsen. 1998. Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology* 53:267-296.

Wipfli, M.S. and C.V. Baxter. 2010. Linking ecosystems, food webs, and fish production: studies in salmonid watersheds. *Fisheries* 35:373-387.

Zeug, S.C. and K.O. Winemiller 2008. Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. *River Research and Applications* 24:90-102.

Table 2.1. Results for models examining benthic and drifting invertebrate densities before, during, after flooding are affected by year of sampling, reach (upstream main channel, downstream main channel), and river stage (before, during, after flooding) in main channel reaches (Hypothesis 1) of the Kansas River and during flooding conditions (Hypothesis 2) in upstream, downstream, and inundated secondary channel habitats of the Kansas River.

Hypothesis 1	Benthic			Drift		
Model Parameters	AICc	ΔAICc	w_i	AICc	ΔAICc	w_i
Intercept; Year; Stage	415.48	0	0.72	510.89	0	0.69
Intercept; Year; Stage; Reach	417.52	2.04	0.26	512.44	1.56	0.31
Intercept; Year	423.60	8.12	0.01	729.62	218.73	0
Intercept; Year; Reach	425.60	10.12	0	731.55	220.67	0
Intercept	514.11	98.63	0	722.81	211.92	0
Intercept; Stage	519.15	103.67	0	642.03	131.15	0
Intercept; Stage; Reach	521.16	105.68	0	643.74	132.86	0
Intercept; Reach	521.56	106.08	0	809.41	298.53	0
Hypothesis 2						
Intercept; Year; Reach	248.77	0	1	298.13	0	1
Intercept; Year	268.32	19.55	0	345.11	46.98	0
Intercept; Reach	269.31	20.53	0	395.55	97.42	0
Intercept	276.53	27.76	0	431.47	133.34	0

Table 2.2. Dominant taxa for drifting and benthic invertebrates for A) invertebrates collected before, during, and after flooding in main channel habitats upstream and downstream of the secondary channel and B) invertebrates collected during flooding in the inundated secondary channel and main channel reaches upstream and downstream of the secondary channel. Percentage of overall catch is identified parenthetically. Some dipterans were identified to family (i.e. Ceratopogonidae, Chaoboridae, and Chironomidae) whereas other Dipterans (predominantly terrestrial and adult Dipterans) were classified as "grouped Ddiptera".

a)

	Overall	**Before Flooding**	**During Flooding**	**After Flooding**
Drifting	Chironomidae (46.3)	Grouped Diptera (28.1)	Chironomidae (48.7)	Ephemeroptera (38.1)
	Oligochaeta (14.7)	Ceratopogonidae (16.7)	Oligochaeta (15.8)	Chironomidae (22.9)
	Grouped Diptera (12.6)	Chironomidae (15.2)	Grouped Diptera (12.4)	Trichoptera (20.8)
Benthic	Chironomidae (50.8)	Chironomidae (39.8)	Chironomidae (59.7)	Oligochaeta (32.7)
	Oligochaeta (27.1)	Oligochaeta (33.7)	Oligochaeta (23.4)	Chironomidae (31.3)
	Grouped Diptera (8.1)	Corixidae (9.1)	Grouped Diptera (10.1)	Trichoptera (13.7)

b)

	Overall	**Upstream**	**Downstream**	**Secondary Channel**
Drifting	Chironomidae (45.7)	Chironomidae (50.0)	Chironomidae (47.0)	Chaoboridae (32.6)
	Oligochaeta (15.0)	Oligochaeta (16.2)	Oligochaeta (15.4)	Corixidae (23.6)
	Grouped Diptera (13.1)	Grouped Diptera (12.3)	Grouped Diptera (12.5)	Grouped Diptera (21.8)
Benthic	Oligochaeta (48.9)	Chironomidae (51.8)	Oligochaeta (71.6)	Chironomidae (34.6)
	Chironomidae (30.3)	Oligochaeta (23.9)	Chironomidae (23.1)	Corixidae (26.3)
	Corixidae (5.2)	Ephemeroptera (13.1)	Ephemeroptera (2.5)	Oligochaeta (12.3)

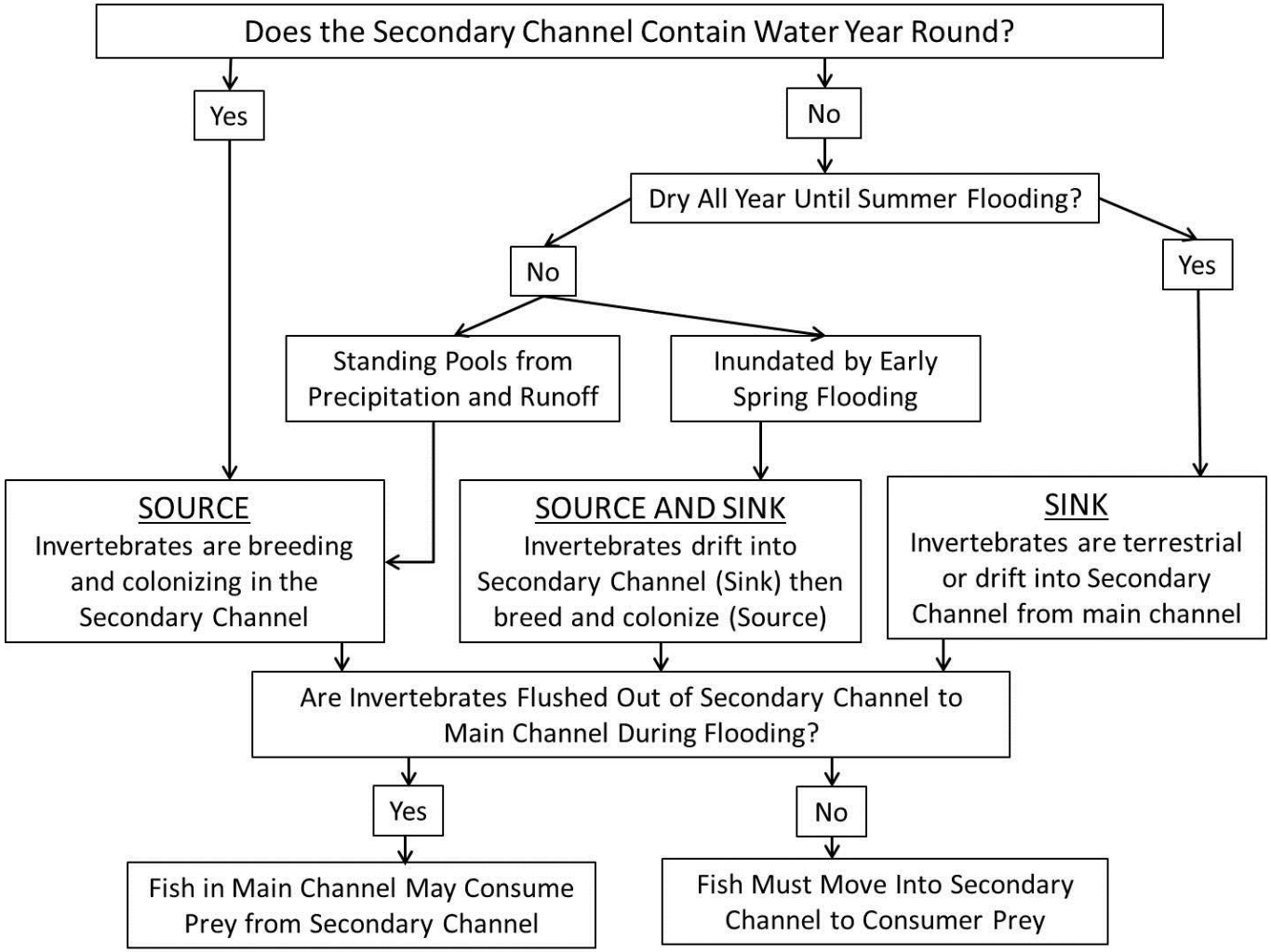

Figure 2.1. Conceptual framework showing how invertebrate assemblages develop in secondary channels and contribute to main channel habitats in various hydrologic conditions and how main channel fishes may benefit from these invertebrates. Invertebrates can colonize standing water in secondary channel habitats and then flush into the main channel during flooding (i.e. source) come directly from the main channel and settle in the secondary channel (i.e. sink) or a combination of the two.

Figure 2.2. Aerial photograph of study sites on the Kansas River near Manhattan, Kansas. Lines indicate the upstream main channel (solid), downstream main channel (dashed), and inundated secondary channel (dotted) study reaches.

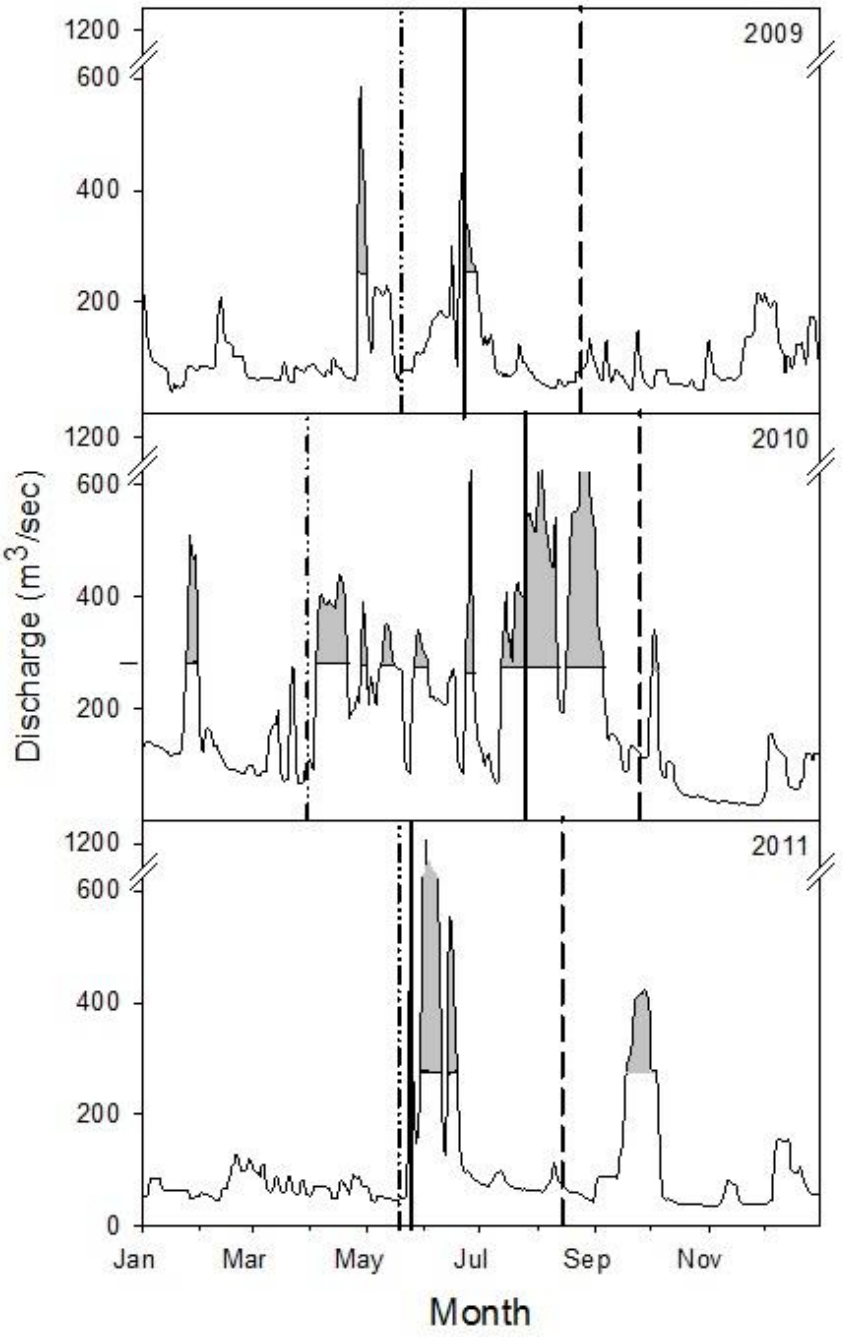

Figure 2.3. Mean daily discharge (m^3 sec^{-1}) for the Kansas River near Wamego, KS in 2009, 2010, and 2011. Lines indicate sampling dates for pre-flood (dash dotted), during flood (solid), and post flood (dashed) for each year. Shaded areas indicate periods of flooding. Discharge values were obtained from United States Geological Survey Station #06887500.

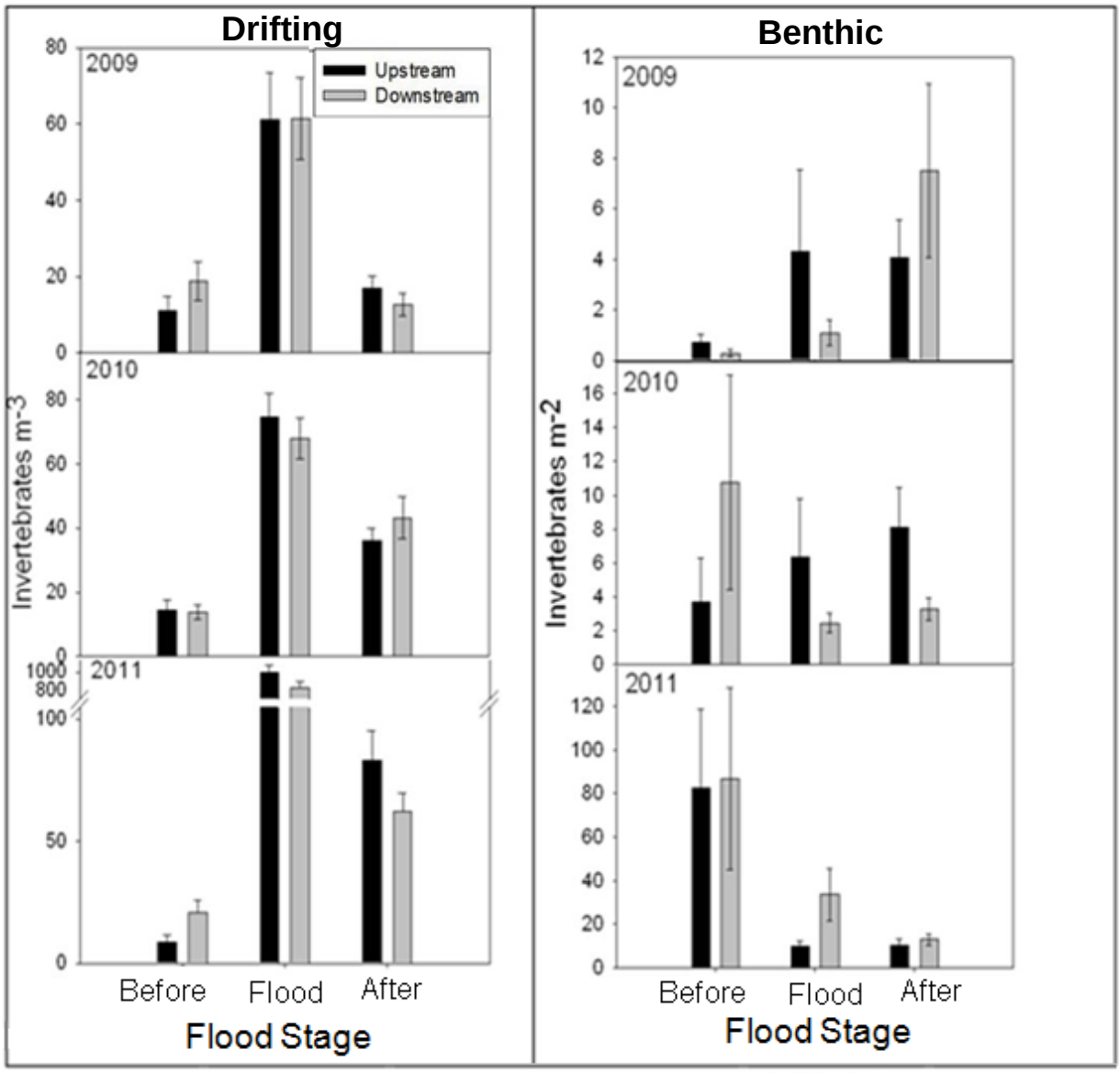

Figure 2.4. Mean (±SE) drifting and benthic invertebrate densities for upstream and downstream main channel reaches of the Kansas River before, during, and after flooding in 2009 – 2011.

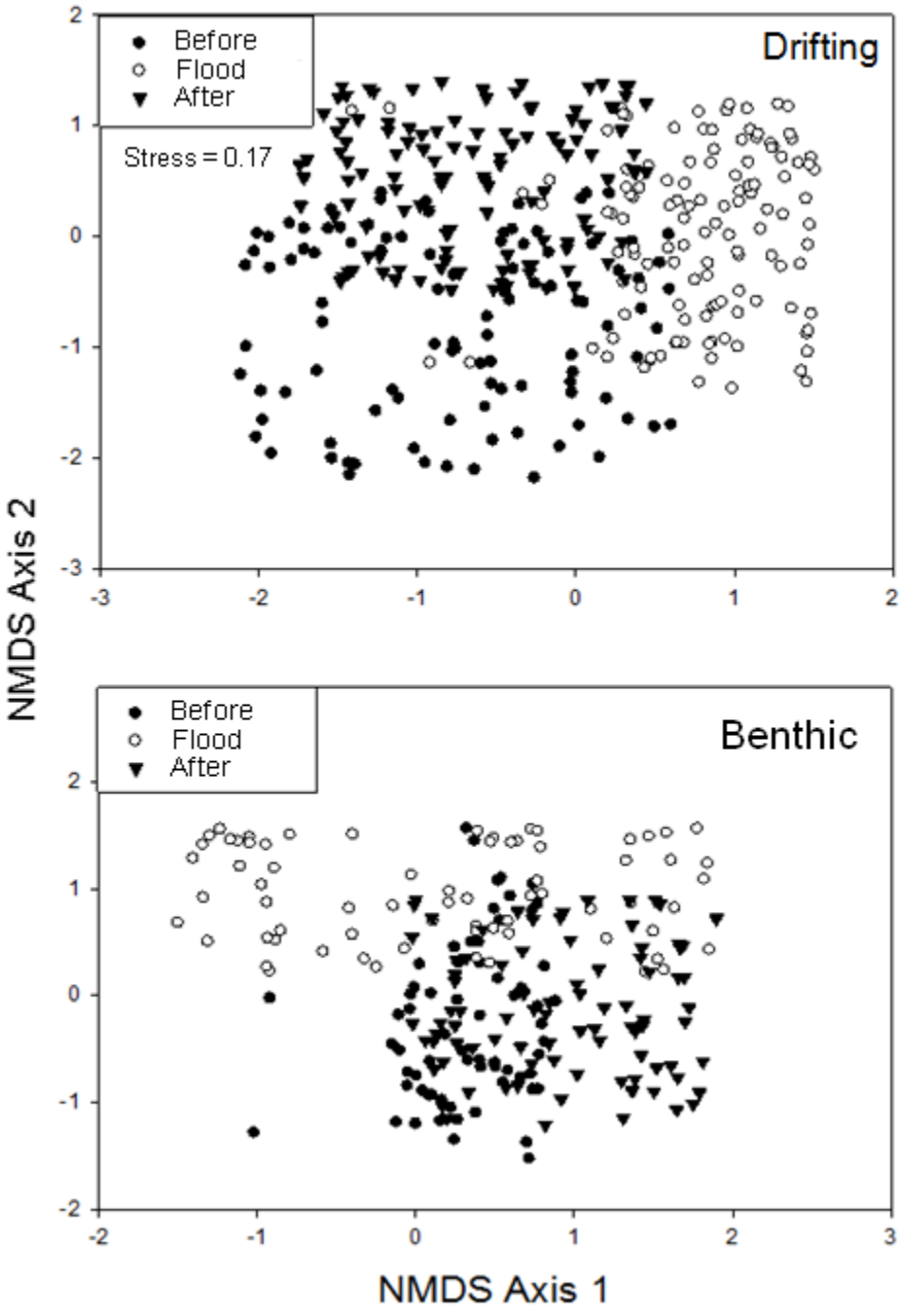

Figure 2.5. Non-metric multidimensional scaling biplot for drifting and benthic invertebrate assemblages (abundance) in upstream and downstream main channel reaches of the Kansas River before, during, and after flooding in 2009 – 2011.

