1 **Title:**

2 Quantifying habitat benefits of channel reconfigurations on a highly regulated river system,
3 Lower Missouri River, USA

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ABSTRACT

We present a quantitative analysis of habitat availability in a highly regulated lowland river, comparing a restored reach with two reference reaches: an un-restored, channelized reach, and a least-altered reach. We evaluate the effects of channel modifications in terms of distributions of depth and velocity as well as distributions and availability of habitats thought to be supportive of an endangered fish, the pallid sturgeon (*Scaphirhynchus albus*). It has been hypothesized that hydraulic conditions that support food production and foraging may limit growth and survival of juvenile pallid sturgeon. To evaluate conditions that support these habitats, we constructed two-dimensional hydrodynamic models for the three study reaches, two located in the Lower Missouri River (channelized and restored reaches) and one in the Yellowstone River (least-altered reach). Comparability among the reaches was improved by scaling by bankfull discharge and bankfull channel area. The analysis shows that construction of side-channel chutes and increased floodplain connectivity increase the availability of foraging habitat, resulting in a system that is more similar to the reference reach on the Yellowstone River. The availability of food-producing habitat is low in all reaches at flows less than bankfull, but the two reaches in the Lower Missouri River – channelized and restored - display a threshold-like response as flows overtop channel banks, reflecting the persistent effects of channelization on hydraulics in the main channel. These high lateral gradients result in punctuated ecological events corresponding to flows in excess of bankfull discharge. This threshold effect in the restored reach remains distinct from that of the least-altered reference reach, where hydraulic changes are less abrupt and overbank flows more gradually inundate the adjacent floodplain. The habitat curves observed in the reference reach on the Yellowstone River may not be attainable within the channelized system on the Missouri River, but the documented hydraulic patterns can be used to inform ongoing channel modifications. Although scaling to bankfull dimensions and discharges provides a basis for comparing the three reaches, implementation of the reference reach concept was complicated by differences in flow-frequency distributions among sites. In particular, habitat availability in the least-altered Yellowstone River reach is affected by increased frequency of low-flow events (less than 0.5 times bankfull flow) and moderately high-flow events (greater than 1.5 times bankfull flow) compared to downstream reaches on the Lower Missouri River.

KEYWORDS: aquatic habitat, hydrodynamic modeling, pallid sturgeon, Missouri River

1. INTRODUCTION

The management of large, regulated rivers in the United States is governed by complex legal frameworks and is subject to numerous, and often competing, socio-economic drivers. In many river systems the fate of endangered species may play a substantial role in guiding management decisions, thus scientists are often called on to provide quantitative models that explicitly link management actions with biotic responses (Murphy and Weiland, 2011; Williams, 2011). Management and recovery of target fish populations may entail a variety of tactics, such as population augmentation and flow manipulation, but often include some form of modification or restoration of channel form (Bond and Lake, 2003; Palmer et al., 2010).

Models linking physical characteristics of aquatic habitat with biotic responses have been used extensively over the past three decades, starting with those developed to identify minimum instream flow requirements. The earliest versions of these models relied on empirical data or one-dimensional hydraulic models to quantify availability of physical habitat criteria over a range of flow (Bovee, 1986; Orth, 1987). Advances in technology for data acquisition, widespread availability of numerical models, and accessibility of computational resources have increased use of higher resolution models for ecohydraulic applications, such as multidimensional hydrodynamic models applied in two (Leclerc et al., 1995; Crowder and Diplas, 2006; Harrison et al., 2011; Boavida et al., 2012) and three dimensions (Shen and Diplas, 2008; Kolden et al., 2015), and agent-based models to simulate individual behavior (Goodwin et al., 2006; Nestler et al., 2008). Common among these modeling approaches is use of a suite of abiotic variables – often physical and sometimes chemical – to predict a species response. The most important physical habitat variables typically include water depth, velocity, substrate, and cover (Tonina and Jorde, 2013).

The most robust models of aquatic habitat are informed by rigorous evaluation of model predictions based on occupancy-related biotic-response variables, such as presence-absence, density, or abundance data. Ultimately, however, most management actions pursue objectives fundamentally related to population dynamics -- such as growth, survival, and fecundity. Understanding the linkages from habitat to population dynamics remains a challenge. Endangered and threatened species present an even greater challenge because they are by

definition very rare and thus limited data may be available to inform model development. For species for which there is an absence of empirical information about habitat selection or limitation, habitat criteria may rely on literature or professional judgement (Bovee, 1986).

Ongoing efforts to inform management of the Missouri River as part of Missouri River Recovery Program have been focused on the recovery of three endangered or threatened species, the piping plover (*Charadrius melodus*), least tern (*Sternula antillarum*), and pallid sturgeon (*Scaphirhynchus albus*) (U.S. Fish and Wildlife Service, 2000a; U.S. Fish and Wildlife Service, 2003a). In contrast to plovers and terns, where quantitative relations have been demonstrated between habitat (i.e. availability of emergent sand bar habitat for nesting) and population demographic variables (e.g., nest success and fledge ratios) (Buenau et al., 2014), pallid sturgeon are more enigmatic. This species is endemic to the Mississippi River basin and has been the focus of conservation efforts on the Missouri River. Subjected to years of heavy commercial fishing, declining water quality, a highly altered flow regime, and extensive channelization, the pallid sturgeon was formally listed as a federally endangered species in 1990 (U.S. Fish and Wildlife Service, 1993). Current recovery efforts focus on population augmentation through stocking of hatchery fish as an interim measure, and restoration of physical habitat through management of flow regime and channel configuration. Because of pervasive uncertainties in how - or if - physical habitat is linked to population dynamics, recovery actions are being implemented through an adaptive management framework. It remains unclear what factors are primarily responsible for decline of the species and what actions may be most effective in promoting successful recruitment (Gemeinhardt et al., 2015; Jacobson et al., 2016a). Uncertainty in the factors driving decline results from the fact that the pallid sturgeon is a very rare, benthic fish that resides in a large, turbid river system. In contrast with many other fishes of intense management interest (e.g. salmonids in the Northern Rockies and Pacific Northwest US) relatively little is known about the pallid sturgeon life cycle and there have been few opportunities to observe behaviors and population processes in the wild (DeLonay et al., 2016a).

For several decades managers have engaged in activities thought to improve habitat, starting with modifications to existing river-training structures (e.g. notching wing dikes) (Hesse et al., 1989; Sheehan and Rasmussen, 1999) and purchasing adjacent riparian lands to restore some degree of

floodplain access (Galat 2005). Following a Biological Opinion and subsequent amendment that were issued by the U.S. Fish and Wildlife Service (collectively referred to as the BIOP), efforts to restore habitat for pallid sturgeon focused on the creation of shallow-water habitat (SWH), defined as areas where velocity $\leq 0.6 \text{ ms}^{-1}$ and depth $\leq 1.5 \text{ m}$ (U.S. Fish and Wildlife Service, 2000b; U.S. Fish and Wildlife Service, 2003b; Galat et al., 2005; Gemeinhardt et al., 2015). The concept of SWH restoration emerged from the understanding that extensive channel engineering and flow regulation along the Missouri River resulted in the loss of as much as 40,000 hectares habitat marked by warm, shallow, and turbid flow that were historically available in the riverine landscape (U.S. Army Corps of Engineers, 2003; Jacobson and Galat, 2006). The most recent published inventory of SWH reports that more than 1,300 hectares (ha) have been restored (Jalili and Pridal, 2010), yet this number is a small fraction of the habitat lost because of river modifications. Moreover, current data indicate that recruitment of pallid sturgeon in the Lower Missouri River is likely insufficient to maintain a viable population (Steffensen et al., 2014). Restoration actions on the Missouri River to date have focused on the habitat acreage targets prescribed by the BIOP (5.0 to 7.6 ha/linear km SWH as measured during the mid-July to mid-August from Sioux City, IA downstream to the confluence with the Mississippi River near St. Louis, MO) rather than a biotic or population response, which is much more difficult to measure (Doyle et al., 2011; National Research Council, 2011; Gemeinhardt et al., 2015).