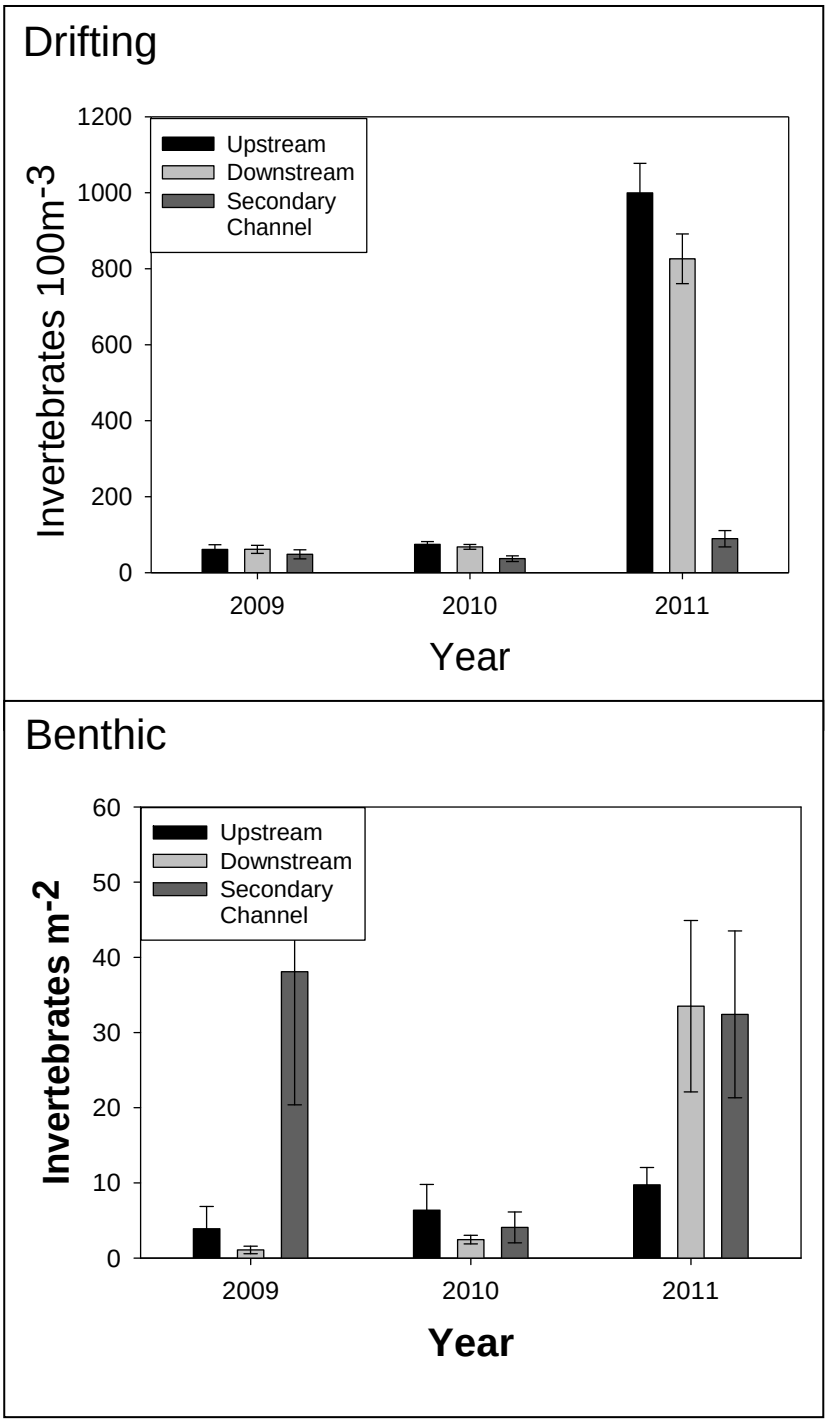

Figure 2.6. Mean (±SE) drifting and benthic invertebrate densities samples collected in the upstream and downstream main channel reaches and the inundated secondary channel of the Kansas River during flooding from 2009 – 2011.

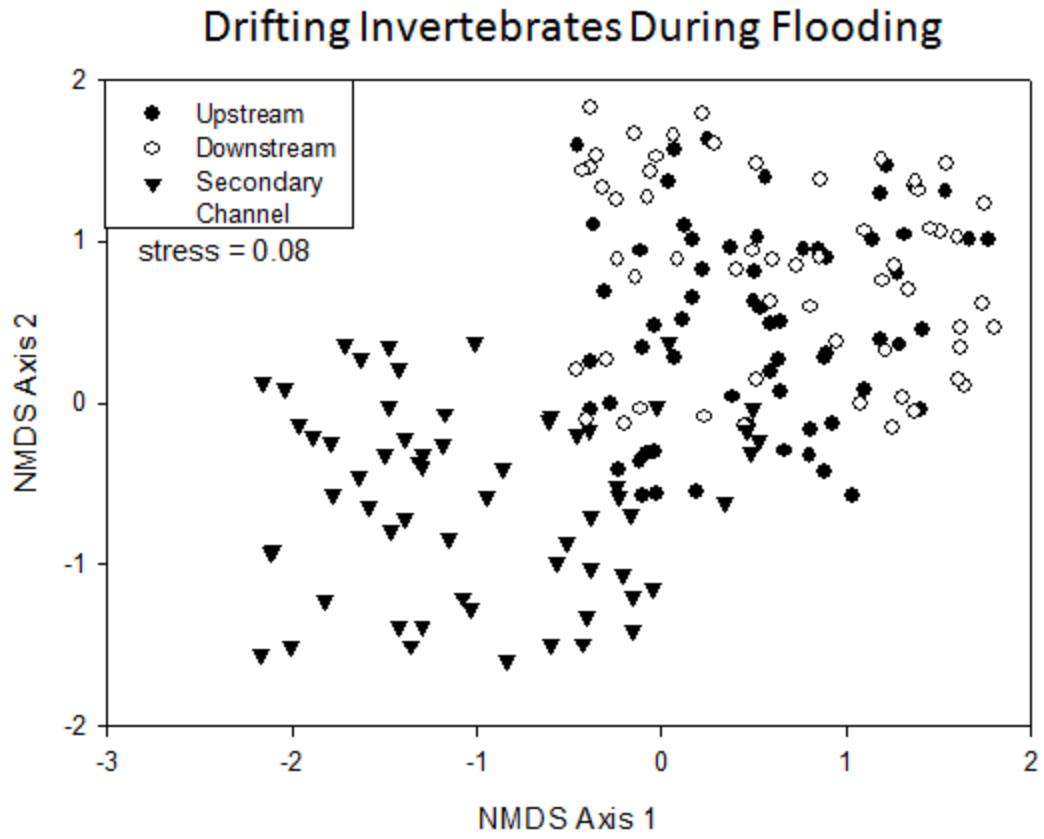

Figure 2.7. Non-metric multidimensional scaling biplot for drifting invertebrate assemblage in upstream and downstream main channel and inundated secondary channel reaches of the Kansas River during flood conditions.

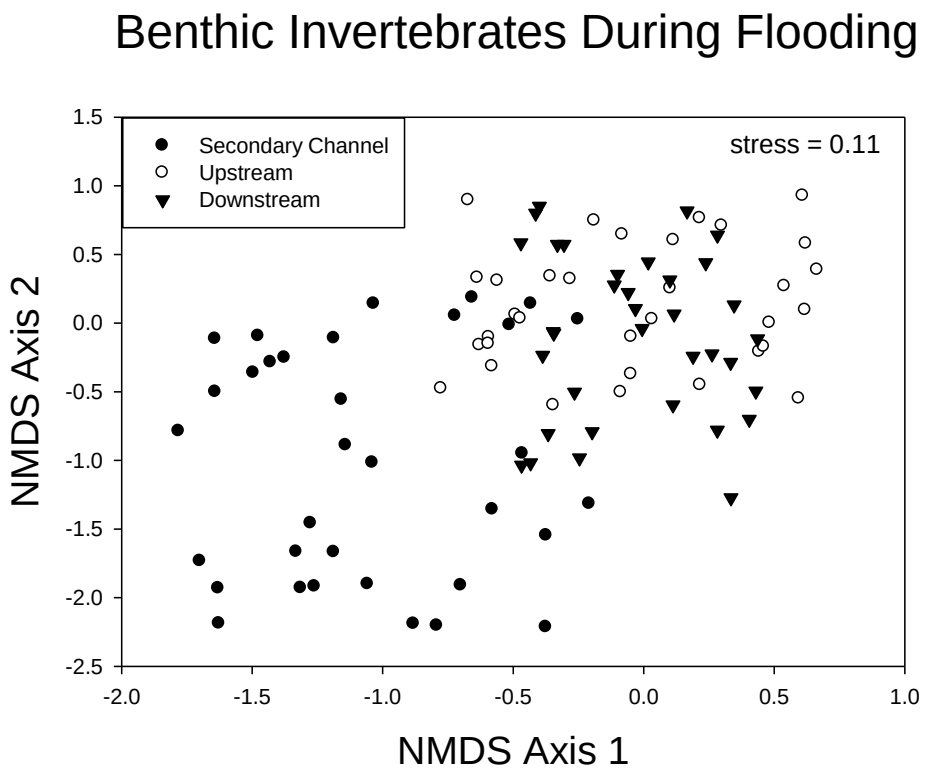

Figure 2.8. Non-metric multidimensional scaling biplot for benthic invertebrate assemblage (abundance) in upstream and downstream main channel and inundated secondary channel reaches of the Kansas River during flood conditions in 2009 - 2011.

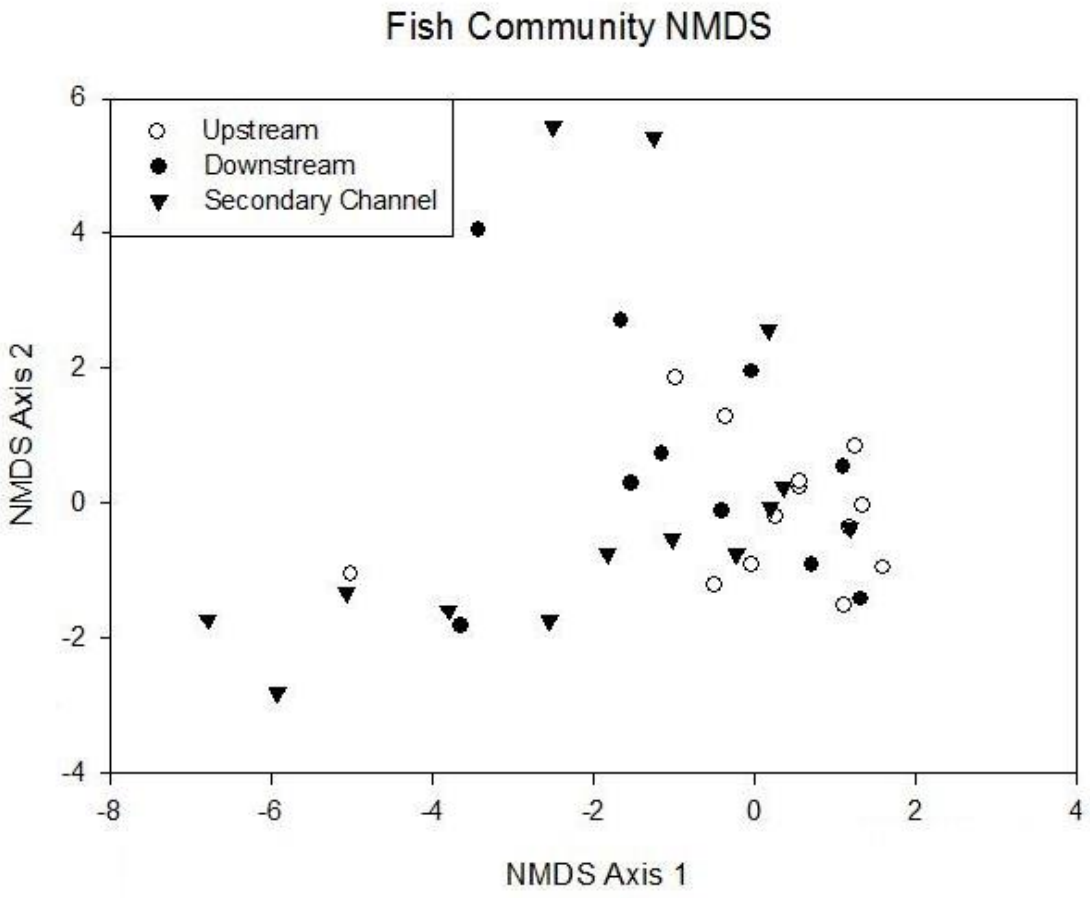

Figure 2.9. Non-metric multidimensional scaling biplot for fish presence or absence in upstream and downstream main channel and inundated secondary channel reaches of the Kansas River during flood conditions in 2009 - 2011. Species listed are strongly associated with axis and indicated direction.

Chapter 3 - Flood-induced lateral connectivity alters fish and invertebrate assemblages in the Kansas River

ABSTRACT

Lateral connectivity between main channel and floodplain habitats is an important driver of ecosystem function in many large river systems. Many fishes and invertebrates rely on floodplain habitats for life history needs, but our understanding of how the duration and timing of lateral connectivity affects fishes and food web dynamics in large rivers is limited. We examined changes in fish and invertebrate densities and assemblage structure before, during, and after flooding in main channel and adjacent permanently-connected and seasonally-connected secondary channels to identify the role of lateral connectivity on fish and invertebrates in the Kansas River. Benthic invertebrate densities declined during and after flooding in these reaches. During flooding, drifting invertebrate concentrations were higher in main channel than seasonally and permanently connected secondary channel reaches but benthic invertebrate densities were higher in secondary channels compared to main channel reaches. Drifting invertebrate concentrations were almost twice as high (186%) in seasonally connected secondary channel reaches ($p<0.01$) whereas benthic invertebrate densities were higher (170%) in seasonally connected secondary channels ($p<0.01$). Permanently connected secondary channels had fish assemblages with higher prevalence of shortnose gar and emerald shiner whereas quillback were more prevalent in fish assemblages of seasonally connected secondary channels. Our results suggest that flooding affects the densities of drifting and benthic invertebrates both in secondary channels and main channels and may provide alternative prey sources for fishes in the river. Additionally, secondary channels with permanent and seasonal connectivity maintain different fish and invertebrate assemblages in this large river ecosystem, suggesting that the degree of connectivity is important in shaping aquatic communities. Maintaining a diversity of

secondary channels with varying degrees of lateral connectivity may be useful in preserving native biota in these habitats.

INTRODUCTION

Lateral connectivity between main channel and secondary channel or floodplain habitats is an important component of many large river ecosystems. Many organisms rely on floodplain habitats for important life history needs and river floodplains are among the most biologically diverse habitats in the world (Tockner and Stanford 2002). The combination of aquatic and terrestrial inputs in floodplain habitats provides many ecological benefits to lotic ecosystems and many organisms, including fishes (Tockner and Stanford 2002; Winemiller 2005).

Many fishes are dependent on floodplain habitats for important life history needs. High flows may cue movement of fishes into floodplain habitats to spawn (Górski et al. 2011, Steffensen et al. 2014), but also these floodplain habitats provide nursery areas as they are often more productive than main channel habitats and juvenile fishes reared in these habitats may benefit from increased food sources (Winemiller 2005, Jeffres et al. 2008, Górski et al. 2011). Floodplain habitats are also important feeding habitats for many adult fishes as they move into floodplains to benefit from higher productivity (Bellmore et al. 2013). Energy derived from floodplain habitats may also benefit organisms in the main channel that do not move directly into floodplain habitats (Junk et al. 1989, Bellmore et al. 2013). The flood pulse concept (FPC) suggests that lateral connectivity between main channel and floodplain habitats is the primary factor regulating large river productivity (Junk et al. 1989). Specifically, the FPC postulates that floods benefit riverine ecosystems by bringing nutrients and allochthonous inputs from floodplain to main channel habitats (Junk et al. 1989). In addition, variation in other hydrologic variables including flow variability and flood timing can influence fish and invertebrate

composition (Lytle and Poff 2004). Examining hydrologic changes to the system can provide us with a better estimate of how fish and invertebrates are using and being transferred throughout a large river system.

Floodplain habitats are diverse and connectivity between the main channel and floodplain habitats varies both spatially and temporally (Paillex et al. 2007), which may affect species composition and the benefits of a particular floodplain habitat to overall ecosystem function. The complexity of lateral connectivity results in high habitat heterogeneity among floodplain habitats and the benefits of a floodplain habitat may vary depending on its degree of connectivity to the main channel or with changes in discharge (Baxter et al. 2005, Winemiller 2005). Fish species richness and diversity may be higher in floodplain habitats with more spatial connectivity to main channel habitats (Ward et al. 1999, Bolland et al. 2012, Franssen et al. 2015). Connectivity between floodplain and main channel habitats can alter food web structure with fish shifting from lotic to lentic invertebrates as connectivity decreases (Bellmore et al. 2013). In addition, habitat heterogeneity is among the primary factors impacting the abundance and composition of invertebrate prey items in lotic ecosystems (Baxter et al. 2005). Differences in seasonal and permanent connectivity on input of allochthonous material to the system have yet to be explicitly tested, but high flows can promote fish movement between the channels (Lyon et al. 2009; Gorski et al. 2014). More connected floodplain habitats are predicted to experience more frequent and longer duration flooding than less connected floodplain habitats, which may lead to differences in invertebrate and fish composition. For example, zooplankton abundance and diversity was higher in backwaters (connected to main channel only on downstream end) than in chutes (connected to main channel upstream and downstream) in the lower Missouri River (Dzialowski et al. 2013). Many fishes prey on zooplankton during their larval development and

as a result, fish growth and recruitment may be higher in backwaters where these prey are more abundant than in chutes (Burrow et al. 2011, Nunn et al. 2012, Steffensen et al. 2014). Therefore, not all floodplain habitats provide the same benefits to fishes and invertebrates.

Humans have altered the flow regime of many large river systems resulting in reduced lateral connectivity and decreased habitat heterogeneity in floodplain habitats (Tockner and Stanford 2002), which has led to declines in biodiversity in these habitats (Vörösmarty et al. 2010). Furthermore, populations of many native fishes dependent on lateral connectivity and floodplain habitats have declined or been otherwise negatively impacted by human activities (Bunn and Arthington 2002, Poff and Zimmerman 2010). However, many restoration projects have been implemented to restore lateral connectivity and minimize the impact of anthropogenic changes on large-river ecosystems (Bernhardt et al. 2005). For example, human development throughout the Upper Mississippi River System aimed at controlling flooding and facilitating navigation have reduced lateral connectivity and led to declines in fish populations (Sparks 1995; Galat and Zweimueller 2001). Restoration efforts to increase lateral connectivity and reduce the impacts associated with anthropogenic changes have been developed in some cases (e.g. Rasmussen et al. 1999).

To examine the impact of connectivity on invertebrates and fish communities, we first tested the importance of flooding for main channel habitats by examining macroinvertebrate communities in main channel habitats before, during, and after flooding. Specifically, we tested the hypothesis that macroinvertebrate diversity and densities will increase in main channel reaches during flooding as a result of inputs from benthic habitats. Next, to evaluate the importance of lateral connectivity we tested two hypotheses focused on the difference between secondary and main channels on prey flow and food web dynamics. First we hypothesize that

macroinvertebrate diversity and density will be higher in permanently connected secondary channel reaches compared to main channel reaches during flooding. Next, we examined fish assemblage structure between permanently connected secondary channel and main channel reaches. Species richness and diversity is often higher in floodplain habitats, especially those with high degrees of connectivity, and inundated habitats often support higher abundances of habitat generalists than similar main channel habitats during flooding (Baxter 2005; Bolland et al. 2012; Phelps et al. 2015). As such, we hypothesize that fish assemblages will have more habitat generalists (fish that utilize lotic and lentic habitats and are able to complete their entire life cycle without flowing water) in permanently connected secondary channel researches and more fluvial specialists (fish that require lotic habitats for a majority of their life cycle) in main channel reaches during flooding (Travnichek et al. 1995, Galat and Zweimüller 2001).

Since habitats in secondary channels and floodplains are often diverse (Paillex et al. 2007) and different levels of flow connectivity may alter food webs and energy flow dynamics (Bolland et al. 2012, Bellmore et al. 2013) it is unclear how well trends observed in one secondary channel can be applied to other channels or floodplain habitats. To gain clarity on differences in secondary channel connectivity, we compared the results of the permanently connected secondary channel for the first three hypotheses with a seasonally connected secondary channel to identify how different flow regimes affect fish and invertebrate assemblies in these two types of secondary channels. Our final hypothesis is that permanently connected and seasonally inundated secondary channels will support similar fish and macroinvertebrate assemblages during flooding.

METHODS

Study Site

The Kansas River is a 7th order sandbed river found in the Flint Hills Region of Northeast Kansas and is characterized by wide shallow channels with an abundance of sandbar habitats. The main stem of the Kansas River is relatively unimpacted with the exception of one lowhead dam and one water diversion weir both located >127 km downstream of our study sites. However, 18 large reservoirs (>650ha), are present in the Kansas River Watershed (Eitzmann and Paukert 2010) but most of the reservoirs are located >105 km downstream of our study sites. The flow regime of the Kansas River is primarily controlled by reservoir releases from tributaries. Our study sites were located in forest and agricultural riparian land use and wider, shallower, and more braided channels than downstream reaches (Eitzmann and Paukert 2010).

Samples were collected from three reaches (1.7 – 2.1 km long) of the Kansas River near St. George, Kansas (39°9'33"N, 96°20'34"W; Figure 3.1) and an adjacent permanently connected secondary channel in a primarily unregulated portion of the Kansas River (Eitzmann and Paukert 2010). Macroinvertebrate and fish samples were collected in two main channel reaches and a permanently connected secondary channel reach before (April), during (June-July), and after (September) flooding in 2010. Each study reach was divided into four equidistant transects and samples were collected at the left, middle, and right of each transect for a total of twelve samples from each study reach during each sampling period (i.e. flood stage).

Samples were collected from a seasonally connected secondary channel near Manhattan, KS (39°11'24"N, 96°30'53"W), 22.6 river km upstream from the sites mention above before (May), during (June), and after flooding (August) in 2010 to address our final hypothesis of differences between permanent and seasonally inundated secondary channels (i.e. varying degrees of connectivity). Discharge for main channel and secondary channel habitats were collected during flooding (June) using an acoustic doppler current profiler.

Main channel macroinvertebrate diversity and density during flooding

Drifting invertebrates were collected at each site using a paired-bongo net with a 50 cm diameter opening and 202 µm mesh deployed just below the water surface for 150 seconds from the bow of the boat. A mechanical flow meter attached to the opening of the net was used to measure water velocity and quantify the volume of water sampled. The paired-bongo net was attached to the bow of the boat with a 10 m tow rope and reverse thrust from the outboard motor was used to hold the net in place during sampling. Benthic invertebrates were collected at each site using a mini-ponar dredge (15.24 cm × 15.24 cm opening), elutriated in the field using a 250 µm sieve to remove inorganic material (i.e. sand), and the contents of the sieve and the collection pan were washed into a collection bottle and retained for identification and enumeration in the laboratory.

All drifting and benthic invertebrate samples were preserved in 10% neutral buffered formalin stained with Rose Bengal, and returned to the laboratory for identification. Preserved samples were examined under 10x magnification and identified to order or family (when possible) and enumerated. A Folsom Plankton Splitter was used to split prohibitively large samples as necessary. For split samples, one half of the sample was randomly selected for sorting and all abundance values were subsequently doubled to obtain estimated abundance values of the entire sample and facilitate comparisons among samples.

Data Analysis

Invertebrate abundances were standardized by calculating catch per unit volume (invertebrates m^{-3}) for drifting invertebrates and catch per unit area (invertebrates m^{-2}) for benthic invertebrates. All continuous variables were $\log_{10}(x + 1)$ transformed prior to analyses to

better meet assumptions of normality. Drifting and benthic invertebrate samples were analyzed separately because different catch per unit effort (i.e. density) values were calculated for each. We used an information theoretic approach to identify hypotheses affecting macroinvertebrate densities in main channel reaches before, during, and after flooding. Three candidate models were developed to examine the importance of habitat type (permanently connected secondary channel, upstream channel, and downstream main channel) and flooding condition (before, during, after flooding) on macroinvertebrate density (Table 3.1). An intercept model was also examined to provide a baseline for interpreting model performance. Akaike's Information Criterion corrected for small sample size (AIC_c) was used to identify best fit models (Burnham and Anderson 2002). We considered models with $\Delta AIC_c < 2$ to be competing models and Akaike weights (w_i) were used to calculate relative support for each competing model. In such cases we used model averaging on predictor variables of competing models to minimize the impact of one model and provide a more conservative representation of the importance of each predictor variable (Burnham and Anderson 2002)

We also examined differences in invertebrate assemblages among reaches and flood stages using non-metric multidimensional scaling (NMDS). Pair-wise differences among groups were identified with analysis of variance using distance matrices (ADONIS). The similarity percentage (SIMPER) function was used to identify the relative importance of each invertebrate taxa to the overall dissimilarity among groups. All statistical analyses were conducted in R version 2.13.1 (The R Foundation for Statistical Computing 2011).

Macroinvertebrate diversity and density in main channel and permanently connected secondary channel habitats during flooding

Drifting and benthic invertebrates were collected from upstream and downstream main channel reaches and a permanently connected secondary channel reach during flood conditions in 2010 using the collection methods of our first hypothesis. Invertebrate densities were compared among reaches using analysis of variance (ANOVA) with an alpha level of 0.05. Pair-wise differences were identified using Tukey HSD tests if ANOVA results were significant.

Similarities in macroinvertebrate assemblages among reaches were examined using analysis of similarity (ANOSIM) and non-metric multidimensional scaling (NMDS) was used to visually examine assemblage structure among reaches during flooding. Significant differences among all groups were identified for NMDS plots with analysis of variance using distance matrices (ADONIS). We identified the relative contribution of each species to overall dissimilarity among groups by calculating similarity percentage (SIMPER) for each NMDS plot.

Fish assemblages in main and permanently connected secondary channels during flooding

Fish were collected from upstream and downstream main channel reaches and a permanently connected secondary channel reach using a combination of boat electrofishing, experimental gill nets, and shoreline seines. Samples were collected from main channel reaches before, during, and after flooding but only during flooding in the permanently connected secondary channel reach. Large bodied fishes were primarily captured using DC-pulsed boat electrofishing using protocols by Guy et al. (2009) and Miranda et al. (2009). One bank was randomly selected at each transect and sampled for 300 seconds resulting in a total of four electrofishing samples in each reach during each sampling period (i.e. before, during, after flooding). Upon capture, fishes were identified, measured (mm), and released.

Monofilament experimental gill nets were set overnight at a randomly selected location (left bank, middle, or right bank) along each transect for a total of four nets in each reach. Nets were set using standardized protocols established by Lester et al. (2009) and Curry et al. (2009). Experimental gill nets were 1.8m tall and 30.5m long with four 7.6m panels of mesh sizes of 1.9, 3.8, 5.1, and 7.6cm. During all sampling periods, nets were set parallel with the flow to minimize drag during high flow conditions. Captured fishes were identified, measured (mm), and released. Small bodied fishes were collected from each reach using 6.0m long by 1.2m deep straight seines with 0.64cm mesh using standardized methods established by Curry et al. (2009). Three to five seine hauls were conducted at each transect per reach. Habitats suitable for seining were sparse during high flow conditions so seining locations were selected opportunistically in each reach. Habitats suitable for seining were randomly selected during periods of low flow or when more than one habitat was identified at a transect during high flow. Large fishes (e.g. > 200mm) were identified in the field, measured (mm), and released. All other fishes were euthanized in a 250mg/L buffered solution of tricane methane sulfonate (MS-222), preserved in 10% formalin, and returned to the laboratory to be measured (mm) and identified.

Data Analysis

Catch rates for fishes were highly variable during flooding primarily as a result of gear inefficiency. Therefore, fish abundance data were converted to presence or absence which still provides a conservative approach when quantitative data are biased (Kwak and Peterson 2007). We used NMDS of a Jaccard distance matrix to test the hypothesis that fish assemblages (using species presence/absence) were consistent among all reaches during flooding. Differences in fish assemblages between sites were identified using ADONIS. The contribution of each species to

overall dissimilarity among groups was calculated using SIMPER values. All statistical analyses were conducted using R version 2.13.1 (The R Foundation for Statistical Computing 2011).

Permanently connected and seasonally inundated secondary channel invertebrate and fish assemblages during flooding

In addition to fish and invertebrates collected in the permanently connected secondary channel, samples were collected from a seasonally connected secondary channel located ~24 km upstream near Manhattan, KS before, during, and after flooding in 2010. Fish and invertebrate samples were collected using the same methodology described previously for the permanently connected secondary channel (see second and third hypotheses this chapter and chapter 2). All fish samples were converted to presence/absence and invertebrate samples were converted to density using the same methods as in previous hypotheses. Drifting and benthic invertebrate densities were compared separately between secondary channel types (i.e. permanent or seasonally connected) using student t-tests.

Fish assemblage structure (using presence/absence data) was compared among secondary channel types using NMDS of a Jaccard distance matrix. Stress values were used to indicate how much variation was explained by the NMDS plot. We identified variation in fish assemblages among sites with an ADONIS using 1000 permutations. Individual species contribution to overall dissimilarity among groups for each axis was identified using SIMPER.

RESULTS

Main channel macroinvertebrate diversity and density during flooding

<u>Drifting Invertebrates</u>

A total of 72 drifting invertebrate samples were collected from upstream and downstream main channel reaches before, during, and after flooding in 2010 which included a total of 2,893 drifting invertebrates from 15 orders and at least 21 families captured at least once in main channel reaches (Table 3.2). Invertebrates from 10 taxa accounted for greater than 5% of the total catch and were retained for further analyses (boldface text Table 3.2). For all sampling periods combined, Ephemeroptera were the most abundant taxa in main channel drift before and after flooding and densities were 3 – 4 times higher before and after flooding compared to densities during flooding when Chaoboridae and Diptera both had higher densities.

Two competing models had support as best fit models explaining drifting invertebrate concentrations in main channel reaches before, during, and after flooding (Table 3.1). The top model indicated that flood stage had the greatest effect on drifting invertebrate density in main channel reaches. Drifting invertebrate concentrations in both main channel reaches was higher during flood conditions compared to before and after flooding (Figure 3.2). However, the competing model had both flood stage and reach, and upstream densities were lower than downstream reaches during post-flood conditions (Figure 3.2). Thus, support for the competing model is likely a result of post-flood conditions when drifting invertebrate concentration is higher in the downstream main channel reach (Figure 3.2). Furthermore, drifting invertebrate assemblages were similar between upstream and downstream main channel reaches before and during flooding but differed after flooding (ADONIS $p=0.041$, Figure 3.3) likely driven by higher densities of Chironomidae in upstream reaches and higher densities of Ephemeroptera and Oligochaeta in downstream reaches (Table 3.2).

Benthic Invertebrates

Seventy-two total benthic invertebrate samples were collected from main channel reaches before, during, and after flooding in 2010 with a total of 466 invertebrates collected representing 11 orders and 15 families (Table 3.3). Among all invertebrates, seven taxa accounted for at least 5% of the total catch and were retained for further analyses (boldface text Table 3.3).

Flood stage and reach both influenced benthic invertebrate densities in main channel reaches before, during, and after flooding. The best supported model suggested that flood stage was the best predictor of benthic invertebrate density in main channel reaches (weight=0.8) but a competing model with flood stage and reach also had limited support (weight=0.2) indicating that patterns in benthic invertebrate density may vary during different flow conditions (Table 3.1). Benthic invertebrate densities were about twice as high in main channel reaches before flooding compared to densities during and after flooding (Figure 3.2). However, densities were similar between upstream and downstream reaches before and during flooding but higher in the downstream main channel reach after flooding (Figure 3.2) which is most likely driving the competing model of flood stage and reach.

Benthic invertebrate assemblage structure was generally similar between upstream and downstream main channel reaches during all sampling periods, with post-flood upstream and downstream reaches being marginally significantly different (Figure 3.3; ADONIS p=0.062). However, Ephemeroptera densities were higher in the downstream reach during and after flooding compared to upstream reaches (Table 3.3). With the exception of Hymenoptera, densities of all dominant benthic invertebrate taxa decreased during flooding compared to densities observed before flooding. Additionally, densities for most taxa increased after flooding although only Odonata densities were higher after flooding compared to pre-flood conditions.

Macroinvertebrate diversity and density in main channel and permanently connected secondary channel habitats during flooding

Drifting Invertebrates

We collected 36 drifting invertebrate samples among upstream and downstream main channel and secondary channel reaches during flooding in 2010. Among all samples, 1,299 drifting invertebrates representing 10 orders and 12 families were collected. Six taxa represented at least 5% of the total catch and were retained for further analyses (boldface text Table 3.4).

During flooding, drifting invertebrate densities were on average 33% – 47% higher in upstream and downstream main channel reaches compared to the permanent secondary channel ($p<0.01$; Figure 3.4). In addition to supporting different concentrations of drifting invertebrates, NMDS for drifting invertebrate assemblage structure (Figure 3.5), mainly differentiated between the upstream and downstream main channels and the secondary channel. Variation along the first axis was most positively associated taxa found in secondary channel habitats (Chaoboride and Corixidae) and most negatively associated with main channel taxa (Chironomidae, Trichoptera). The second axis primarily differentiated sites by year and was positively associated with Ephemeroptera and Coleoptera and negatively associated with Ceratopogonidae. Drifting invertebrate assemblages varied among habitats the permanently connected secondary channel, upstream, and downstream main channel reaches (ADONIS, $p<0.01$).

The six most abundant taxa in the upstream and downstream main channel accounted for 95.9% of the total catch and were identical for both the upstream and downstream main channel reaches but showed differences in the permanently connected secondary channel (Table 3.4). Mean densities of the two most abundant taxa in main channel reaches, Chaoboridae and Diptera, were about 7 to 10 times higher in main channel reaches compared to the permanently

connected secondary channel. Conversely, the mean density of Corixidae, the most abundant taxa in the permanently connected secondary channel, was about 9 times higher in the secondary channel than in the main channel reaches.

Benthic Invertebrates

A total of 36 benthic invertebrate samples were collected among upstream and downstream main channel reaches and the permanently connected secondary channel reach in 2010. A total of 216 benthic invertebrates were collected representing 10 orders and at least 12 families. However, only 5 taxa represented at least 5% of the total catch and were retained for further analysis (boldface text Table 3.5).

During flooding, mean benthic invertebrate densities in the permanently connected secondary channel were more than double the densities in upstream and downstream main channel reaches (P=0.016; Figure 3.4), driven by Chironomidae and Oligochaeta densities that were 3 to 5 times higher in the permanently connected secondary channel compared to main channel reaches (Table 3.5). NMDS for benthic invertebrate assemblage structure primarily differentiated between main channel and secondary channel habitats (Figure 3.5). Variation along the first axis was most positively associated with secondary channel species (Chironomidae and Oligochaeta) and most negatively associated with dipterans. The second axis was primarily differentiated among secondary channel sites and was most positively associated with Ephemeroptera and negatively associated with hymenoptera. However, assemblage structure did not vary among reaches (ADONIS, P=0.19).

Fish assemblages in main and permanently connected secondary channels during flooding

We collected a total of 1427 individual fishes from all sites during flooding including 1076 from seines, 67 from overnight gill nets, and 284 from electrofishing. These fish represented 23 species from 11 families. Cyprinidae was the most abundant family and sand shiner (*Notropis stramineus*) was the most abundant species among all reaches and was found at every site (Table 3.6). Among all samples, 12 species represented at least 5% of the total catch and were retained for further analyses (boldface text Table 3.6). Because sampling was consistent with each gear at each sampling site, collection data were pooled among all gears for each site and analyzed together.

The NMDS analysis indicated fish assemblages (using presence/absence) primarily separated the upstream and downstream main channel reaches from the permanently connected secondary channel reach (Figure 3.6). Fish assemblages were similar in both main channel reaches (ADONIS, p=0.48) where suckermouth minnow (*Phenacobius mirabilis*) and shovelnose sturgeon (*Scaphirhynchus platorynchus*) were present at a majority of main channel sites but were not as prevalent in the permanently connected secondary channel. Sand shiner was the only species captured in all samples and emerald shiner (*Notropis atherinoides*) and red shiner (*Cyprinella lutrensis*) were present in all main channel samples. Gizzard shad and red shiner were also found at all sites except one (11/12) in the permanently connected secondary channel. Among all species, blue sucker (*Cycleptes elongates*), fathead minnow (*Pimephales promelas*), goldeye (*Hiodon alosoides*), and shovelnose sturgeon (*Scaphirhynchus platorhychus*) were found exclusively in main channel reaches and bluegill (*Lepomis macrochirus*), white bass (*Morone chrysops*), and white crappie (*Pomoxis annularis*) were found exclusively in the permanently connected secondary channel (Table 3.6).

Permanently connected and seasonally inundated secondary channel invertebrate and fish assemblages during flooding

We collected a total of 1052 drifting invertebrates during flooding in 2010 including 368 from the permanently connected secondary channel and 684 from the seasonally connected secondary channel reach. Mean drifting invertebrate densities were about twice as high in the seasonally connected secondary channel (x=57.0 per m^3) compared to the permanently connected secondary channel (x=30.7 per m^3, t-test, $p<0.01$). A total of 309 benthic invertebrates were collected during flooding in 2010 including 212 from the permanently connected secondary channel and 97 from the seasonally inundated secondary channel. Mean benthic invertebrate densities in the permanently connected secondary channel (x=17.7 per m^2) were more than double those observed in the seasonally connected secondary channel (x=8.1 per m^2, t-test, $p<0.01$).

We collected a total of 2,620 fish during flooding in 2010 including 1,427 fish from the permanently connected secondary channel and its adjacent main channel and 1,193 collected from the seasonally connected secondary channel and its adjacent main channel. From all samples, 24 species representing 11 families were collected at least once but 11 species accounted for at least 5% of the total catch and were retained for further analyses (Table 3.6).

Fish assemblages (using presence/absence) in main channel reaches (St. George versus Manhattan) were similar before (ADONIS, p=0.42) and during (ADONIS, p=0.22) flooding suggesting that, although these sites were ~24 river km apart the fish assemblages in these reaches were similar (Figure 3.7). In contrast, shortnose gar and emerald shiner were more common in the permanently connected secondary channel but generally absent from the

seasonally connected secondary channel and quillback (*Carpiodes cyprinus*) was more common in seasonally connected secondary channels ($p<0.01$).

DISCUSSION

Flooding can affect fish and invertebrate communities both directly and indirectly (e.g. mortality, voluntary and involuntary movement, prey availability, refugia). Our results suggest that flooding may lead to differences among fish and invertebrate assemblages and that the duration of lateral connectivity (seasonal versus permanent) may be an important factor in determining the function of secondary channels. Flooding increased the concentration of drifting invertebrates in main channel reaches providing support for a pulse of prey in the main channel reaches as described by the Flood Pulse Concept (Junk et al. 1989). Our results support the river-wave hypotheses and suggest that the pulse observed during flooding is a combination of inputs from floodplain habitats and upstream reaches. Upstream inputs are likely the result of involuntary or catastrophic drift because all samples were collected during daylight hours when most drift is accidental or involuntary (Waters 1965; Callisto and Goulart 2005, Gibbins et al. 2007). Drifting invertebrate concentrations did not differ between upstream and downstream main channel reaches during flooding which may suggest the absence of changes in input of drifting invertebrates from the permanently connected secondary channel during a high flow event. Concentrations downstream would be expected to equal upstream concentrations plus input from the permanently connected secondary channel reach and would be higher than upstream main channel densities if floodplain habitats were the primary source of an energy pulse as proposed by the Flood Pulse Concept. These results may indicate that floodplain habitats are not primarily responsible for higher densities of drifting invertebrates during flooding. Our findings may also be an artifact of flood control measures in our system and that

our definition of flooding included high flows that inundated sub-bankful habitats but did not exceed bankful width and inundate true floodplain habitats.

Secondary channel flows are dynamic and influenced by channel morphology and main channel discharge (Le Coz et al. 2010). During peak discharges observed in this study in July 2011 ($\bar{Q}$=989m^3/s), 3.7% of the main channel flow was diverted into the permanently connected secondary channel. However, during more typical flood discharges ($\bar{Q}$=221-424m^3/s) observed in 2009 and 2010, only 0.6 – 1.3% of main channel discharge was diverted into the permanently connected secondary channel. With flows from the permanently connected secondary channel representing a relatively small amount of overall main channel discharge, the increase in drifting invertebrate density is likely the result of collective input from terrestrial habitats, including floodplain habitats and main channel riparian habitats inundated below bankfull flows (Tockner et al. 2000, Thorpe et al. 2006). Alternatively, it is possible that we did not detect a sizable input from the secondary channel we sampled because it is permanently connected and therefore not found in a classic floodplain habitat which may have higher productivity (Tockner and Stanford 2002). However, our results indicate that the collective inundation of multiple terrestrial habitats (i.e. the secondary channel plus riparian vegetation) may still benefit fishes by increasing macroinvertebrate densities in main channel habitats. These findings are consistent with other studies that suggest that the collective inundation of riparian habitats in both main channel and secondary habitats, and not just the inundation of floodplain habitats, is important for the transfer of prey from terrestrial to aquatic habitats (e.g. Puckridge et al. 1998, Tockner et al. 2000, Thorpe et al. 2006). Tockner et al. (2000) explained such events as "flow pulses" and highlighted the importance of such events in creating a diversity of habitats and regulating functional processes in large river systems. The inundation of terrestrial sub-bankful habitats along the bank

could provide important sources of energy and inundation of these habitats, along with floodplain habitats, should be considered when determining the importance of floods as prey sources for fishes and other large river organisms.

Benthic invertebrate densities were highest in main channel reaches before flooding and declined during and after flooding suggesting flooding may disrupt benthic assemblages and affect the recovery of benthic invertebrate assemblages in main channel reaches. These decreases are likely the result of "catastrophic drift" where benthic organisms are involuntarily entered into the drift as a result of high benthic shear stress during high flows (Callisto and Goulart 2005, Gibbins et al. 2007). Organisms in sand-bed rivers are especially susceptible to catastrophic drift compared to organisms in systems with larger gravel or cobble substrate because relatively small increases in velocity can disrupt sand benthos compared to other benthic substrates (Allan 2007, Gibbins et al. 2007, 2010). Substrate composition may also explain the higher densities of benthic invertebrates we observed during flooding in secondary channel compared to main channel reaches. Most of the benthic substrate in the secondary channel was predominantly muddy instead of the sandy substrate found in the main channel. Additionally, flow rates tended to be lower in secondary channel habitats ($\bar{Q}$=9.3m^3/s) compared to main channel reaches ($\bar{Q}$=545m^3/s). High flows in the main channel likely resulted in entrainment of many benthic invertebrate during flooding leading to the decrease in benthic invertebrate density in main channel habitats during and after flooding. Bowen et al. (2003) found that varying flows may alter habitats and nutrient cycling in floodplain habitats so the combination of muddy substrates and lower flows (and resulting reduction in entrainment compared to main channel) in the secondary channel reach of this study may explain higher densities of benthic organisms found in secondary channel habitats compared to those observed in the main channel.

More fluvial dependent fish species were captured in the permanently connected secondary channel than the seasonally inundated secondary channel. These findings are similar to other studies which found that ecological benefits of floodplain habitats vary with abiotic variables (e.g. water temperature, Tockner et al. 2000) and that some fish (e.g. habitat generalists) rely on floodplain habitats whereas others (i.e. fluvial specialists) thrive in main channel habitats (e.g. Dettmers et al. 2001, Galat and Zweimuller 2001). Many fishes use floodplain habitats for many life history needs including refugia, reproduction, and feeding (Scheimer 2000, Galat and Zweimuller 2001, Burgess et al. 2012). We found that habitat generalist species common carp and red shiner were prevalent in all reaches indicating that these species can persist in a variety of habitats. Fluvial dependents, such as quillback, were more prevalent in seasonally connected secondary channels compared to permanently connected secondary channels. Our results provide evidence that secondary channel habitats with varying degrees of connectivity may be beneficial in supporting fish assemblages. Whereas fish may move into inundated habitats for different reasons (e.g. increased prey, spawning habitat, random movement) and these habitats can be beneficial, movement into these habitats does not come without risk as fish may become stranded when flows recede (Humphries et al. 1999, Bolland et al. 2015). Bellmore et al. (2013) also found differences in food web structure and fish assemblages among secondary channels with varying degrees of lateral connectivity. Specifically, they found that larger predators such as chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) used a wide variety of habitats whereas important prey fish such as sculpin and whitefish were common in main channel and connected secondary channels but generally absent from reaches that were not connected to the main channel (Bellmore et al. 2013).