Scientists working to inform species recovery have tried to more explicitly link habitat types with functional requirements of the species. Recent research suggests that success (or lack thereof) in early life stages may be limiting successful recruitment (Jacobson et al., 2016b). Specifically, it is hypothesized that environments that produce food or support foraging for age-0 sturgeon (between hatch and survival through their first winter) may be limiting. In the present paper we employ current working definitions of food-producing or foraging habitats (described below) to evaluate the effects of channel modifications with the understanding that improved biological understanding is likely to provide more accurate estimates of habitats occupied by age-0 pallid sturgeon and improved understanding of whether either of the habitats is actually limiting to growth and survival. Gradational, bivariate habitat suitability indices under development (G. Mestl, Nebraska Game and Parks Commission, pers. com.) promise to provide additional precision about biological selection. At present (2016) the simple definitions

implemented here are considered hypotheses, albeit with substantial physical and biological support. Analysis in terms of these definitions serves to indicate controls on habitat availability in time and space.

Here, we present a quantitative analysis of habitat availability in a highly regulated lowland river, the Missouri River, USA. Our analysis is framed in terms of the temporal and spatial availability of habitats thought to support age-0 pallid sturgeon, a highly endangered benthic, rheophilic fish. We compare a restored reach with two reference reaches: a non-restored, channelized reach, and a least-altered reach. We quantify the availability of food-producing habitat and foraging habitat during the post-spawn growing season in each of our three study reaches, and we evaluate how flow regulation and channel modifications alter the distribution and availability of these habitat types. The present study represents the first effort to compare habitat availability in modern channel types that differ substantially in channel form and engineering structures due to evolving management objectives in the Missouri River Basin. Our analysis addresses several issues that are generic to river restoration, including approaches to quantifying habitat benefits and challenges of defining and using reference conditions on large, highly altered rivers.

2. STUDY AREA

The Missouri River has been profoundly transformed by over two centuries of river management and channel alterations (Galat et al., 2005; Jacobson and Galat, 2006). With a drainage area of more than 1,300,000 km², draining the eastern Rocky Mountains, Great Plains, and a small area of Canada (Figure 1A), the Missouri River is the longest river in the United States. However, six large mainstem dams have substantially altered the natural flow regime, reducing the magnitude of annual floods and elevating base flows for navigation and water supply (Galat and Lipkin, 2000). The Lower Missouri River (LMOR) is defined as the 1,300 km of the Missouri River downstream from Gavins Point Dam near Yankton, South Dakota to the confluence with the Mississippi River, near Saint Louis, Missouri (MO). Extensive channelization and construction of river training structures (e.g. dikes and bank revetment) in the LMOR have converted the channel from one that was historically broad, shallow, dynamic, and braided to one that is

relatively deep, narrow, and stable with substantially less morphologic diversity (Jacobson and Galat, 2006; Erwin and Jacobson, 2014).

We constructed two-dimensional hydrodynamic models for three reaches in the Missouri River Basin: the Fairview reach of the Yellowstone River, North Dakota (ND), and the Miami and Lisbon-Jameson reaches of the Lower Missouri River, MO (Figure 1A; Table 1). The three locations were selected because they represent distinct geomorphic settings along the continuum of river habitats within the Missouri River basin; the Miami reach is representative of much of the typical channelized LMOR, the Lisbon-Jameson reach has been subjected to extensive restoration actions, and the Yellowstone reach is presented as a least-altered reference reach.

The 7.7-km Fairview reach of the Yellowstone River represents one of the few relatively unaltered and minimally regulated segments of river in the Missouri River Basin (Figure 1B) (Bowen et al., 2003). The Yellowstone River is the major tributary to the Upper Missouri River, which we define as the section of the Missouri River upstream from the Lake Sakakawea, the reservoir formed by Garrison Dam, ND. The Yellowstone and Missouri Rivers are approximately equal in size at their confluence in western North Dakota – they have comparable channel dimensions, mean annual flow, and drainage areas. However, flow in this segment of the Upper Missouri River is regulated by Fort Peck Reservoir, located ~ 350 km upstream in eastern Montana (MT), whereas the Yellowstone is minimally regulated. The Yellowstone River displays a distinct snowmelt-driven peak in late spring to early summer with relatively low base flows the remainder of the year (Figure 2). The Fairview modeling reach is located approximately 5 miles upstream from the confluence of the Yellowstone and Upper Missouri Rivers, near the town of Fairview, MT. The site encompasses an area where multiple pallid sturgeon spawning events have been documented from 2007 to 2015 (DeLonay et al., 2016b).

In contrast to the relatively unaltered Fairview reach, both the Miami and Lisbon-Jameson reaches contain extensive bank revetment and regularly spaced river-training structures, or dikes, designed to maintain a self-dredging navigation channel (Erwin and Jacobson, 2014). The 8.4-km Miami reach is located at the town of Miami, MO (Figure 1C). Restoration activities in this reach have been limited to some modification (notching) of existing dikes. The reach represents

the channelized and leveed conditions that are typical of the LMOR downstream from the border of Nebraska and Kansas; there is relatively little in-channel complexity, apart from that associated with scour around wing dikes, and floodplain access is limited by near-continuous earthen levees. Although the Miami and Lisbon-Jameson reaches are nearly 900 km downstream from the lowermost dam on the Missouri River system, the effects of regulation persist with statistically significant decreases in peak flow and increases in base flow during the navigation season (April – November) (Galat and Lipkin, 2000). In addition, the downstream reaches are subject to a somewhat different hydroclimatic regime with less snow-melt and greater input of sub-tropical moisture from the Gulf of Mexico compared to the Yellowstone reach. Hence, the upstream and downstream reaches have noticeably different flow frequency distributions (Figure 2B). As discussed later, the difference in flow frequency distributions presents a challenge to interpretation of the Yellowstone reach as a reference condition.

The 14.6-km Lisbon-Jameson reach is located approximately 22 km upstream from Boonville, MO and encompasses both the Lisbon Bottoms and Jameson Island chutes (Figure 1D). The site is located within the U.S. Fish and Wildlife Service's Big Muddy National Fish and Wildlife Refuge and levee setbacks allow floodwater to inundate adjacent floodplains in the refuge, thus providing a greater degree of floodplain connectivity than occurs on most of the LMOR. The Lisbon Bottom chute (upstream chute) was formed as the result of levee breaks during the floods of 1993 and 1995 (Jacobson et al., 2004). The chute was allowed to evolve with minimal intervention until 1999, when a grade-control structure was installed at the downstream end of the chute and a notched hydraulic control structure was installed at the entrance to the chute (Gosch et al., 2015). The Jameson Island chute (downstream chute) was intentionally constructed by the U.S. Army Corps of Engineers with the objective of creating rearing habitat for pallid sturgeon (U.S. Army Corps of Engineers, 2012). Construction of the pilot channel occurred in 2006-2007 and the channel was subsequently widened during naturally occurring high flows. A pilot channel for a chute extension was completed in summer 2014. These channel modifications, coupled with a high degree of floodplain connectivity and a relatively wide mainstem, produce a reach that represents one of the best-available sections of aquatic habitat within the LMOR.

3. METHODS

Topographic and bathymetric data for the Lisbon-Jameson and Yellowstone models were collected during field campaigns in spring and summer 2014 (Lisbon-Jameson) and summer 2015 (Yellowstone). The Miami model was originally developed by USGS in 2006 and 2007 to evaluate the effects of modifications of releases from Gavins Point Dam on pallid sturgeon habitat dynamics (Jacobson et al., 2009). Field methods were similar among all years of data collection. Field methods, hydrodynamic modeling, and calculation of availability of hypothesized habitats are described in detail below. Data are available at the USGS data repository ([dataset] Erwin, 2017).