Seasonally connected secondary channels had higher densities of drifting invertebrates whereas permanently connected secondary channels had higher densities of benthic invertebrates during flooding in our study. Fish species, such as red shiner, that feed primarily on drifting invertebrates may benefit more from moving into these seasonally connected secondary channels. However, most fishes that primarily feed on drifting invertebrates in the Kansas River predominantly feed on aquatic invertebrates and seldom feed on terrestrial invertebrates (Eitzmann 2008). Permanently connected secondary channels may be more beneficial to fishes feeding predominantly on benthic invertebrates, such as smallmouth buffalo, and during high flows, movement into these laterally connected habitats may benefit these species of fish with greater access to prey. Our results suggest that it may be important to maintain a secondary channels with varying degrees of lateral connectivity and show that benefits to fish and invertebrates may diverge in relation to the degree of connectivity between the main channel and secondary channel habitat.

Because upstream and downstream reaches were relatively equal in the amount of drifting and benthic invertebrates, the main tenet of the Flood Pulse Concept that floods are the primary source for energy in large river systems does not follow in this large river system. The Flood Pulse Concept was originally designed for unaltered large-rivers (Junk et al. 1989), but almost all large rivers have been altered to some degree to meet human needs which has affected the ecology of secondary channels and floodplains and the organisms that rely on these habitats (Bunn and Arthington 2002, Poff and Zimmerman 2010, Carlisle et al. 2011).

Our results may help improve the success of restoration efforts for fishes in large river systems by identifying the importance of secondary channel and floodplain habitats for fishes and invertebrates. Restoration efforts to mitigate the effects of human actions on aquatic

ecosystems are widespread and an estimated average of at least $1 billion is spent on river and stream restoration in the United States each year (Bernhardt et al. 2005). We found that the degree of lateral connectivity (i.e. permanently or seasonally connected) changes how fish use these habitats. For example, flooding resulted in an increase in drifting invertebrate density but subsequently decreased the density of benthic invertebrates in main channel reaches. These patterns were switched in secondary channel reach where benthic invertebrate densities were higher than drifting invertebrate densities. Because invertebrates are an important food source for many fishes, these patterns and the flooding responsible for them, may be important in predicting the importance of secondary channel habitats for fishes. Food web dynamics are important in shaping fish communities and increasing our understanding of food web dynamics may increase our ability to protect native fishes (Winemiller 2005).

Although we did not directly quantify feeding or food web structure in this study, we provide evidence that flooding and lateral connectivity are important factors influencing invertebrate densities (i.e. fish prey). Although some fish taxa were commonly found in all habitats (e.g. common carp, emerald shiner, sand shiner), assemblages differed depending on the degree of lateral connectivity with shortnose gar and emerald shiner indicative of permanently connected secondary channels and quillback indicative of seasonally connected secondary channels. Our results suggest that flooding and inundation of terrestrial habitats during flooding is important for many large river systems and may help guide restoration efforts by identifying the importance of flooding and floodplain inundation. Specifically, the degree of lateral connectivity can influences fish assemblages and invertebrate densities and these differences may help guide conservation efforts for native fishes. However, the importance of different secondary channels may be scale dependent or may benefit non-native fishes more than natives

(Franssen et al. 2015) and restoration efforts should consider other factors (e.g. distribution of other secondary channels) when determining the importance of lateral connectivity. Restoration and conservation efforts focused on ecological benefits of lateral connectivity should consider the degree of connectivity between the secondary channel and main channel habitats to ensure that target taxa will benefit from such efforts. Future efforts to examine fish assemblages at numerous secondary channels with varying amounts of connectivity within and among large rivers may further elucidate which fish taxa use inundated secondary channel habitats. Such efforts would help increase our understanding of how connectivity influences fish and invertebrate communities and may help increase our understanding of the importance of lateral connectivity and the importance of flooding as part of the flow regime for large-river systems.

LITERATURE CITED

Allan, J.D. 2007. Stream ecology: structure and function of running waters. *Springer, New York, New York.*

Baxter, C.V., K.D. Fausch, and W.C. Sanders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian habitats. *Freshwater Biology* 50:201-220.

Bellmore, J.R., C.V. Baxter, K. Martens, and P.J. Connolly. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recover. *Ecological Applications* 23:189-207.

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.

Bolland, J.D., A.D. Nunn, M.C. Lucas, and I.G. Cowx. 2012. The importance of variable lateral connectivity between artificial floodplain waterbodies and river channels. *River Research and Applications* 28:1189:1199.

Bolland, J.D., A.D. Nunn, M.C. Lucas, and I.G. Cowx. 2015. The habitat use of young-of-the-year fishes during and after floods of varying timing and magnitude in a constrained lowland river. *Ecological Engineering* 75:434-440.

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.

Bunn, S.E. and A.H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492-507.

Burgess, O.T., W.E. Pine III, and S.J. Walsh. 2012. Importance of floodplain connectivity to fish populations in the Apalachicola River, Florida. *River Research and Applications* 29:718-733.

Burnham, K.C. and D.R. Anderson. 2002. Model selection and multi-model inference. *Springer, New York, New York.*

Burrow, J.F., J.W. Horwood, and J.W. Pitchford. 2011. The importance of variable timing and abundance of prey for fish larval recruitment. *Journal of Plankton Research* 33:1153-1162.

Callisto, M. and M. Goulart. 2005. Invertebrate drift along a longitudinal gradient in a Neotropical stream in Serra do Cipó National Park, Brazil. *Hydrobiologia* 539:47-56.

Carlisle, D.M., D.M. Wolock, and M.R. Meador. 2011. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264-270.

Curry, R.A., R.M. Hughes, M.E. McMaster, and D.J. Zafft. 2009. Coldwater fish in rivers. Pages 139-158 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

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.

Dzialowski, A.R., J.L. Bonneau, and T.R. Gemeinhardt. 2013. Comparisons of zooplankton and phytoplankton in created shallow water habitats of the lower Missouri River: implications for native fish. *Aquatic Ecology* 47:13-24.

Eitzmann, J.L. 2008. Spatial habitat variation in a Great Plains river: Effects on the fish assemblage and food web structure. Master's thesis, Kansas State University, Manhattan, Kansas.

Eitzmann, J.L., and C.P. Paukert. 2010. Longitudinal differences in habitat complexity and fish assemblage structure of a Great Plains River. *American Midland Naturalist* 163: 14-32.

Franssen, N.R., E.I. Gilbert, and D.L. Propst. 2015. Effects of longitudinal and lateral stream channel complexity on native and non-native fishes in an invaded desert stream. *Freshwater Biology* 60:16-30.

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.

Gibbins, C.N., D. Vericat, R.J. Batalla. 2007. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. *Freshwater Biology* 52:2369-2384.

Gibbins, C.N., D. Vericat, R.J. Batalla. 2010. Relations between invertebrate drift and flow velocity in sand-bed and riffle habitats and the limits imposed by substrate stability and benthic density. *Journal of the North American Benthological Society* 29:945-958.

Górski, K., J.J. De Leeuw, H.V. Winter, D.A. Vekhov, A.E. Minin, A.D. Buijse, and L.A.J. Nagelkerke. 2011. Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. *Freshwater Biology* 56:210-2225.

Guy, C.S., P.J. Braaten, D.P. Herzog, J. Pitlo, and R.S. Rogers. 2009. Warmwater fish in rivers. Pages 59-84 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Jeffres, C.A., J.J. Opperman, and P.B. Moyle. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California River. *Environmental Biology of Fishes* 83:449–458.

Junk, W.J., P.B. Bayley, and R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106:110-127.

Kwak, T.J., and J.T. Peterson. 2007. Community indices, parameters, and comparisons. Pages 677-763 *in* C.S. Guy and M.L. Brown (editors). Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Le Coz, J., M. Michalková, A. Hauet, M. Čomaj, G. Dramais, K. Holubová, H. Piégay, and A. Paquier. 2010. Morphodynamics of the exit of a cutoff meander: experimental findings from field and laboratory studies. *Earth Surface Processes and Landforms* 35:249-261.

Lester, N.P., P.E. Bailey, and W.A. Hubert. 2009. Coldwater fish in small standing waters. Pages 85-96 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Miranda, L.E. 2009. Standardizing electrofishing power for boat electrofishing. Pages 223-230 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Nunn, A.D., L.H. Tewson, and I.G. Cowx. 2012. The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries* 22:377-408.

Paillex, A., E. Castella, and G. Carron. 2007. Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. *Journal of the North American Benthological Society* 26:779-796.

Phelps, Q.E., S.J. Tripp, D.P. Herzog, and J.E. Garvey. 2015. Temporary connectivity: the relative benefits of large river floodplain inundation in the lower Mississippi River. *Restoration Ecology* 23:53-56.

Poff, N.L. and J.K.H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55:194-205.

Puckridge, J.T., F. Sheldon, K.F. Walker, and A.J. Boulton. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* 49:55-72.

Rasmussen, J. D. Steinbach, K. Westphall, D. Ellis, R. Cantu, M. Kerschbaum, C. Suprenant, J. Milligan, A. Sprunger-Allworth, and R. Adams. 1999. Floodplain land management practices of the U.S. Fish and Wildlife Service on Upper Mississippi River National Wildlife Refuges. Upper Mississippi River Ecosystem Levee Committee Final Report, June 24, 1999.

Scheimer, F. 2000. Fish as indicators for the assessment of ecological integrity of large rivers. *Hydrobiologia* 422/423:271-278.

Sparks, R.E. 1995. Need for ecosystem management of large rivers and their floodplains. *Bioscience* 45:168-182.

Steffensen, K.D., B.L. Eder, and M.A. Pegg. 2014. Fish community response to floodplain inundation in a regulated river. *Journal of Freshwater Ecology* 29:413-427.

Thorpe, J.H., M.C. Thoms, and M.D. Delong. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* 22:123-147.

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.

Tockner, K., F. Malard, and J.V. Ward. 2000. An extension of the flood pulse concept. *Hydrological Processes* 14:2861-2883.

Tockner, K. and J.A. Stanford. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29:308-330.

Tockner K., F. Schiemer, and J.V. Ward. 1998. Conservation by restoration: the management concept for a river floodplain system on the Danube River in Austria. *Aquatic Conservation: Marine and Freshwater Ecosystems* 8:71–86.

Vörösmarty, C.J., P.B. McIntyre, M.O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S.E. Bunn, C.A. Sullivan, C.R. Liermann, and P.M. Davies. 2010. Global threats to human water security and river biodiversity. *Nature* 467:555-561.

Ward, J.V. 1992. Aquatic Insect Ecology, Part 1, Biology and Habitat. Wiley: New York, New York. 438pp.

Waters, T.F. 1965. Interpretation of drift in streams. *Ecology* 46:327-334.

Winemiller, K.O. 2005. Floodplain river food webs: generalizations and implications for fisheries management. Pages 285–312 in R. L. Welcomme and T. Petr, editors. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries. Volume 2. Mekong River Commission, Phnom Penh, Cambodia.

Table 3.1. AIC results for candidate models examining trends in benthic and drifting invertebrate densities in upstream and downstream main channel reaches of the Kansas River before, during, and after flooding in 2010.

	Benthic			Drift		
Model Parameters	AICc	ΔAICc	w_i	AICc	ΔAICc	w_i
Stage	312.1	0	0.8	618.0	0	0.6
Reach; Stage	314.0	1.9	0.2	619.1	1.1	0.4
Reach	323.6	11.5	0	625.1	7.1	0
Intercept	326.8	14.7	0	643.9	25.9	0

Table 3.2. Mean ± standard error (SE) of density of drifting invertebrates per 100 cubic meters in main channel reaches of the Kansas River upstream and downstream of a permanently connected secondary channel before, during, and after flooding in 2010. Bold values indicate taxa that accounted for at least 5% of the total catch and were retained for analyses.

	Before Flooding		During Flooding		After Flooding	
Taxa	Downstream	Upstream	Downstream	Upstream	Downstream	Upstream
Amphipoda	6.1 ± 4.1	2.8 ± 2.8	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Arachnid	6.3 ± 4.2	2.9 ± 2.9	10.0 ± 7.0	6.5 ± 4.4	0 ± 0	0 ± 0
Ceratopogonid	**73.9 ± 41.5**	**37.1 ± 15.3**	**3.6 ± 3.6**	**6.9 ± 4.7**	**54.0 ± 18.1**	**21.5 ± 9.8**
Chaoboridae	**12.9 ± 7.2**	**5.7 ± 3.8**	**57.1 ± 39.4**	**32.8 ± 22.2**	**46.1 ± 13.2**	**36.5 ± 19.8**
Chironomidae	**223.3 ± 48.6**	**200.7 ± 40.9**	**148.9 ± 26.3**	**144.3 ± 37.8**	**182.1 ± 26.5**	**170.1 ± 30.3**
Coleoptera	15.5 ± 8.5	15.8 ± 10.1	14.7 ± 6.3	7.0 ± 4.8	8.7 ± 4.6	17.9 ± 7.1
Corixidae	**24.5 ± 6.9**	**20.5 ± 7.9**	**682.8 ± 69.4**	**678.0 ± 94.6**	**38.5 ± 13.4**	**8.0 ± 4.2**
Diptera	**36.7 ± 14.8**	**48.3 ± 17.3**	**281.7 ± 50.9**	**287.2 ± 48.6**	**48.4 ± 11.7**	**19.6 ± 9.0**
Ephemeroptera	**1160.4 ± 214**	**1231.7 ± 211.8**	**210.8 ± 33.7**	**224.2 ± 85.6**	**795 ± 101.8**	**471.9 ± 92.2**
Gastropoda	**0 ± 0**	**3.0 ± 3.0**	**10.9 ± 7.8**	**3.7 ± 3.7**	**3.2 ± 3.2**	**8.7 ± 4.6**
Geriidae	9.2 ± 4.8	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Hirudinae	0 ± 0	3.2 ± 3.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Hymenoptera	9.5 ± 5.0	18.5 ± 10.9	18.1 ± 6.5	17.3 ± 6.2	15.7 ± 5.6	2.8 ± 2.8
Lepidoptera	5.8 ± 3.9	0 ± 0	7.2 ± 4.9	3.3 ± 3.3	3.0 ± 3.0	0 ± 0
Megaloptera	0 ± 0	5.8 ± 3.9	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Naucoridae	0 ± 0	2.9 ± 2.9	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Odonata	19.3 ± 9.0	11.8 ± 6.7	3.1 ± 3.1	0 ± 0	0 ± 0	0 ± 0
Oligochaeta	**27.4 ± 13.0**	**17.5 ± 6.9**	**13.9 ± 5.9**	**19.3 ± 7.2**	**46.2 ± 15.4**	**6.2 ± 4.2**
Plecoptera	15.3 ± 5.5	6.0 ± 4.0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Trichoptera	**233 ± 47.2**	**130.5 ± 29.5**	**90 ± 22.2**	**125.6 ± 42.0**	**212.6 ± 34.8**	**145.3 ± 34.3**
Veliidae	**36.1 ± 10.3**	**17.1 ± 6.7**	**3.4 ± 3.4**	**6.5 ± 4.4**	**54.6 ± 13.9**	**32.8 ± 11.3**
Total	1902.9 ± 295.9	1776.1 ± 242.8	1445.7 ± 122.4	1476.9 ± 89	1508.3 ± 134.2	941.2 ± 108.6

Table 3.3. Mean ± SE density of benthic invertebrates per square meter in main channel reaches of the Kansas River upstream and downstream of a permanently connected secondary channel before, during, and after flooding in 2010. Bold values indicate taxa that accounted for at least 5% of the total catch and were retained for analyses.

	Before Flooding		During Flooding		After Flooding	
Taxa	Downstream	Upstream	Downstream	Upstream	Downstream	Upstream
Arachnidae	3.6 ± 3.6	0 ± 0	7.2 ± 4.8	7.2 ± 4.8	0 ± 0	0 ± 0
Ceratopogonidae	14.4 ± 8.1	14.4 ± 8.1	0 ± 0	0 ± 0	14.4 ± 8.1	7.2 ± 4.8
Chaoboridae	0 ± 0	3.6 ± 3.6	0 ± 0	3.6 ± 3.6	0 ± 0	3.6 ± 3.6
Chironomidae	**118.4 ± 34.6**	**89.3 ± 12.4**	**50.3 ± 19**	**50.3 ± 10.4**	**78.2 ± 15.2**	**56.8 ± 11.3**
Coleoptera	0 ± 0	0 ± 0	0 ± 0	3.6 ± 3.6	0 ± 0	0 ± 0
Decapoda	3.6 ± 3.6	0 ± 0	0 ± 0	0 ± 0	3.6 ± 3.6	0 ± 0
Diptera	**36.1 ± 18.6**	**48.8 ± 15.6**	**25.1 ± 6.4**	**18 ± 9.9**	**30.7 ± 11.6**	**20.6 ± 11.8**
Ephemeroptera	**81.6 ± 41.8**	**98.2 ± 31.3**	**39.5 ± 12.4**	**7.2 ± 4.8**	**62.3 ± 24.1**	**19.9 ± 8.3**
Gastropoda	0 ± 0	7.2 ± 7.2	0 ± 0	3.6 ± 3.6	0 ± 0	0 ± 0
Hirudinae	3.6 ± 3.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Hymenoptera	**7.2 ± 4.8**	**3.6 ± 3.6**	**14.4 ± 8.1**	**21.6 ± 9.9**	**7.2 ± 4.8**	**0 ± 0**
Odonata	**0 ± 0**	**3.6 ± 3.6**	**0 ± 0**	**14.4 ± 6.1**	**7.2 ± 4.8**	**7.2 ± 4.8**
Oligochaeta	**151.6 ± 82.1**	**182.5 ± 78.7**	**39.5 ± 35.8**	**35.9 ± 13.9**	**93.6 ± 46.2**	**88.4 ± 37.1**
Tricoptera	3.6 ± 3.6	0 ± 0	7.2 ± 4.8	0 ± 0	3.6 ± 3.6	0 ± 0
Veliidae	0 ± 0	3.6 ± 3.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Total	423.7 ± 103.2	454.8 ± 91.2	183.2 ± 47.5	165.2 ± 23.0	293.3 ± 56.6	197.1 ± 48.1

Table 3.4. Mean ± standard error (SE) of concentrations of drifting invertebrates per 100 cubic meters in upstream and downstream main channel and permanently connected secondary channel reaches of the Kansas River during flooding in summer of 2010. Bold values indicate taxa that accounted for at least 5% of the total catch and were retained for analyses.

Taxa	Secondary Channel	Downstream	Upstream	Total
Ceratopogonid	0.0 ± 0.0	3.6 ± 3.6	6.9 ± 4.7	3.5 ± 3.4
Chaoboridae	**48.2 ± 18.0**	**682.8 ± 69.4**	**678 ± 94.6**	**469.7 ± 109.7**
Chironomidae	**172.4 ± 40.9**	**148.9 ± 26.3**	**144.3 ± 37.8**	**155.2 ± 34.7**
Coleoptera	9.1 ± 6.5	14.7 ± 6.3	7.0 ± 4.8	10.3 ± 5.8
Corixidae	**279.6 ± 69**	**57.1 ± 39.4**	**32.8 ± 22.2**	**123.2 ± 56.5**
Diptera	**29.9 ± 10.8**	**281.7 ± 50.9**	**287.2 ± 48.6**	**199.6 ± 53.2**
Ephemeroptera	**108.1 ± 34.6**	**210.8 ± 33.7**	**224.2 ± 85.6**	**181.0 ± 57.2**
Gastropoda	53.5 ± 24.5	10.9 ± 7.8	3.7 ± 3.7	22.7 ± 15.9
Hymenoptera	9.0 ± 4.7	18.1 ± 6.5	17.3 ± 6.2	14.8 ± 5.8
Oligochaeta	36.0 ± 19.0	14.5 ± 6.2	20.3 ± 7.6	23.6 ± 12.3
Trichoptera	**20.5 ± 11.0**	**90.0 ± 22.2**	**125.6 ± 42.0**	**78.7 ± 30.2**
Veliidae	21.6 ± 10.4	3.4 ± 3.4	6.5 ± 4.4	10.5 ± 7.0
Total	787.9 ± 105.4	1536.6 ± 136.3	1553.9 ± 100.8	1292.8 ± 153.2

Table 3.5. Mean ± SE density of benthic invertebrates per square meter in a permanently connected secondary channel and main channel reaches of the Kansas River upstream and downstream of the permanently connected secondary channel during flooding in summer of 2010. Bold values indicate taxa that accounted for at least 5% of the total catch and were retained for analyses.