3.1. Collection of field data

Topographic data for the hydrodynamic models were generated by integrating data from hydroacoustic bathymetric surveys, topographic ground surveys, and existing aerial LiDAR. Hydroacoustic surveys were performed using methods established by USGS (Elliott et al., 2009). Surveys were conducted using an Odom Hydrographics 200 kHz single-beam echo sounder with an 8 degree transducer coupled with real-time kinematic global positioning system (RTK-GPS) equipment to provide precise positioning. The echo sounder was calibrated for draft and sound velocity using a bar check. Transects were terminated laterally when the depth became too shallow for the boat survey, at approximately 0.3 m. We used Hypack surveying software¹ for navigation, data collection, and data processing. Single-beam data were edited in the office to remove false bottom returns, spikes, and other data anomalies.

At Lisbon-Jameson, transects were surveyed at regularly-spaced 50-m increments in the main channel and 20-m increments in the chutes. Topography for banks, islands, and subaerial bars was provided by aerial LiDAR collected in 2014. This more recent LiDAR was supplemented by LiDAR flown in 2007 that covered additional portions of the floodplain (National Elevation Dataset; <http://ned.usgs.gov>). Bathymetric data at Fairview were surveyed in 2015 at regularly-spaced 15 or 20-m transects and supplemented by aerial LiDAR to create a continuous elevation

¹ Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

mesh. Field data for the Miami reach were collected in 2006 and 2007, and transects were surveyed at 20-m intervals throughout the model domain (Jacobson et al., 2009).

Water-surface profiles were surveyed over a range of discharges in each reach for model calibration. Discharges ranged from 827 to 1266 m³s⁻¹ at Fairview, 743 to 3136 m³s⁻¹ at Miami, and 1135 to 5974 m³s⁻¹ at Lisbon-Jameson (Table 2). Discharge measurements to accompany water surface profiles were acquired using either a 600 or 1200 kHz Teledyne RDI Rio Grande acoustic Doppler current profiler (ADCP), also integrated with RTK-GPS.

3.2. Hydrodynamic modeling

We developed two-dimensional steady-state hydrodynamic models to predict water-surface elevations, depths, and depth-averaged velocity throughout each study area. Modeling was performed using Sedimentation and River Hydraulics – Two-Dimensional Model (SRH-2D) developed by the U.S. Bureau of Reclamation (Lai, 2008). SRH-2D solves the St. Venant depth-averaged shallow water equations and employs an unstructured mesh. As is typical with most 2D hydrodynamic models, the models were calibrated by iteratively adjusting channel roughness such that modeled water surface elevations matched field measurements of water surface. In SRH-2D, lateral eddy viscosity (LEV) is dynamically adjusted and spatially variable based on local depth and velocity, thus LEV was not a calibration parameter in our simulations.

Topographic and bathymetric data were used to generate an unstructured computational mesh for each modeling domain, consisting of a mix of quadrilateral and triangular elements of varying size. Meshes were developed in SMS (Aquaveo LLC, 2013). We calibrated the models to measured water-surface elevations for the range of available flows by iteratively adjusting channel roughness. Channel roughness was calibrated by selecting the roughness value that minimized the root mean square error (RMSE) between observed and modeled water surface over the available range of water-surface profiles measured at each site. Because we did not observe clear trends in discharge and channel roughness, we used the mean roughness value from the calibration discharges to determine a single roughness to be used for all steady state simulations (Figure 3; Table 2). Recent observations show that bedforms in the Missouri River do not scale with depth, but result from a combination of current hydraulics and antecedent

conditions (Elliott and Jacobson, 2016); additional research is needed to elucidate stage-roughness relations. For floodplain roughness, we used Manning's n coefficients ranging from $n = 0.05$ (low-resistance conditions from fallow agricultural fields) to $n = 0.2$ (dense floodplain forest with thickets of young willows and cottonwoods (Fippin-Dudley et al., 1998; Jacobson et al., 2009; Jacobson et al., 2015)).

3.3. Calculation of habitat availability

We generated steady-state simulations for discharges ranging from base flow to overbank floods in $150\text{-m}^3\text{s}^{-1}$ increments at Fairview (ranging from 150 to $1650\text{ m}^3\text{s}^{-1}$) and $200\text{-m}^3\text{s}^{-1}$ increments Miami and Lisbon-Jameson ($550 - 5550\text{ m}^3\text{s}^{-1}$ and $600 - 7,000\text{ m}^3\text{s}^{-1}$ at Miami and Lisbon-Jameson, respectively). Analysis of habitat availability was performed on the hydraulic outputs from the SRH simulations using custom Python scripts. Working definitions of food-producing and foraging habitat types were based on available literature and professional judgment (Jacobson et al., 2016a). Relations are bivariate, as data at this time are not sufficient to support more complex relations between habitat type and use or selection, such as commonly applied in the development of habitat suitability indices or curves. Food-producing habitat is currently defined as areas where velocity $< 0.08\text{ ms}^{-1}$; foraging habitat is defined as areas where velocity is > 0.5 and $< 0.9\text{ ms}^{-1}$, and flow depth is $> 1.0\text{ m}$ and $< 3.0\text{ m}$ (Jacobson et al., 2016a). The criterion for food-producing habitat is based on velocities that result in deposition of fine sand and thereby provide a stable substrate for burrowing *Chironomidae* larvae, which have been documented as dominant prey items for age-0 pallid sturgeon larvae (Sechler et al., 2012; Harrison et al., 2014). The criteria for foraging habitat are based on empirical occupancy data for age-0 *Scaphirhynchus* (undifferentiated shovelnose and pallid sturgeon) (Ridenour et al., 2011); conceptually, foraging habitat exists where velocities are sufficient to bring drifting invertebrates from food-producing source areas to the age-0 pallid sturgeon but where velocities are not so high as to require excessive energy expenditure.

To facilitate comparison of hydraulic and habitat data among reaches, we scaled data by the approximate bankfull discharge. In each of our multi-kilometer reaches local variability exists in the discharge at which flow overtops channel banks. For purposes of this analysis we defined the bankfull flow as the discharge when approximately 10 percent of the inundated area extended beyond the digitized boundary of the active channel. Area of each habitat type (foraging and

food-producing) was scaled by area inundated at bankfull discharge in each reach, resulting in percent area.

To evaluate temporal patterns in availability of hypothesized habitat types, we fit polynomial functions to the modeled availability of habitat, thus establishing a unique discharge-habitat relation for each reach and each habitat type (Doyle et al., 2005). We used these discharge-habitat relations to compute trends in habitat availability by month. Because the dominant hypotheses focus on survival of age-0 pallid sturgeon and the potential limiting factors of food production and foraging, the temporal analysis was limited to the post-spawn growing season, May through October (Jacobson et al., 2016a). All time series analyses were conducted for the period from 1967 to 2015, 1967 being the year when the system of six mainstem dams on the Missouri River commenced operations (Galat and Lipkin, 2000).

4. RESULTS

4.1. Simulated hydraulic patterns

Maps of inundation and velocity generated by flow simulations depict markedly different flow patterns in the three model reaches. In the Fairview reach on the Yellowstone River, heterogeneity within the active channel is provided by alternating riffles and pools, bars, and secondary channels (Figure 4). As discharge increases, flow overtops bank and inundates portions of the floodplain where the channel is not confined by bluffs (Figures 4C-D). Access to the floodplain provides area of relatively low velocities and flow depths during periods of high discharge. However, as compared to the other study reaches, in-channel velocities are relatively low across the full range of the hydrograph. At discharges less than bankfull, approximately 90 percent of depth-averaged velocities are $< 1 \text{ ms}^{-1}$ and at the highest discharges modeled > 95 percent of depth-averaged velocities are $< 1.5 \text{ ms}^{-1}$ (Figure 5C). Similarly, flow depths are relatively shallow; even at the highest discharge, > 25 percent of flow depth is less than 2 m and approximately 75 percent of the inundated area has depths $< 4 \text{ m}$ (Figure 6C).