Taxa	Secondary Channel	Upstream	Downstream	Total
Arachnidae	0 ± 0	7.2 ± 4.8	7.2 ± 4.8	4.8 ± 4.0
Chaoboridae	3.6 ± 3.6	3.6 ± 3.6	0 ± 0	2.4 ± 2.9
Chironomidae	**158 ± 69**	**50.3 ± 10.4**	**50.3 ± 19**	**86.2 ± 43.2**
Coleoptera	3.6 ± 3.6	3.6 ± 3.6	0 ± 0	2.4 ± 2.9
Diptera	**0 ± 0**	**18 ± 9.9**	**25.1 ± 6.4**	**14.4 ± 7.3**
Ephemeroptera	**32.3 ± 32.3**	**7.2 ± 4.8**	**39.5 ± 12.4**	**26.3 ± 20.0**
Gastropoda	7.2 ± 4.8	3.6 ± 3.6	0 ± 0	3.6 ± 3.5
Hirudinae	7.2 ± 7.2	0 ± 0	0 ± 0	2.4 ± 4.1
Hymenoptera	**3.6 ± 3.6**	**21.6 ± 9.9**	**14.4 ± 8.1**	**13.2 ± 7.8**
Odonata	3.6 ± 3.6	14.4 ± 6.1	0 ± 0	6.0 ± 4.4
Oligochaeta	**204.7 ± 52.6**	**35.9 ± 13.9**	**39.5 ± 35.8**	**93.4 ± 43.2**
Tricoptera	3.6 ± 3.6	0 ± 0	7.2 ± 4.8	3.6 ± 3.5
Total	427.4 ± 110	165.2 ± 23	183.2 ± 47.5	258.6 ± 76.8

Table 3.6. Proportion of sites (of 12 sampled) where species were detected in upstream and downstream main channel or permanently connected secondary channel reaches of the Kansas River during flooding in 2010. Bolded species represented at least 5% of the total catch and were retained for further analyses.

Common Name	Scientific Name	Family	Upstream	Downstream	Secondary Channel
Blue sucker	*Cycleptus elongatus*	Catostomidae	16.7	8.3	0.0
Bluegill	*Lepomis macrochirus*	Centrarchidae	0.0	0.0	25.0
Bluntnose minnow	*Pimephales notatus*	Cyprinidae	16.7	25.0	16.7
Bullhead minnow	*Pimephales vigilax*	Cyprinidae	8.3	16.7	8.3
Channel catfish	*Ictalurus punctatus*	Ictaluridae	8.3	8.3	16.7
Common carp	***Cyprinus carpio***	**Cyprinidae**	**50.0**	**58.3**	**58.3**
Emerald shiner	***Notropis atherinoides***	**Cyprinidae**	**100.0**	**100.0**	**75.0**
Fathead minnow	*Pimephales promelas*	Cyprinidae	8.3	0.0	0.0
Flathead catfish	***Pylodictis olivaris***	**Ictaluridae**	**33.3**	**58.3**	**75.0**
Freshwater drum	***Aplodinotus grunniens***	**Sciaenidae**	**16.7**	**25.0**	**66.7**
Gizzard shad	***Dorosoma cepedianum***	**Clupeidae**	**16.7**	**33.3**	**91.7**
Goldeye	*Hiodon alosoides*	Hiodontidae	25.0	25.0	0.0
Longnose gar	***Lepisosteus osseus***	**Lepisosteidae**	**41.7**	**25.0**	**66.7**
Quillback	*Carpiodes cyprinus*	Catostomidae	0.0	8.3	16.7
Red shiner	***Cyprinella lutrensis***	**Cyprinidae**	**100.0**	**100.0**	**91.7**
River carpsucker	***Carpiodes carpio***	**Catostomidae**	**33.3**	**66.7**	**83.3**
Sand shiner	***Notropis stramineus***	**Cyprinidae**	**100.0**	**100.0**	**100.0**
Saugeye	*Sander sp.*	Percidae	8.3	8.3	50.0
Shortnose gar	*Lepisosteus platostomus*	Lepisosteidae	25.0	16.7	75.0
Shovelnose sturgeon	***Scaphirhynchus platorynchus***	**Acipenseridae**	**75.0**	**83.3**	**0.0**
Smallmouth buffalo	***Ictiobus bubalus***	**Catostomidae**	**50.0**	**41.7**	**75.0**
Suckermouth minnow	***Phenacobius mirabilis***	**Cyprinidae**	**100.0**	**91.7**	**16.7**
White bass	*Morone chrysops*	Moronidae	0.0	0.0	8.3
White crappie	*Pomoxis annularis*	Centrarchidae	0.0	0.0	25.0

Figure 3.1. Aerial photograph of the Kansas River near St. George, KS. Lines indicate upstream main channel (solid), downstream main channel (dashed), and permanently connected secondary channel (dotted) study reaches.

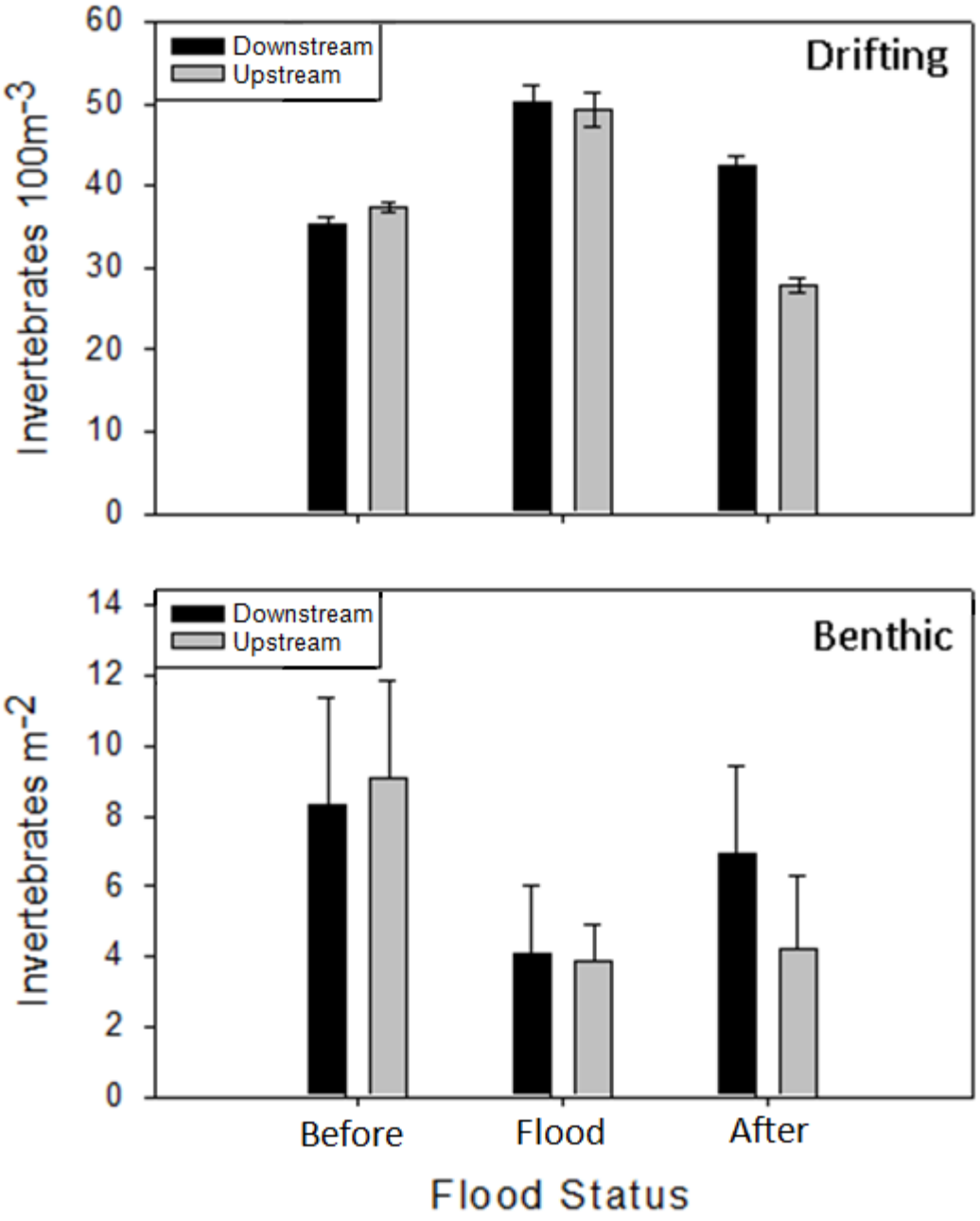

Figure 3.2. Mean density (±SE) of drifting and benthic invertebrates in upstream (US) and downstream (DS) main channel reaches of the Kansas River before, during, and after flooding in 2010.

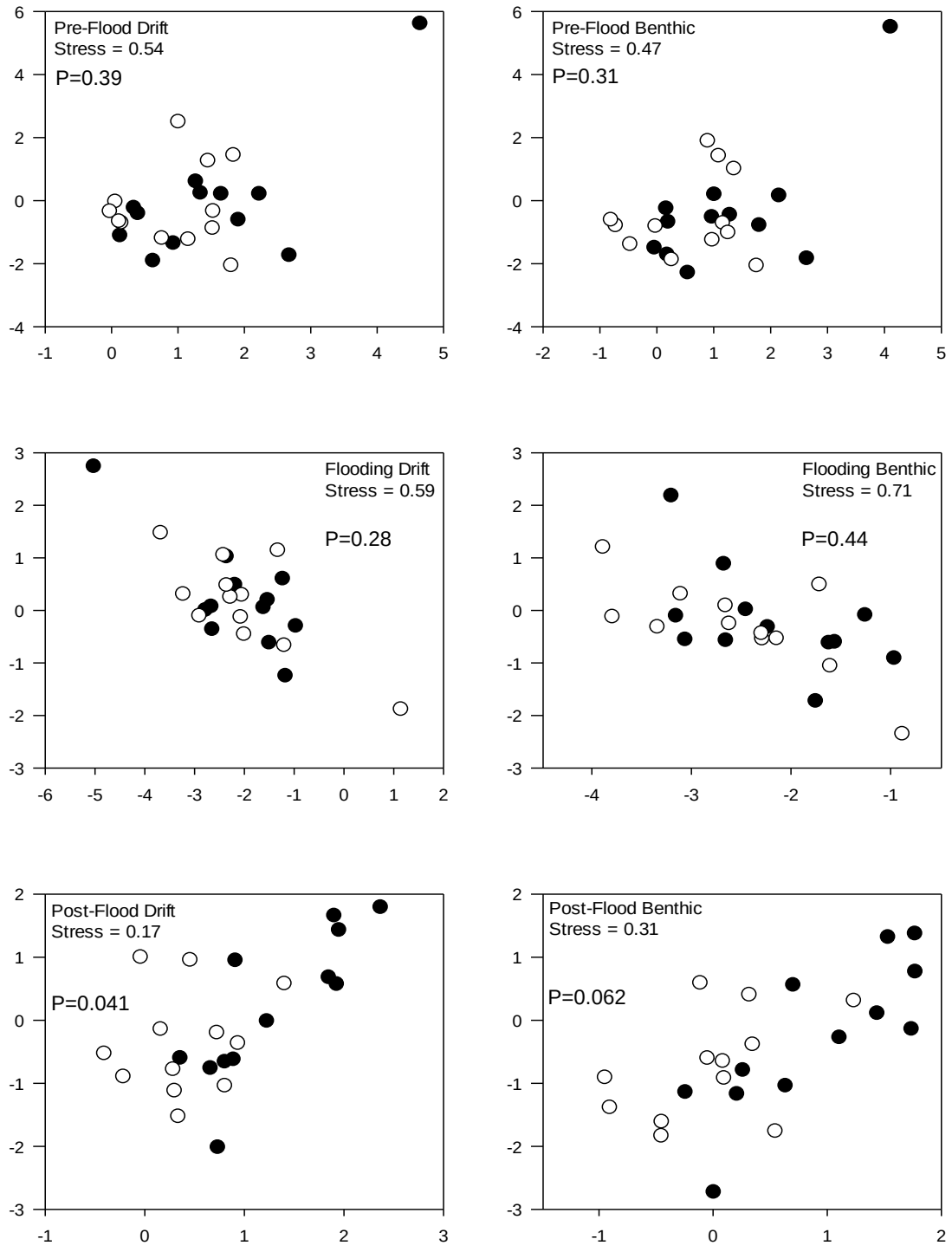

Figure 3.3. NMDS plots for drifting (left panels) and benthic (right panels) invertebrate assemblages in upstream (white circles) and downstream (black circles) main channel reaches of the Kansas River before, during, and after flooding in 2010. Significance values examining differences among groups using ADONIS are presented.

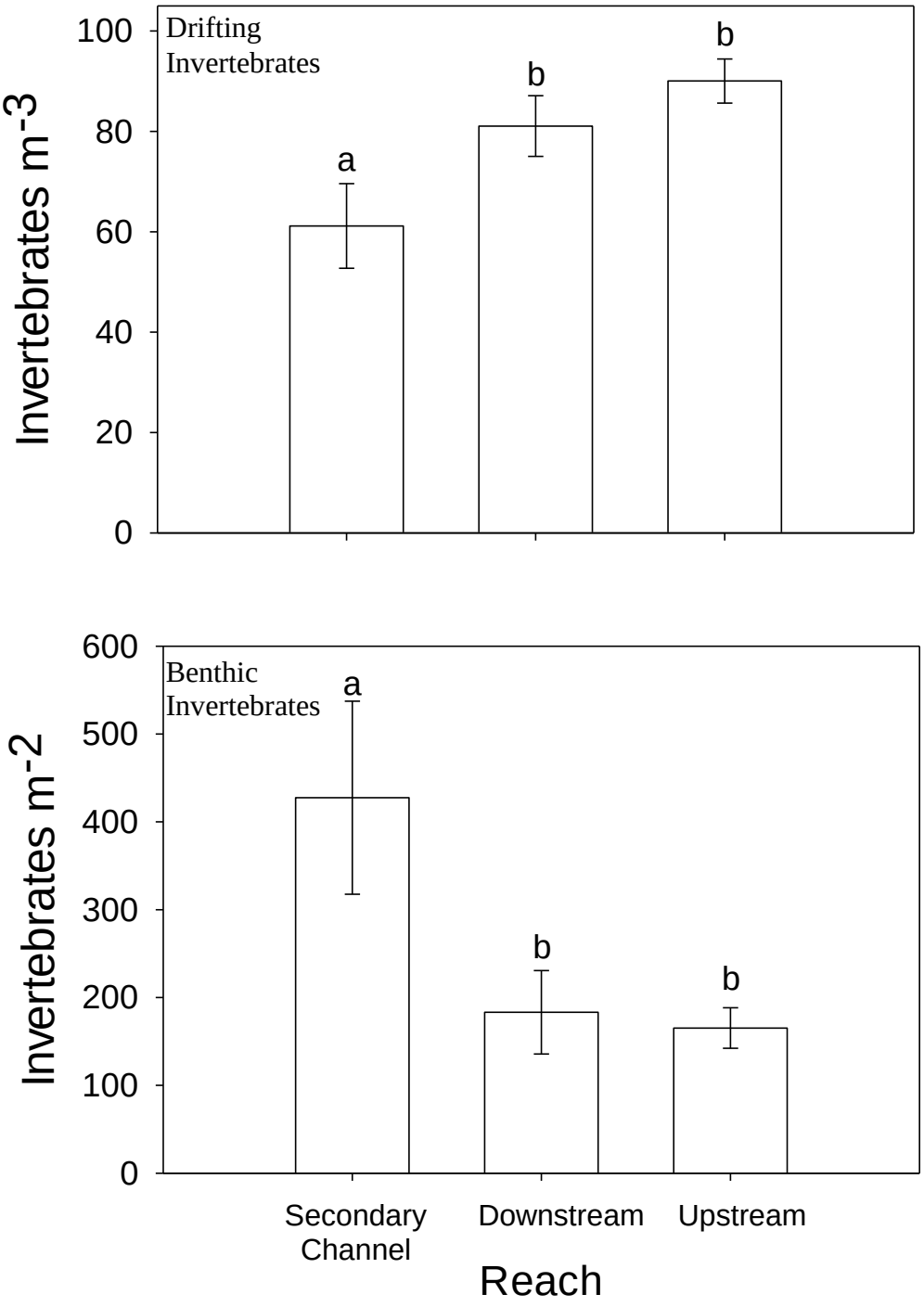

Figure 3.4. Mean (±SE) densities of drifting and benthic invertebrates collected in 2010 from upstream and downstream main channel reaches and a permanently connected secondary channel reach of the Kansas River. Letters above bars indicate significant differences among groups.

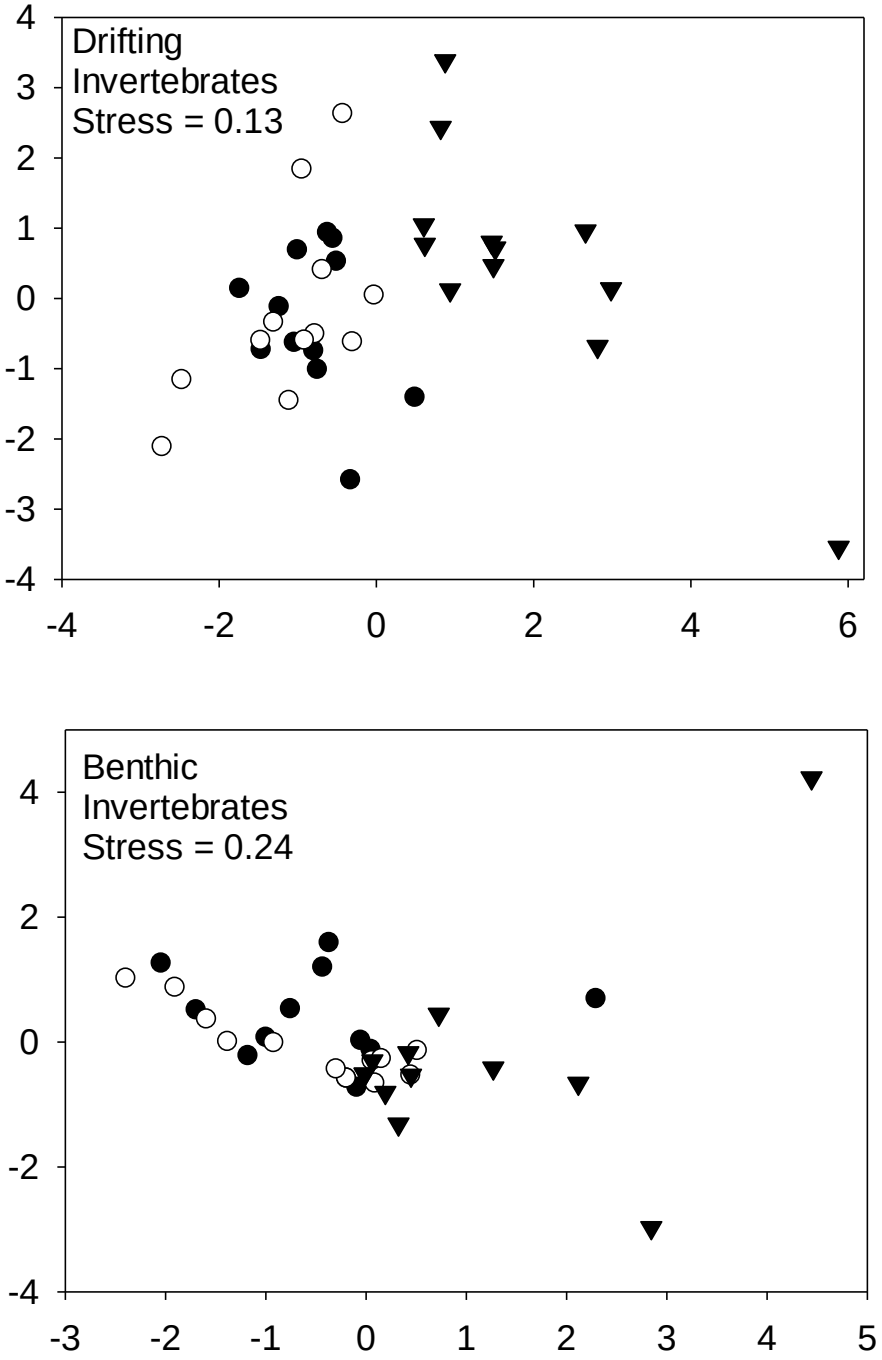

Figure 3.5. NMDS plots for drifting and benthic invertebrate assemblages in upstream (white circles) and downstream (black circles) main channel and secondary channel (black triangles) reaches of the Kansas River during flooding in 2010.

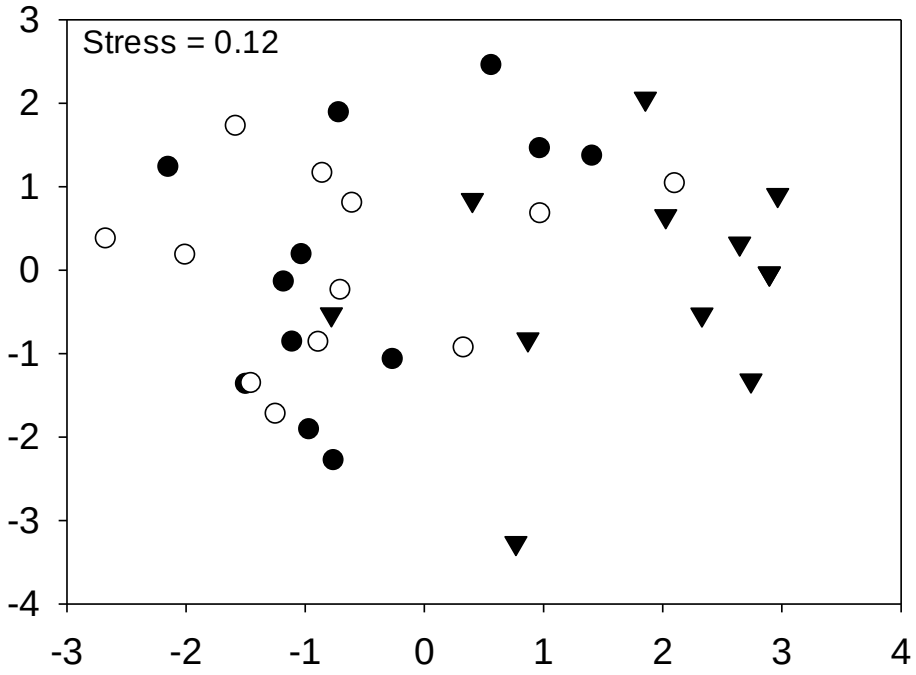

Figure 3.6. NMDS plot for fish assemblages (using presence/absence data) in upstream (white circles) and downstream (black circles) main channel and secondary channel (black triangles) reaches of the Kansas River during flooding in 2010.

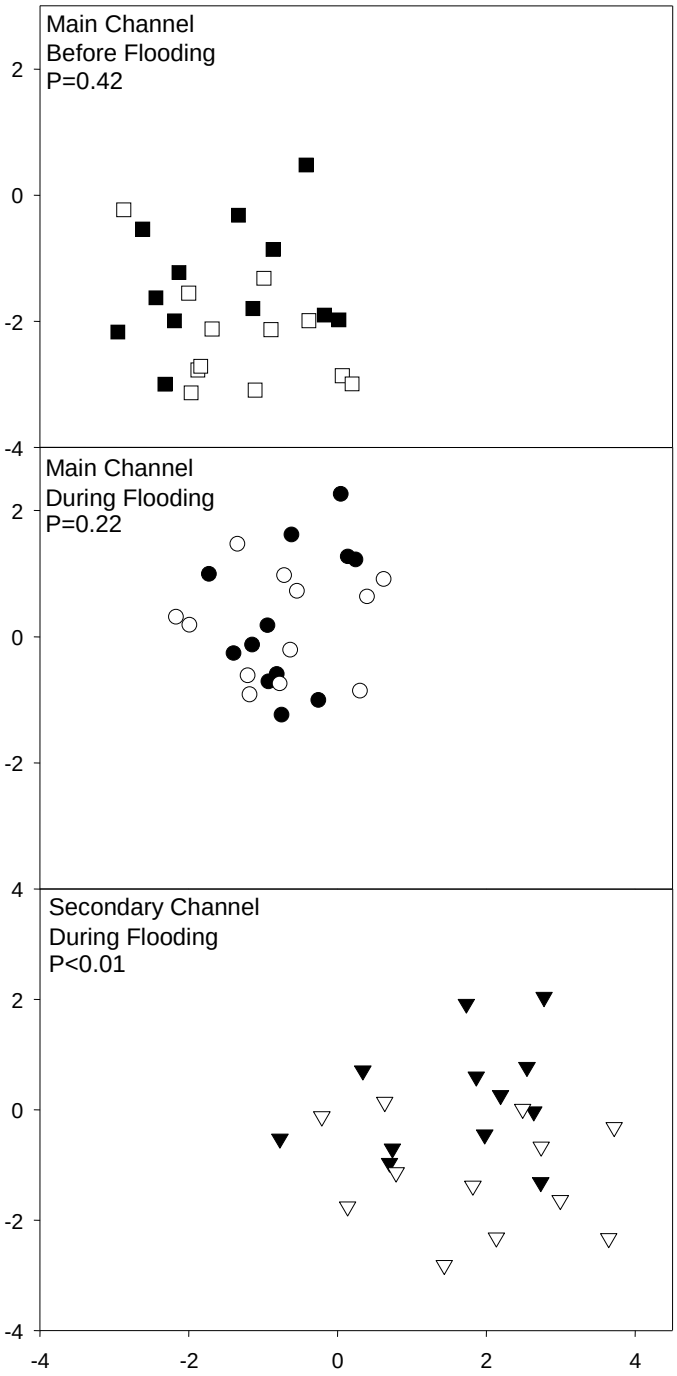

Figure 3.7. NMDS plots for fish assemblages (using presence/absence) in main channel reaches before flooding and in main channel and secondary channels during flooding in 2010. Samples for the permanently connected secondary channel and adjacent main channel were collected near St. George, KS (dark symbols) and samples for the seasonally connected secondary channel and adjacent main channel were collected near Manhattan, KS (hollow symbols). Significance values for ADONIS pair-wise comparisons are presented.

Chapter 4 - Impacts of Hydrologic Variability on Recruitment Patterns of Fishes in the Kansas River

ABSTRACT

Humans have altered the hydrology and function of many lotic ecosystems in the United States and these changes may affect native fish recruitment. We examined recruitment patterns for four native fishes at three reaches of the Kansas River with varying in-stream and hydrologic characteristics. Patterns in hydrologic variation were examined using principal component analysis which primarily differentiated among years with high flows (>125% of 20-year mean annual flow) and years with numerous summer low-flow (<25% of 20-year mean annual flow) days. Age class structure for freshwater drum (*Aplodinotus grunniens*), flathead catfish (*Pylodictis olivaris*), river carpsucker (*Carpiodes carpio*), and shovelnose sturgeon (*Scaphirhynchus platorynchus*) were examined using an information theoretic approach. Models were constructed from catch curve residuals and principal component scores of hydrologic variables to identify the relationships among native fish recruitment and flows. Flathead catfish and shovelnose sturgeon recruitment increased in relation to metrics of high flows. We did not identify any consistent trends between freshwater drum and river carpsucker recruitment and hydrologic variables characterizing high and low flows. Overall, our results indicate that variability in flow events among years adequately supports these native river fishes examined, with high flow events significantly benefiting some species but not others. A diversity of hydrological conditions may be necessary to increase recruitment success of all native fishes and restoring flow regimes to mimic natural hydrology may be a viable option of mitigating human influences in many rivers and maintaining a strong native fish community.

INTRODUCTION

Most riverine ecosystems in the United States have been altered by human activities and as a result, only about 2% of the rivers in the United States remain in their original and unmodified conditions including many in the Great Plains (Graf 1993; Lytle and Poff 2004). Dam construction, dredging, and agricultural and urban land use are widespread and have altered the hydrology and function of many lotic ecosystems (Bunn and Arthington 2002; Vörösmarty et al. 2010; Costigan and Daniels 2012). These changes often have detrimental impacts on native fishes and may reduce the biodiversity and recruitment success of fishes and other organisms in altered systems (Bunn and Arthington 2002; Poff and Zimmerman 2010). Though the mechanisms by which human alterations have impacted aquatic ecosystems are diverse, changes to the natural flow regime of aquatic ecosystems are especially pervasive and have altered abiotic factors and biotic communities in many large rivers (Bunn and Arthington 2002; Poff and Zimmerman 2010; Górski et al. 2011).

Changes to the natural flow regime can considerably modify the habitat of large rivers and subsequently alter fish recruitment patterns (Warren et al. 2000; King et al. 2003; Dutterer et al. 2013). Among abiotic aspects, flows are especially important in defining physical habitats including river channel structure, substrate characteristics, and connectivity between main channel and inundated floodplain habitats (Bain et al. 1988; Poff et al. 1997; Bunn and Arthington 2002). Recruitment of fishes is often linked to flow regimes in large rivers and may be considered among the most important factors shaping fish population structure (King et al. 2003; Zeug and Winemiller 2007). High flows are especially important for many aspects of spawning and successful recruitment (Welcomme 1985, Górski et al. 2011) and floods are often the primary environmental factor impacting recruitment success for fishes (Sparks 1995,

Agostinho et al. 2004, Górski et al. 2011). Whereas high flow events can benefit species such as shovelnose sturgeon by initiating spawning, providing nursery habitats, and facilitating larvae and egg movement (Bramblett and White 2001; DeLonay et al. 2007; Goto et al. 2015), other fishes, especially those without drifting egg or larval stages, may show increased recruitment success in response to low flows that provide increased densities of prey for developing larvae (Humphries et al. 1999; King et al. 2010; Baumgartner et al. 2014).The timing, duration, and intensity of high and low flow events are especially important for fish recruitment (Poff et al. 1997, Rolls et al. 2013) as these events can provide cues to initiate spawning and connect the main channel to important spawning and nursery habitats in side channels and backwater habitats (Junk et al. 1989, Zeug and Winemiller 2007, Górski et al. 2011).

Although flow events are essential for successful spawning and recruitment of many fishes, dam construction has altered the hydrology of many streams and constrained high and low flow extremes throughout the Great Plains (Costigan and Daniels 2012). As a result, anthropogenic impacts and changes to hydrology can decrease recruitment success of native fishes in impacted systems (Agostinho et al. 2004; Zeug and Winemiller 2007, Carlisle et al. 2010). By limiting and constraining flood events, anthropogenic changes may limit fish access to floodplain and backwater habitats and subsequently decrease the recruitment success for fishes that rely on flooded habitats for spawning and nursery sites (King et al. 2003, Galat et al. 2005; Górski et al. 2011). When hydrological variation is reduced, floodplains may become disconnected and fish that rely on inundated habitats may be forced to less suitable spawning grounds or refrain from spawning altogether (Górski et al. 2011). Gaining an understanding of how hydrology (i.e. high and low flows) relates to recruitment of native fishes is important for protecting the biodiversity of fishes in many rivers including those in the Great Plains.

We examined recruitment patterns of four native fishes: flathead catfish (*Pylodictis olivaris*), freshwater drum (*Aplodinotus grunniens*), river carpsucker (*Carpiodes carpio*), and shovelnose sturgeon (*Scaphirhynchus platorynchus*) in three reaches of the Kansas River to identify how spatial and temporal variation in hydrologic characteristics influence fishes with different reproductive strategies. These species are common native fishes in many large rivers of the Great Plains and they represent a variety of recruitment strategies and fish management interests throughout the Great Plains.

Flathead catfish, river carpsucker, and shovelnose sturgeon all have adhesive eggs (Kansas Fishes Committee 2014). Shovelnose sturgeon have a drifting larval stage (Kynard et al. 2002; Braaten et al. 2008) and therefore may rely on high flows for successful recruitment. High flows may also be important for freshwater drum eggs that mature as they drift downstream (Balon 1975; Kansas Fishes Committee 2014). In contrast, hydrologic variation and floodplain inundation may not be as important for successful recruitment of flathead catfish and river carpsucker because they have adhesive eggs and flathead catfish build sedentary nests that are guarded by males as they develop (Balon 1975; Fuselier 2014). Floodplain habitats with slower discharges may be especially important for successful recruitment in upstream reaches of the Kansas River where impoundments (i.e. Bowersock Dam) may prevent upstream recruitment of juveniles that drift downstream, for fishes such as shovelnose sturgeon and freshwater drum but not as much for species such as flathead catfish. Shovelnose sturgeon often migrate long distances (>200km) to reach spawning locations (DeLonay et al. 2007) but Bowersock Dam likely limits many of these fishes from migrating into the upper reaches of the Kansas River. Additionally, low-flows and anoxic habitats in the transition zone upstream of Bowersock Dam may trap eggs and larvae and be a sink for recruitment of fishes with drifting egg and larval

stages (Guy et al. 2015). Additionally, shovelnose sturgeon is treated as a threatened species in downstream portions of the Kansas River under the Endangered Species Act because of its similarity to the federally endangered pallid sturgeon (Quarterman 2010). As such, increasing our understanding of shovelnose sturgeon recruitment patterns may also help increase our understanding of other similar species including the federally endangered pallid sturgeon.

Our study assesses the relationship of recruitment patterns of four native fishes to hydrology variables that encompass high and low flows in the Kansas River, including mean annual flow variability, mean spring flow variability, and number of low flow days during summer months (for complete list see Table 4.1). Our first hypothesis is that recruitment of species with drifting egg or larval stages (freshwater drum and shovelnose sturgeon) will increase in years with high flows (e.g. flows exceeding 175% of 20-year mean annual flow) because high flows will facilitate the drift component of their life history and help developing eggs and larvae develop and survive. Our second hypothesis is that recruitment of fishes without a drifting egg or larval stage (flathead catfish and river carpsucker) will be higher in years with low flows (e.g. many days with flow below 25% of 20-year mean annual flow) because low flows will increase the density of prey for these non-drifting, developing larvae easing the effort of the larvae to obtain food for growth (Humphries et al. 1999; Baumgartner et al. 2014). Identifying trends in recruitment patterns and factors that impact recruitment success of native fishes may aid in conservation efforts focused on protecting these and other native fish species.

METHODS

The Kansas River is a 7th order river located in northeast Kansas that flows 274 km from its source near Junction City, KS to the confluence with the Missouri River near Kansas City Kansas. The Kansas River watershed encompasses 155,695 km^2 throughout the Great Plains

including portions of Colorado, Kansas, and Nebraska. Although impoundments on the main stem of the Kansas River are rare, the Kansas River Watershed contains 18 large reservoirs (>650ha) and numerous small impoundments (Eitzmann and Paukert 2010) and the flow regime is largely regulated by releases from these reservoirs. Samples were collected from upper, middle, and lower reaches of the Kansas River to ensure that a gradient of habitats were sampled so we could identify the impact of environmental variation (i.e. hydrology) on native fish recruitment (Table 4.1). Upstream reaches are characterized by agriculture and forest riparian habitat with more instream habitats, i.e. grass islands and sandbars (Eitzmann and Paukert 2010). Downstream reaches are characterized by greater urban land use (Eitzmann and Paukert 2010). In addition, upstream reaches tended to have lower mean annual flows and floods of lower intensity and shorter duration than downstream reaches (Table 4.1).

Fishes were collected at each reach using pulsed-DC boat electrofishing following the standardized methodology presented by Guy et al. (2009) and Miranda (2009) from April to August 2009 and 2010. Six 300-second electrofishing samples were collected from each reach for a total of 18 samples for each round of sampling. After capture, fishes were measured and had an aging structure removed (otoliths for freshwater drum and principle fin rays for flathead catfish, river carpsucker, and shovelnose sturgeon).

Aging structures were used to calculate fish age and evaluate recruitment patterns among species. At least 50 individuals were aged at each reach for all species except shovelnose sturgeon which had at least 34 individuals aged at each reach. In the laboratory, freshwater drum otoliths were sectioned using a Buehler low-speed isomet saw and polished with sandpaper until annuli could be easily identified. Fin rays were air dried and mounted in epoxy following the methods proposed by Koch and Quist (2007), and cut into 1 mm sections using a Buehler low-

speed isomet saw. Otolith annuli and fin ray radii were counted using a computer mounted microscope and Image ProPlus image analysis software (Image ProPlus; Media Cybernetics, Inc., Bethesda, MD). Aging structures were aged independently by two readers without knowing the fish's length. If readers disagreed on the age of the fish by less than two years they discussed the differences and tried to reach an agreeable age. Fish were excluded from analyses if readers could not agree on an age, or if the original age discrepancy between readers was greater than two years. Only age-classes that were fully recruited to the gear and consistently represented with at least 2 fish among samples and captured in 2 of 3 of the reaches, were retained for analysis. Catch curves were constructed by plotting abundance by year class for each species at each reach. Older age classes that were not captured at all sites were excluded from analyses. Standardized residuals of weighted catch curves were used to examine recruitment variability. Positive residuals represented strong year classes whereas negative residuals indicated weak year classes (Maceina 1997; Maceina and Pereira 2007). Differences in maximum and minimum residuals were calculated by year for each species to identify spatiotemporal differences in recruitment patterns among species.

Hydrologic parameters were calculated using daily discharge values collected for 1999 – 2009 from the Kansas River near Wamego, KS (United States Geological Survey (USGS) Station 06887500), Topeka, KS (USGS Station 06889000), and DeSoto, KS (USGS Station 06892350). The hydrologic metrics used were calculated by reach for each year analyzed (Table 4.1). The 20 year mean was calculated from all years collected (1999-2009). We used the inundation of sampled secondary channels in the Kansas River near Manhattan, the most upstream reach, as our base metric to define flooding. Secondary channels in this reach were inundated when flows were 137% above the 20 year mean annual flow (Figure 4.1). Lateral

connectivity is more prevalent in this reach than more channelized downstream reaches. As such, we used a cutoff of 175% of the 20 year mean annual flow at each reach as a conservative and consistent threshold to defining flooding among all reaches (sensu Carlisle et al. 2010).

We used numerous hydrologic variables to examine the role of high and low flows on native fish recruitment for each reach of our system (Table 4.1). High flow events have been identified as a primary factor impacting the recruitment of many large river fishes (Górski et al. 2011); thus, we chose variables to examine various metrics of high flows, including duration, timing, and magnitude (Poff et al. 1997) on fishes of the Kansas River (Table 4.1). Mean flow and coefficient of variation were also calculated for spring months (March, April, and May) as flows in these months may regulate spawning success of native fishes in the Kansas River. We also examined metrics related to low flow during summer months for each reach to test our hypothesis that low flows are affecting fish recruitment patterns in the Kansas River. Number of days below 25% of the 20 year mean during summer months, mean summer flow, and summer flow variability (coefficient of variation) were also used for low flow metrics (Table 4.1). Summer months are defined as June, July and August and correspond with the time of development for fish eggs and larvae.

Spatiotemporal relationships among hydrologic variables were identified using principal component analysis (PCA) to assess which hydrologic variables best characterized reaches among years. Hydrologic variables were selected *a priori* for inclusion in the PCA to ensure metrics of high and low flows were examined. All continuous variables were $\log_{10}(X + 1)$ transformed prior to analyses to address the assumption of normality. We retained two axes as they explained greater than 70% of the variance while still allowing for easy visual interpretation of the relationships among samples (Kwak and Peterson 2007). We interpreted variables that had

had PC loadings with absolute values greater than 0.4 to be important factors for each principal component (Stevens 1992; Kwak and Peterson 2007). Native fish standardized catch curve residuals and principal component scores were plotted to identify the strength and direction of the relationship between hydrologic variables and recruitment patterns of each fish species.

We examined the importance of the hydrologic parameters (e.g. flood intensity, duration, magnitude) and habitat characteristics (i.e. reach) on native fish recruitment with an information theoretic approach using Akaike Information Criterion (AIC). Principal component scores for the first and second axes were included in models to examine relationships between spatiotemporal hydrologic conditions and native fish recruitment. We also included a model with reach as a predictor variable to help identify if recruitment patterns varied among sampling locations and a null model with just the intercept to serve as a baseline for comparison of model performance (Table 4.2). In total, five candidate models were developed to identify how native fish recruitment (i.e. catch curve residuals) varied in relation to hydrologic parameters at each reach (Table 4.2). AIC corrected for small sample size (AIC_c) was used for evaluation of model performance. The lowest AIC_c score indicates the best fit model; however, models within two AIC_c values are considered competing models with similar support and a best fit model cannot be calculated using AIC_c values alone (Burnham and Anderson 2002). We calculated ΔAIC_c scores ($\Delta AIC_c = AIC_c - AIC_{c(minimum)}$) to identify competing models within 2 AICc values of the best fit models. When competing models were identified, Akaike weight (w_i) was used to identify support for competing models (Burnham and Anderson 2002). Results of these analyses were compared to identify recruitment patterns among species. All statistical analyses were conducted using R version 2.13.1 (The R Foundation for Statistical Computing 2011).

RESULTS

Mean daily discharge varied among years in our study and resulted in a gradient of high, intermediate, and low flow years (Figure 4.1). Lowest flows were observed in 2006 (mean daily discharge = 34.52 m^3/s) and highest flows were observed in 1999 (mean daily discharge = 216.61 m^3/s). Three years (1999, 2005, and 2007) were high flow years that had mean daily discharge values that exceeded the 20 year mean daily discharge of 148.9 m^3/s. Conversely, 2002, 2003, and 2006 were low flow years with mean daily discharge values below 33% of the 20 year mean daily discharge (49.64 m^3/s).

A total of 816 aging structures were collected in 2009 (n=283) and 2010 (n=533; Table 4.3). Of these, 724 aging structures were precisely aged between two readers and retained for further analyses including structures from flathead catfish (n=186), freshwater drum (n=179), river carpsucker (n=239), and shovelnose sturgeon (n=120). In general, recruitment was more consistent (i.e. difference in minimum and maximum residual) for river carpsucker than other fish species (Figure 4.2).

Principal component analyses of hydrologic variables largely separated samples among years and grouped samples by reach (Figure 4.3). The first principal component accounted for 70.3% of the variation among samples and was generally positively associated with high flow metrics including mean summer flow, flood duration, and flood intensity and negatively associated with higher numbers of summer days below 25% of the 20 year mean annual flow (Table 4.4). The second principal component accounted for 12.7% of variation among samples and primarily separated sites based on higher annual and summer flow variability (positive scores) and decreased mean spring flow (negative scores; Table 4.4).

Freshwater drum maximum age ranged from 10 years in Kansas City and Manhattan reaches to one fish aged 18 years in Topeka (Table 4.3). Catch rates became sporadic (many

zeros) for fishes greater than 10 years (2001 year class) and fishes 11 years and older were removed from analysis. The only year that strong year classes (positive residuals) were observed for freshwater drum at all reaches was 2004 but strong or average year classes were observed at all reaches in 2002, 2003, and 2006 (Figure 4.2). Year class strength was weak at all reaches in 2007. Recruitment was variable among reaches in 1999, 2000, and 2001 with some reaches exhibiting strong year class strength and others exhibiting weak year class strength (Figure 4.2). Two competing models were identified relating freshwater drum recruitment to PC loadings of the hydrologic variables PCA (Table 4.5). However, the null model with just the intercept was also identified as a competing model indicating that freshwater drum recruitment patterns in our study are not related to the hydrologic variables we examined.

Maximum age of flathead catfish varied from 8 years in Manhattan to 17 years in Topeka. Flathead catfish exhibited strong year classes at all reaches of the Kansas River in 2001, 2003, and 2007 and consistently weak year classes among all reaches in 1999, 2006, and 2007 (Figure 4.2). Flathead catfish recruitment was variable among reaches for the 2000, 2002, and 2004 year classes. Three competing models were identified relating flathead catfish recruitment to hydrology including high flows (i.e. PC1) and flow variability (i.e. PC2) in the Kansas River (Table 4.5). Flathead catfish recruitment increased with (r^2=0.12) with PC1 indicating that flathead catfish recruitment increases during years with high summer flows and longer, higher intensity flooding (Figure 4.4). Flathead catfish recruitment decreased with PC2 (r^2= 0.15) meaning that flathead catfish recruitment decreased in relation to increasing annual and summer flow variability (Figure 4.4).

River carpsucker maximum age ranged from 10 years in the Manhattan reach to 16 years in Topeka and Kansas City. Strong year class strength was observed at all reaches for 2000 –

2004, with the exception of the Kansas City reach in 2003 that had a slightly weak year class, whereas year class strength was weak at all reaches in 1999 and 2005 (Figure 4.2). Two models had reasonable support as top models relating river carpsucker recruitment patterns to hydrologic variables (Table 4.5). However, the intercept model was one of the candidate top models indicating that flow had little impact on river carpsucker recruitment in our study.

Maximum age of shovelnose sturgeon ranged from 9 years in the Manhattan reach to 14 years in the Kansas City reach. Shovelnose sturgeon year class strength was more variable among reaches than the other species examined in this study (Figure 4.2). With the exception of 2005 and 2007 when year class strength was consistently positive and 2006 when year class strength was consistently negative among all reaches, year class strength was highly variable among reaches for each year of the study (Figure 4.2). The top candidate model for shovelnose sturgeon indicated that recruitment patterns were positively associated with high flows (i.e. PC1; Table 4.5). In general, shovelnose sturgeon recruitment increased in response to higher PC1 scores ($r^2 = 0.19$) indicating that shovelnose sturgeon recruitment may benefit from high flows (Figure 4.4).

DISCUSSION

We found that recruitment was positively related to high flows for two of the four native fish species (flathead catfish, shovelnose sturgeon) in our study. Whereas the responses of these two species were similar, the mechanism explaining why recruitment increases with high flows is likely different for flathead catfish and shovelnose sturgeon. Recruitment variability is often linked to abiotic factors that decrease survival of larvae (Houde 2009; Lobón-Cerviá 2014). Flathead catfish build sedentary nests that are protected by adult males as eggs and larvae

develop near the nest (Balon 1975; Fuselier 2014). As such, flathead catfish recruitment may increase in response to high flows because they increase nursery habitats and increase survival of age-0 fishes (Schramm and Eggleton 2006; Steffensen et al. 2014). Similar responses were observed for many large river fishes including shovelnose sturgeon in the Missouri River during flooding in 2011 (Steffensen et al. 2014) and side-channel chutes are often constructed or restored in the Missouri River to create low-flow nursery habitats that may benefit sturgeon and other fishes (Ridenour et al. 2011; Gosch et al. 2015). However, age-0 sturgeon are often found in deeper main channel habitats and may not benefit from these nursery habitats as much as other species (e.g. flathead catfish) in similar large rivers (Ridenour et al. 2011; Gosch et al. 2015). Instead, high flows may increase shovelnose sturgeon recruitment by facilitating downstream drift of eggs and larvae. Shovelnose sturgeon require prolonged drift to successfully develop and high flows likely increase the survival of these developing eggs and larvae (Delonay et al. 2007; Goto et al. 2015). Reduced flows in reservoirs upstream of large dams often create a "dead zone" where drifting eggs and larvae settle out of the water column, are covered in silt, and die (Guy et al. 2015). Although large reservoirs are not present in the Kansas River, similar results (i.e. egg and larval death) may occur if flows necessary to maintain downstream drift are not sustained.

We did not identify a relationship between the hydrologic factors we examined and freshwater drum or river carpsucker recruitment patterns indicating that flow patterns (e.g. high and low flows) may not influence recruitment of these fishes as much as other species. Intra-annual recruitment was generally consistent among reaches for river but was not consistent among reaches for flathead catfish, freshwater drum, or shovelnose sturgeon. These findings indicate that spatial scale may play an important role in regulating recruitment patterns with local (i.e. reach) factors driving recruitment patterns for river carpsucker and more large-scale (i.e.

river) factors regulating recruitment patterns for the other fishes. Our results are consistent with other studies that found that river carpsucker recruitment was often variable and not strongly related to flow (e.g. Peterson and Jennings 2007; Quist and Spiegel 2011). Peterson and Jennings (2007) found that abundance of age-0 river carpsucker decreased in response to high flows in the Oconee River in Georgia indicating that high flows may negatively influence river carpsucker recruitment. Whereas we did not find a link between hydrology and recruitment of these species, high flow events are often associated with increased growth rates for both freshwater drum and river carpsucker (Peterson and Jennings 2007; Quist and Spiegel 2011; Jacquemin et al. 2015).

Our study showed that shovelnose sturgeon and flathead catfish recruitment increased in relation to high flow events but no relationship was found between high and low flows and recruitment of river carpsucker and freshwater drum. However, all four native species in our study are abundant throughout the Kansas River and had years with strong recruitment in our study indicating that they may benefit from some aspect of the flow regime. These results are consistent with other studies and suggest that variability in flow patterns among years may be important to maintain successful recruitment for a variety (i.e. community) of native freshwater fishes (King et al. 2010). Variable flow patterns (i.e. natural flow regime) may conserve or restore native fish species (Carlisle et al. 2010, King et al. 2010) and simultaneously inhibit nonnative species that are not adapted to flourish in response to high and low flows (Kiernan et al. 2012). Gido and Propst (2012) found that densities of native fishes generally increased in years with prolonged summer flooding whereas densities of native fishes generally increased in years with prolong low flow periods. The relationship between recruitment and hydrology is not always consistent among species. King et al. (2003) found that some fishes (e.g. golden perch *Macquaria ambigua*) in the Murray River, Australia increase their spawning activity during

major flood events whereas spawning activity of other species (e.g. trout cod *Maccullochella macquariensis*) remains constant or declines. Humphries et al. (1999) developed the Low Flow Recruitment Hypothesis to explain the importance of low flow events for successful recruitment of some fishes in response to increased prey densities during prolonged periods of low-flow. Recruitment of river carpsucker and shovelnose sturgeon both increased in relation to metrics of increased flow indicating that increased hydrology may be more beneficial for these species. Our results indicate that the low-flow recruitment hypothesis may not be relevant for river carpsucker and shovelnose sturgeon in the Kansas River. Whereas the inundation of floodplain habitats may benefit fishes such as freshwater drum by serving as spawning and nursery habitats, these same events may negatively impact recruitment patterns of other fishes by flushing larvae downstream or limiting recruitment opportunities (Humphries et al. 1999; King et al. 2003; Rolls et al. 2013). This high to low, inter-annual variability tends to benefit the fish community as a whole and maintaining large river systems that are allowed to naturally flux and mimic the natural flow regime may be a critical component to restoring native fish communities

Models examining differences in recruitment patterns among reaches were not identified as strong models for any of the fishes in our study showing that recruitment patterns were generally consistent throughout the Kansas River. Reaches in our study were characterized by variation in urbanization and agricultural riparian land use (Eitzmann and Paukert 2010). In contrast with our results, anthropogenic influence to the reaches of the river system may create alternative habitats that may influence fish recruitment. For example, recruitment in highly fragmented systems may decrease due to decreased upstream migration (Dudley and Platania 2007). All of the fish in our study were large-bodied fishes that can migrate long distances which may limit our ability to identify differences among reaches, especially reaches upstream of

Bowersock Dam where fishes can move freely among the sampled habitats without being restricted by the dam. Although we included a measure of habitat and anthropogenic influence (Reach) future studies should include river reaches of distinct anthropogenic influence to explicitly identify the impacts of urbanization and anthropogenic impacts on recruitment of native fishes.

Our results show that for shovelnose sturgeon and flathead catfish high flow was associated with increased recruitment among reaches in the Kansas River. Hydrologic variables examined in this study did not influence recruitment patterns of freshwater drum and river carpsuckers but further examination of flow by years shows low variation among reaches in freshwater drum in a low flow year (2006). In addition, intra-annual recruitment was not consistent among reaches for three of the four species in our study indicating that, in addition to hydrology, differences among reaches (e.g. land use) may be related to recruitment patterns of these species. Overall, our results indicate that variability in flow events among years adequately supports these native river fishes examined, with high flow events significantly benefiting some species but not others. Consistent with these results and current literature (e.g. Gido and Propst 2012, Pool and Olden 2015), restoration of natural flow regimes by controlling dam releases to mimic natural hydrology may be a viable option of mitigating human influences in many rivers and maintaining a strong native fish community (Bernhardt et al. 2005; Kiernan et al. 2012).

LITERATURE CITED

Agostinho, A.A., L.C. Gomes, S. Verissimo, and E.K. Okada. 2004. Flood regime, dam regulation and fish in the Upper Parana River: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries* 14:11–19.

Bain M.B, J.T. Finn, and H.E. Booke. 1988. Streamflow regulation and fish community structure. *Ecology* 69: 382–392.

Balon, E.K. 1975. Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Board of Canada* 32:821-864.

Baumgartner, L.J., J. Conallin, I. Wooden, B. Campbell, R. Gee, W.A. Robinson, and M. Mallen-Cooper. 2014. Using flow guilds of freshwater fish in an adaptive management framework to simplify environmental flow delivery for semi-arid riverine systems. *Fish and Fisheries* 15:410-427.

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.

Braaten, P.J., D.B. Fuller, L.D. Holte, R.D. Lott, W. Viste, T.F. Brandt, and R.G. Legare. 2008. Drift dynamics of larval pallid sturgeon and shovelnose sturgeon in a natural side channel of the upper Missouri River, Montana. *North American Journal of Fisheries Management* 28:808-826.

Bramblett, R.G. and R.G. White. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri Rivers in Montana and North Dakota. *Transactions of the American Fisheries Society* 130:1006-1025.

Bunn, S.E. and A.H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492-507.

Burnham, K.C. and D.R. Anderson. 2002. Model selection and multi-model inference. Springer, New York, New York.

Carlisle, D.M., D.M. Wolock, and M.R. Meador. 2010. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264-270.

Costigan, K.H. and M.D. Daniels. 2012. Damming the prairie: human alteration of Great Plains river regimes. *Journal of Hydrology* 444-445:90-99.

DeLonay, A.J., D.M. Papoulias, M.L. Wildhaber, M.L. Annis, J.L. Bryan, S.A. Grifith, S.H. HOlan, and D.E. Tillitt. 2007. Use of behavioral and physiological indicators to evaluate *Scaphirhynchus* sturgeon spawning success. *Journal of Applied Ichthyology* 23:428-435.

Dutterer, A.C., C. Mesing, R. Cailteux, M.S. Allen, W.E. Pine, and P.A. Strickland. 2013. Fish recruitment is influenced by river flows and floodplain inundation at Apalachicola River, Florida. *River Research and Applications* 29:1110-1118.

Eitzmann, J.L. and C.P. Paukert. 2010. Longitudinal differences in habitat complexity and fish assemblage structure of a Great Plains River. *American Midland Naturalist* 163: 14-32.

Fuselier, L.C. 2014. Flathead catfish, *Pylodictis olivaris* Rafinesque 1818. Pages 306-307 *in* Kansas Fishes Committee. Kansas Fishes. University Press of Kansas, Lawrence.

Galat, D.L., C.R. Berry, E.J. Peters, and R.G. White. 2005. The Missouri River basin. Pages 427-480 *in* A.C Benke and C.E. Cushing (eds.) Rivers of North America. Elsevier Press, Burlington, MA.

Gido, K.B. and D.L. Propst. 2012. Long-term dynamics of native and nonnative fishes in the San Juan River, New Mexico and Utah, under a partially managed flow regime. *Transactions of the American Fisheries Society* 141:645-659.

Górski, K., J.J. De Leeuw, H.V. Winter, D.A. Vekhov, A.E. Minin, A.D. Buijse, and L.A.J. Nagelkerke. 2011. Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. *Freshwater Biology* 56:210-2225.

Gosch, N.J.C, M.L.Miller, T.R. Gemenhardt, S.J. Sampson, and J.L. Bonneau. 2015. Age-0 sturgeon accessibility to constructed and modified chutes in the Lower Missouri River. *North American journal of Fisheries Management* 35:75-85.

Goto, D., M.J. Hamel, J.J.Hammen, M.L.Rugg, M.A. Pegg, and V.E. Forbes. 2015. Spatiotemporal variation in flow-dependent recruitment of long-lived riverine fish: model development and evaluation. *Ecological Modelling* 296:79-92.

Graf, W.L. 1999. Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. *Water Resources Research* 35:1305-1311.

Guy, C.S., P.J. Braaten, D.P. Herzog, J. Pitlo, and R.S. Rogers. 2009. Warmwater fish in rivers. Pages 59-84 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Guy, C.S., H.B. Treanor, K.M. Kappenman, E.A. Scholl, J.E. Ilgen, and M.A.H. Webb. 2015. Broadening the regulated-river management paradigm: A case study of the forgotten dead zone hindering pallid sturgeon recovery. *Fisheries* 40:6-14.

Houde, E.D. 2009. Recruitment variability. *In*: Jakobsen, T., M.J. Fogarty, B.A. Megrey, and E. Moksness (eds). Fish Reproductive Biology: Implications for Assessment and Management. Wiley-Blackwell, Oxford, UK.

Humphries, P., A.J. King, J.D. Koehn. 1999. Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes* 56:129-151.

Jacquemin, S.J., J.C. Doll, M. Pyron, M. Allen, and D.A.S. Owen. 2015. Effects of flow regime on growth rate of freshwater drum, *Aplodinotus grunniens*. *Environmental Biology of Fish* 98:993-1003.

Kansas Fishes Committee. 2014. Kansas Fishes. University Press of Kansas, Lawrence, Kansas.

Kiernan, J.D., P.B. Moyle, and P.K. Crain. 2012. Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. *Ecological Applications* 22:1472-1482.

King, A.J., P. Humphries, and P.S. Lake. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* 60:773-786.

King, A.J., K.A. Ward, P. O'Connor, D. Green, Z. Tonkin, and J. Mahoney. 2010. Adaptive management of an environmental watering event to enhance native fish spawning and recruitment. *Freshwater Biology* 55:17-31.

Koch JD, Schreck W, Quist MC. 2008. Standardized removal and sectioning locations for shovelnose sturgeon fin rays. *Fisheries Management and Ecology* 15: 139–145.

Kwak, T.J. and J.T. Peterson. 2007. Community indices, parameters, and comparisons. Pages 677 – 763 *in* C.S. Guy and M.L. Bwrown, editors, Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Kynard, B., E. Henyey, and M. Horgan. 2002. Ontogenetic behavior, migration, and social behavior of pallid sturgeon, *Scaphirhynchus albus*, and shovelnose sturgeon, *S. platorynchus*, with notes on the adaptive significance of body color. *Environmental Biology of Fishes* 63:389-403.

Lobón-Cerviá, J. 2014. Recruitment and survival rate variability in fish populations: density-dependent regulation or further evidence of environmental determinants? *Canadian Journal of Fisheries and Aquatic Sciences* 71:290-300.

Lytle, D.A. and N.L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19: 94-100

Maceina, M. 1997. Simple application of using residuals from catch curve regressions to assess year class strength in fish. *Fisheries Research* 32:115-121.

Maceina, M., and D. Pereira. 2007. Recruitment. Pages 121-186 in C. Guy and M. Brown editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Miranda, L.E. 2009. Standardizing electrofishing power for boat electrofishing. Pages 223-230 *in* Bonar, S.A., W.A. Hubert, and D.W. Willis editors. Standard Methods for Sampling North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Peterson, R.C. and C.A. Jennings. 2007. Effects of river discharge on abundance and instantaneous growth of age-0 carpsuckers in the Oconee River, Georgia, USA. *River Research and Applications* 23:1016-1025.

Poff, N.L., J.D. Allen, 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.

Poff, N.L. and J.K.H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55:194-205.

Pool, T.K. and J.D. Olden. 2015. Assessing long-term fish responses and short-term solutions to flow regulation in a dryland river basin. *Ecology of Freshwater Fish* 24:56-66.

Quarterman, C.L. 2010. Endangered and threatened wildlife and plants; threatened status for shovelnose sturgeon under the similarity of appearance provisions of the endangered species act. *Federal Register* 75:53598-53606.

Quist, M.C. and J.R. Spiegel. 2011. Population demographics of catostomids in large river ecosystems: effects of discharge and temperature on recruitment dynamics and growth. *River Research and Applications* 28:1567-1586.

Ridenour, C.J., W.J. Doyle, and T.D. Hill. 2011. Habitats of age-0 sturgeon in the lower Missouri River. *Transactions of the American Fisheries Society* 140:1351-1358.

Rolls, R.J., I.O. Growns, T.A. Khan, G.G. Wilson, T.L. Ellison, A. Prior, and C.C. Waring. 2013. Fish recruitment in rivers with modified discharge depends on the interacting effects of flow and thermal regimes. *Freshwater Biology* 58:1804-1819.

Schramm, H.L. Jr. and M.A. Eggleton. 2006. Applicability of the flood-pulse concept in a temperate floodplain river ecosystem: thermal and temporal components. *River Research and Applications* 22:543-553.

Sparks, R.E. 1995. Need for ecosystem management of large rivers and their floodplains. *BioScience* 45: 168–182.

Steffensen, K.D., B.L. Eder, and M.A. Pegg. 2014. Fish community response to floodplain inundation in a regulated river. *Journal of Freshwater Ecology* 29:413-427.

Vasconcelos, L.P., D.C. Alves, and L.C. Gomes. 2014. Spatial and temporal variations among fish with similar strategies: patterns of reproductive guilds in a floodplain. *Hydrobiologia* 726:213-228.

Vörösmarty, C.J., P.B. McIntyre, M.O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S.E. Bunn, C.A. Sullivan, C.R. Liermann, and P.M. Davies. 2010. Global threats to human water security and river biodiversity. *Nature*, 467:555-561.

Warren, M.L., B.M. Burr, S.J. Walsh, H.L. Bart Jr., R.C. Cashner, D.A. Etnier, B.J. Freeman, B.R. Kuhajda, R.L. Mayden, H.W. Robinson, S.T. Ross, W.C. Starnes. 2000. Diversity, distribution and conservation status of the native freshwater fishes of the Southern United States. *Fisheries* 25:7-31.

Welcomme, R.L. 1985. River fisheries. *Food and Agriculture Organization – fisheries technical paper 262.* United Nations, Publication Division, Rome, Italy. 330 pages.

Zeug, S.C. and K.O. Winemiller. 2007. Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1291-1301.

Table 4.1. Description and mean values of hydrologic parameters considered for each study reach and used in analysis of candidate models. Each parameter was calculated separately for each year and study reach for analyses. Mean values were calculated from hydrologic data obtained from reaches of the Kansas River near Manhattan (USGS Station #06887500), Topeka (USGS Station #06889000), and Kansas City (USGS Station #06892350) from 1999 – 2009.

Hydrologic Variable	**Description**	**Manhattan**	**Topeka**	**Kansas City**
Flood Timing	Julian date of first day of the year that flows exceeded 175% of 20-year mean annual flow	60.67	53.78	52.67
Flood Duration (Total)	Total number of flood days in a year	21.67	22.56	26.78
Flood Duration (Consecutive)	Longest number of consecutive flood days in a year	12	12.78	17.22
Flood Intensity	Greatest discharge value for year / 20 year mean annual flow	3.97	5.37	6.12
Flood Frequency	Number of times that flows exceed 175% cutoff following at least one day below threshold	2.22	2.22	3.33
Annual Flow	Mean daily discharge / 20 year mean annual discharge (m^3/sec)	94.95	110.60	151.08
Flow Variability	Coefficient of variation of mean annual flow	0.92	0.98	1.01
Spring Flow	Mean spring (March – May) daily discharge / 20 year mean spring annual discharge (m^3/sec)	130.29	158.75	217.78
Spring Flow Variability	Coefficient of variation of mean spring flow	0.77	0.79	0.84
Summer Flow	Mean summer (June – August) daily discharge / 20 year mean summer discharge (m^3/sec)	141.88	165.02	222.68
Summer Flow Variability	Coefficient of variation of mean summer flow	0.66	0.75	0.78
Summer Low Days	Number of days discharge was 25% below 20 year mean annual discharge	34.56	35.22	36.56

Table 4.2. List of candidate models used to examine relationship between principal components (PC1, PC2) of PCA for hydrologic variables, spatial location (reach), and native fish recruitment (standardized catch-curve residuals) for flathead catfish, freshwater drum, river carpsucker, and shovelnose sturgeon in the Kansas River.

Model Name	Model Variables
Intercept Model	Species standardized catch-curve residuals ~ Intercept
Flooding Model	Species standardized catch-curve residuals ~ Intercept + PC1
Flow Variability Model	Species standardized catch-curve residuals ~ Intercept + PC2
All Hydrologic Variables Model	Species standardized catch-curve residuals ~ Intercept + PC1 + PC2
Reach Model	Species standardized catch-curve residuals ~ Intercept + Reach

Table 4.3. Total abundance by year class of flathead catfish, freshwater drum, river carpsucker, and shovelnose sturgeon captured from three reaches the Kansas River in 2009 and 2010. Fish from 2009 and 2010 year classes were not recruited to the gear and were not included in analyses. Additionally, catch rates for older fishes (2000 and earlier year classes) were sporadic (many zeros) and these fishes were not included in analyses. Bolded values indicate fishes included in analyses.

Year Class	Freshwater Drum	Flathead Catfish	River Carpsucker	Shovelnose Sturgeon
2010	4	8	1	0
2009	7	13	7	1
2008	**33**	**46**	**30**	**8**
2007	**44**	**25**	**35**	**24**
2006	**22**	**18**	**22**	**17**
2005	**34**	**21**	**38**	**23**
2004	**17**	**29**	**31**	**19**
2003	**14**	**13**	**24**	**11**
2002	**8**	**22**	**32**	**7**
2001	**13**	**11**	**18**	**9**
2000	1	5	2	11
1999	4	0	9	3
1998	0	2	7	0
1997	1	0	3	1
1996	2	0	1	0
1995	0	0	3	0
1994	0	1	0	0
1993	0	0	0	0
1992	1	0	0	0
Total	205	214	263	134

Table 4.4. Principal component (PC) loadings for hydrologic factors obtained from three reaches of the Kansas River near Manhattan (USGS Station #06887500), Topeka (USGS Station #06889000), and Kansas City (USGS Station #06892350) from 1999 – 2009. Bolded values indicate variables with high loadings (absolute value ≥ 0.4) that were used for interpretation.

Variable	PC1	PC2
Flood Timing	**0.732**	0.260
Flood Duration (Total)	**0.610**	0.052
Flood Duration (Consecutive)	**0.835**	-0.076
Flood Intensity	**0.810**	0.078
Flood Frequency	**0.772**	0.138
Annual Flow	0.761	**-0.408**
Annual Flow Variability	0.715	**0.457**
Spring Flow	0.700	**-0.468**
Spring Flow Variability	0.376	0.280
Summer Flow	**0.800**	-0.131
Summer Variability	0.365	**0.674**
Summer Low Days	**-0.834**	0.568
Eigenvalue	8.44	1.52
Percent Variance Explained	70.3	12.7
Total Variance Explained	70.3	83.0

Table 4.5. AIC results for models with strong support as best model (ΔAICc < 2) explaining spatiotemporal relationships between PC loadings of PCA of hydrologic variables and recruitment of four native fishes in the Kansas River. Model strength was assessed using Akaike Information Criterion corrected for small sample size (AICc) to identify best fit models. Akaike weights (w_i) were used to identify support among competing candidate models and total Akaike weights show overall support among candidate models.

Species	Model Variables	AICc	ΔAICc	w_i	Total w_i
Freshwater drum	Intercept Model	77.94	0	0.49	0.49
	Flooding Model	79.68	1.74	0.26	0.75
	Flow Variability Model	79.82	1.88	0.23	0.98
Flathead catfish	Flow Variability Model	77.97	0	0.68	0.68
	Flooding Model	79.59	1.62	0.15	0.83
	All Hydrologic Variable Model	79.76	1.78	0.14	0.97
River carpsucker	Flooding Model	78.23	0	0.38	0.38
	Intercept Model	78.29	0.06	0.37	0.75
Shovelnose sturgeon	Flooding Model	78.34	0	0.96	0.96

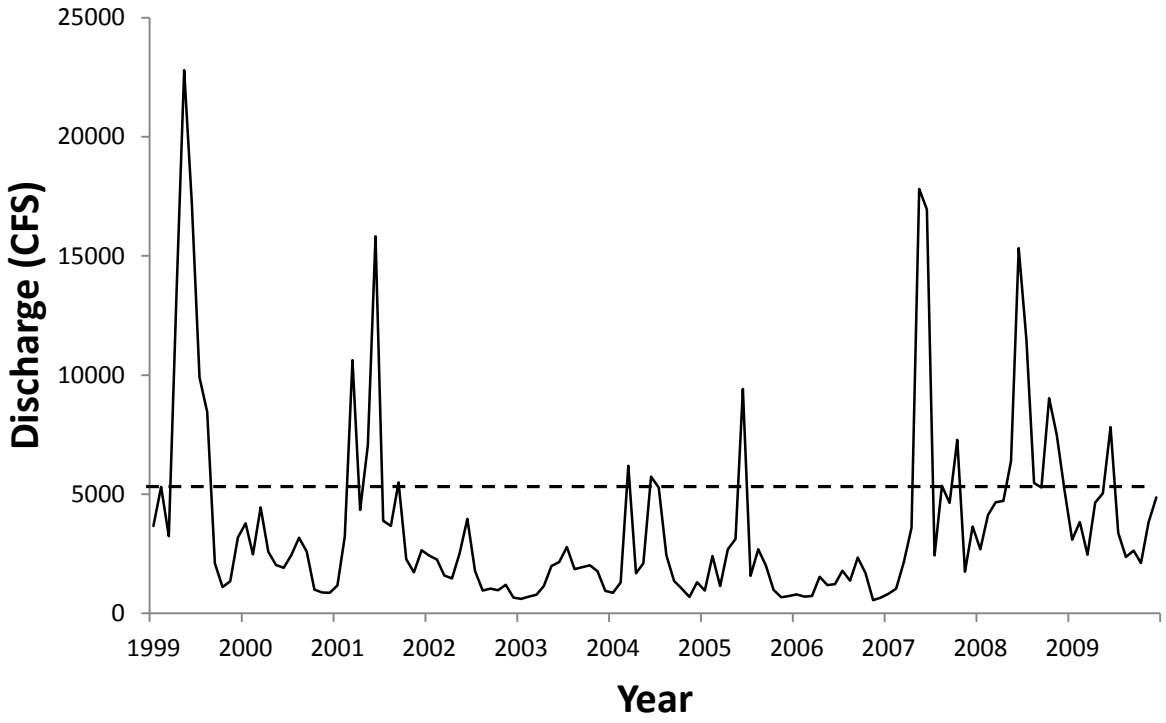

Figure 4.1. Hydrograph of mean daily discharge in the Kansas River near Wamego, KS from 1999 - 2009. Flooding threshold for this study is indicated by the dotted line. Discharge values were obtained from United States Geological Survey Station #06887500.

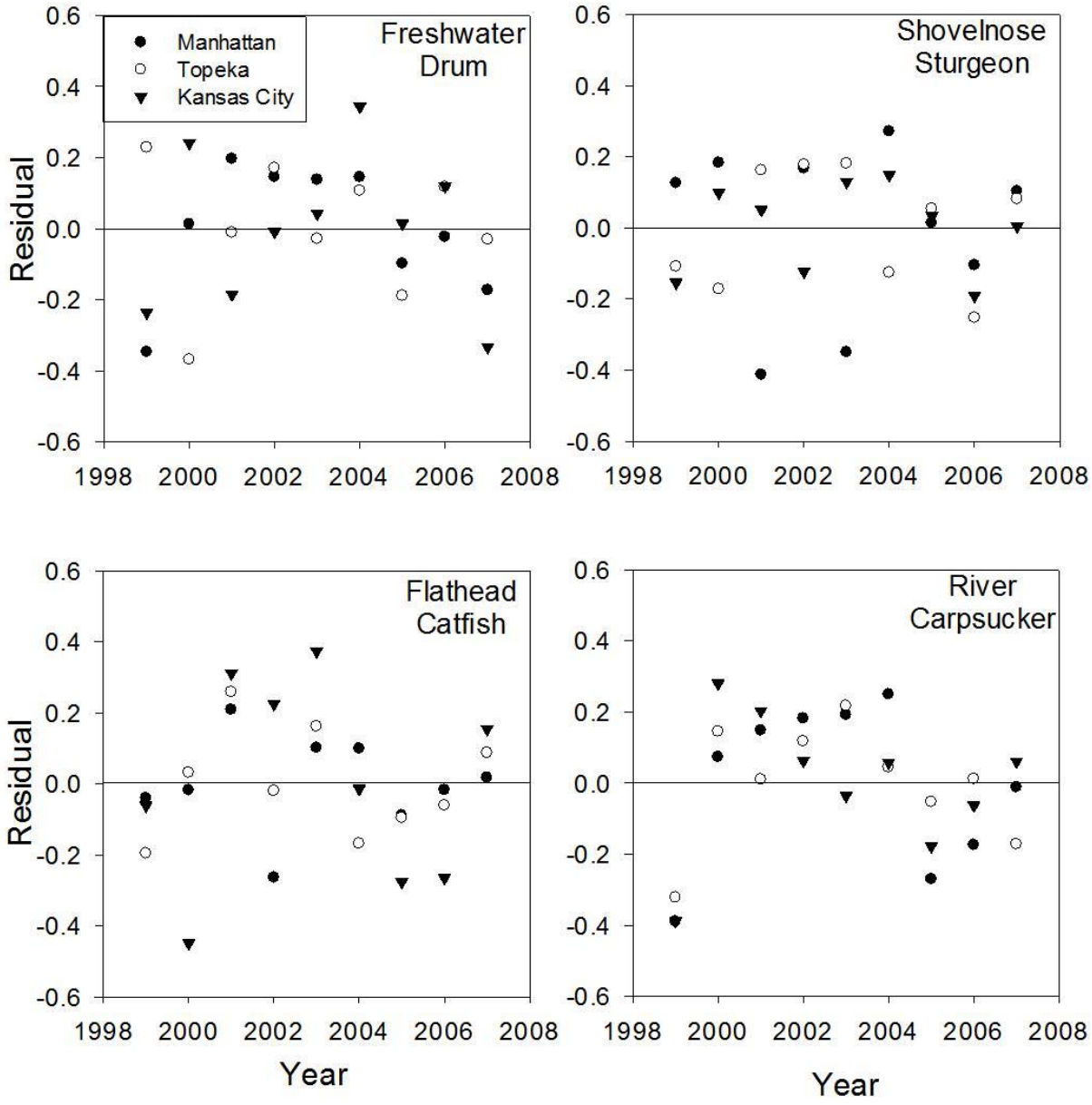

Figure 4.2. Residuals of catch curves from fishes captured at three reaches of the Kansas River in 2009 and 2010. Positive residuals indicate strong year class strength whereas negative values indicate weak year class strength.

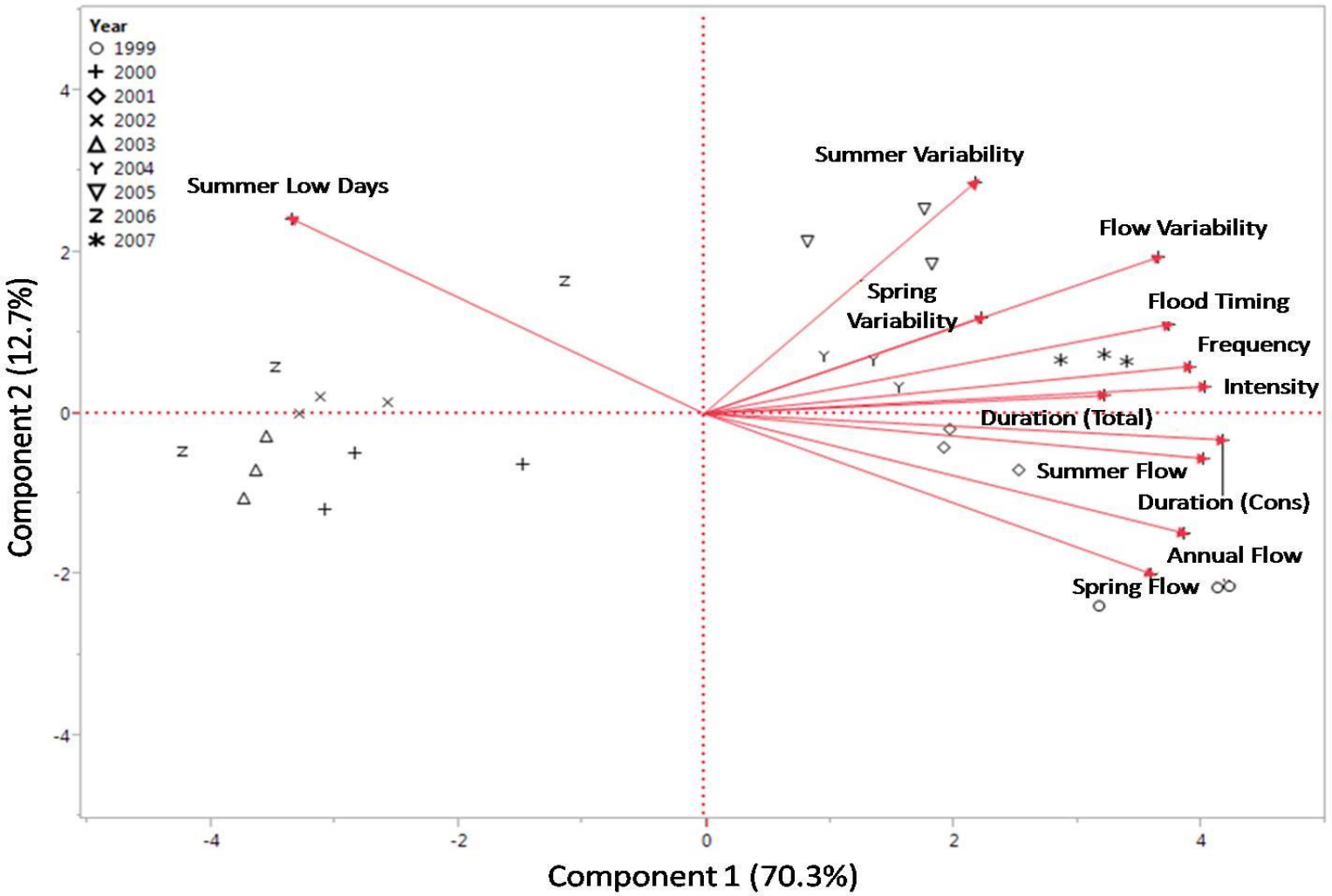

Figure 4.3. PCA ordination examining the relationship among hydrologic variables from three reaches of the Kansas River from 1999 – 2007. See table 4.1 for a complete description of hydrologic variables.

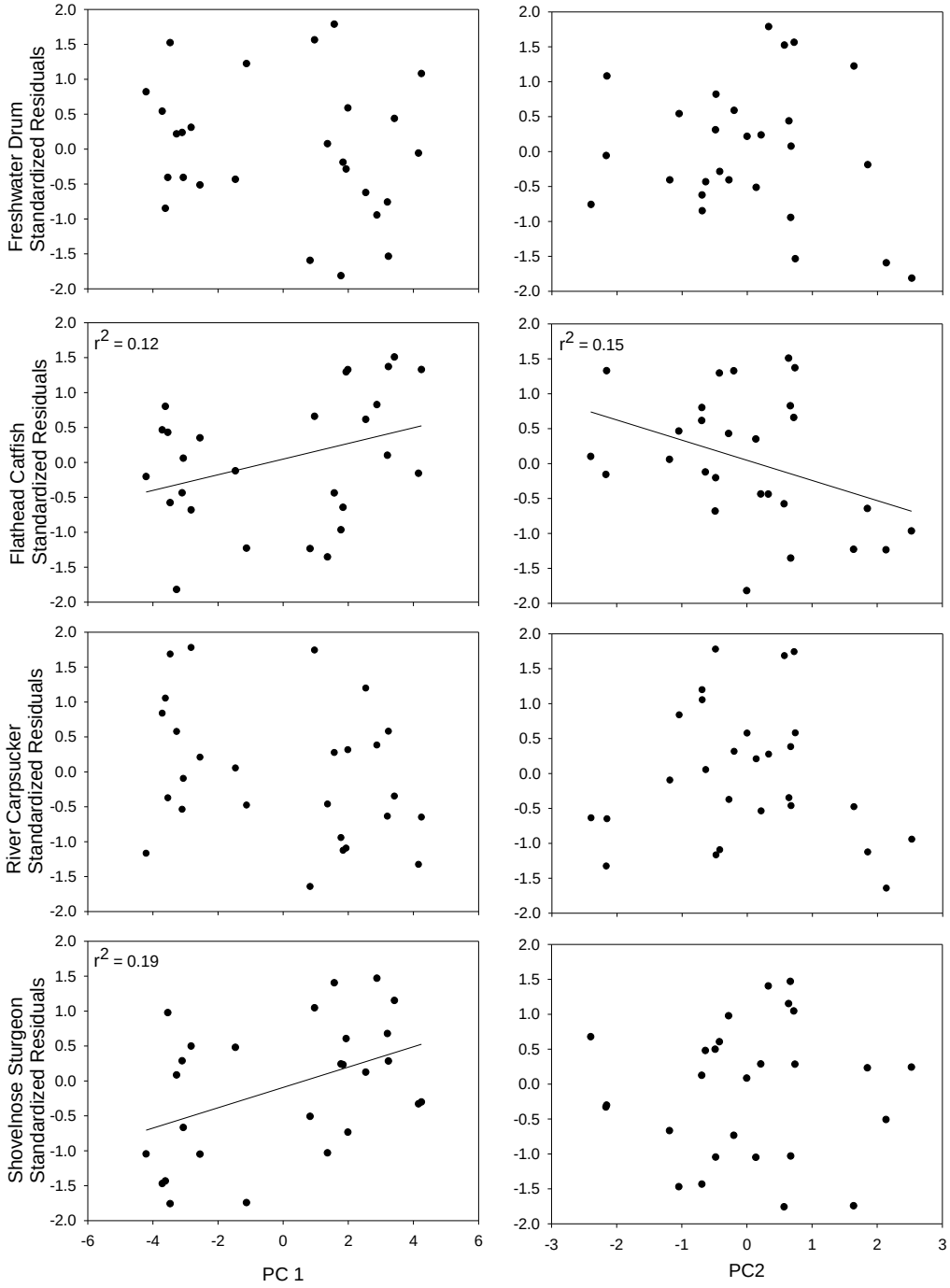

Figure 4.4. Relationship between native fish recruitment (standardized residuals) and principal components scores of PCA examining spatiotemporal variation in hydrologic factors in the Kansas River. Line of best fit and coefficient of determination are shown for variable relationships identified in top-ranked models for species with models that had support and varied from the null.

Chapter 5 – Dissertation Summary

Anthropogenic changes to freshwater ecosystems are widespread and almost all running water systems in North America have been impacted by humans in some way (Strayer and Dudgeon, 2010; Vörösmarty et al. 2010, Dodds et al. 2013). In many cases, natural flow regimes of lotic systems are particularly susceptible to anthropogenic impacts (Poff et al. 1997; Carlisle et al. 2011). Hydrologic changes can alter habitat structure, water quality, and many other abiotic components of lotic systems and subsequently lead to changes in the organisms found in these systems (Vörösmarty et al. 2010). Altering the natural hydrology of lotic systems can also reduce lateral connectivity between main channel and secondary channel habitats which serve many important functions for many freshwater organisms. For example, many organisms feed in secondary channels and many fishes use them as spawning and nursery habitats (Welcomme 1985; Zeug and Winemiller 2007).

The research we presented further advanced our understanding of the role and importance of lateral connectivity for freshwater ecosystems. In chapter 2 we found that a seasonally connected secondary channel supports different invertebrate communities than main channel habitats. Additionally, invertebrate densities were generally higher in these secondary channels compared to the main channel. These differences may benefit fishes moving into these habitats during flooding to use them as a feeding habitat. A majority of the fishes captured during this study were found both in the main channel and in the seasonally connected secondary channel indicating that many fishes are highly mobile during flooding. We observed similar trends in chapter 3 although our focus was more on identifying differences between seasonally connected and permanently connected secondary channels. We found that seasonally inundated secondary channels had higher densities of drifting invertebrates whereas permanently connected secondary

channels had higher densities of benthic invertebrates. These findings may indicate that fishes may benefit from secondary channels differently depending on their feeding habits with fishes preferring drifting invertebrate prey benefiting more from seasonally connected secondary channels and fishes preferring benthic invertebrate prey benefitting more from permanently connected secondary channels. In chapter 4 we examined recruitment patterns of native fishes and found that these fishes respond to hydrologic cues in various ways. We found that flathead catfish and shovelnose sturgeon recruitment increased during high flow years. However, we did not identify any relationship between freshwater drum and river carpsucker recruitment and metrics of high and low flows.

Our findings indicate that high flows and resulting lateral connectivity are important for large river ecosystems and the fishes found in these systems. We found that riverine biota, including fishes, rely on high flows and lateral connectivity in many ways and the degree of lateral connectivity can influence fish assemblage structure and invertebrate densities. We also found that recruitment patterns of some native fishes respond to hydrologic cues. Our research demonstrates the importance of high flows and lateral connectivity and advances the understanding of these events for fishes and other large river organisms.

Taken as a whole, our results indicate that lateral connectivity is important for fish and invertebrates in the Kansas River. Whereas flooding and lateral connectivity play important roles in regulating fish and invertebrate communities, the importance of these events are likely variable depending on individual species of interest. Future studies should build on our findings to link lateral connectivity to fish productivity and energy flow in large river systems.

The increased density of drifting invertebrates in main channel reaches during flooding in 2011 supports the idea of a “pulse” of energy as proposed by the Flood Pulse Concept.

Additionally, inundated secondary channels had different fish and invertebrate communities compared to main channel habitats indicating that lateral connectivity is important in maintaining community diversity in the Kansas River. Fish and invertebrate communities were also variable between secondary channels with different amounts of connectivity to the main channel indicating that the role of inundated habitats are not consistent among habitats. These findings suggest that maintaining variable flows, including flows capable of inundating floodplain habitats, may be most beneficial to fish and invertebrates in the Kansas River and other similar large rivers.

LITERATURE CITED

Carlisle, D.M., D.M. Wolock, and M.R. Meador. 2011. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264-270.

Dodds, W.K., J.S. Perkin, and J.E. Gerken. 2013. Human impact on freshwater ecosystem services: a global perspective. *Environmental Science and Technology* 47:9061-9068.

Poff, N.L., J.D. Allen, 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.

Strayer, D.L. and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society,* 29:344-358

Vörösmarty, C.J., P.B. McIntyre, M.O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S.E. Bunn, C.A. Sullivan, C.R. Liermann, and P.M. Davies. 2010. Global threats to human water security and river biodiversity. *Nature*, 467:555-561.

Welcomme, R.L. 1985. River fisheries. Food and Agriculture Organization – fisheries technical paper 262. United Nations, Publication Division, Rome, Italy. 330 pages.

Zeug, S.C. and K.O. Winemiller 2008. Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. *River Research and Applications* 24:90-102.