At the two sites in the LMOR there is a greater range in velocities and depths available throughout the full range of simulated flows. At Miami, the channelized reach, simulated depth-averaged velocities during base flows are controlled by flow control structures located within the active channel (7A-B). Median depth-averaged velocity steadily increases until flows overtop

channel banks and water inundates the adjacent floodplain. Overbank flows are contained within a relatively narrow corridor along the channel due to extensive levees along the reach (Figures 7C-D). The relatively uniform, deep channel and uniform floodplain result in a bimodal distribution of depth-averaged velocities during overbank flows, producing a wide spread in the distribution of depth-averaged velocities and flow depth (Figures 5B and 6B). During the highest discharge simulated, maximum flow depths approach 12 m and maximum depth-averaged velocities exceed 2.5 ms^{-1} . For the entire range of flows simulated, the primary sources of hydraulic variability within the active channel are dikes used to maintain the navigation channel.

The Lisbon-Jameson reach is morphologically more complex than Miami due to the constructed side chutes and relatively wide main channel. At base flows, bars, exposed dikes, and shallow zones within the side-channel chutes provide areas of low velocity and backwaters (Figures 8A-B). As discharge approaches bankfull conditions, bar and dikes become inundated but these features still provide substantial zones of low velocity that may act as hydraulic refugia (Figure 8C). Substantial areas of low velocity occur along the channel margins, in the upstream chute (Lisbon), and in areas of low-lying floodplain. As discharge overtops channel banks, mean velocities in both the main channel and chutes increase, but extensive areas of low velocity occur across the floodplain (Figure 8D). Overall, modeled velocities are slightly lower as compared to Miami, as are flow depths (Figures 5A, 6A).

In the Lisbon-Jameson reach the side-channel chutes provide a distinct hydraulic environment as compared to the main channel. In the main channel, there is a uniform and steady rise in velocity as discharge increases (Figure 9). In contrast, in the Lisbon and Jameson chutes there is greater range in available velocities at higher discharges (Figures 9B-C). This is especially true of Lisbon, the more geomorphically mature of the two chutes, where even at the highest discharges simulated there is evidence of extensive areas of low velocity, which may provide hydraulic refugia for aquatic organisms. Similar trends are observed in flow depth, with greater availability of shallow areas in both chutes as compared to the main channel (Figure 10).

4.2. Distribution of hypothesized habitat types

Model results show that hydraulic patterns translate into different patterns in the distribution and availability of hypothesized habitat types among the three reaches. In the relatively unaltered

Fairview reach of the Yellowstone River, availability of food-producing habitat is driven by floodplain connectivity, with an increase in this habitat type as flows overtop banks and inundate adjacent floodplain surfaces (Figures 11, 12). Notably, food-producing relative area increases gradually from 1.5 to 2.5 times bankfull discharge. During low flows, food-producing habitat is located in shallow areas along channel margins and emergent bars (Figure 11A). Foraging habitat is most extensive in the Yellowstone River when flow is contained within the channel banks and lower velocity environments are available within the active channel (Figure 11A-C).

The distribution and occurrence of habitat types are different in the Lower Missouri River than in the Upper Basin on the Yellowstone River. Areal extent of food-producing habitat (Figure 12A) is relatively low in both the Miami and Lisbon-Jameson reaches below bankfull discharge because areas of low velocity occur only in narrow areas in wing dike fields adjacent to the active channel (Figures 13-14). The greatest source of food-producing habitat at very low flows in Lisbon-Jameson ($1000 \text{ m}^3\text{s}^{-1}$) is due to low velocities in the lower half of the Lisbon chute (Figure 13A). Floodplain inundation substantially increases the availability of slow velocities thought to constitute food-producing habitat within each of these reaches (Figures 13D, 14D). The overbank increase in food-producing habitat occurs on the downstream margins of the bends at Lisbon-Jameson where overbank flows inundate floodplain swales.

An alternative scaling of discharge is to use flow non-exceedance for the relevant discharges (Figures 12C, D), thereby presenting discharges in terms of frequency or likelihood. The alternative shows that food-producing habitats are low for both Yellowstone and Miami up to 95% flow non-exceedance. At non-exceedances below about 30%, substantially more habitat is available at Lisbon-Jameson compared to the other two reaches. All three reaches increase in area of food-producing habitat at about 95% flow exceedance; the increase at Lisbon is especially rapid reflecting the large area of connected floodplain. Based on flow non-exceedance, foraging habitat is substantially more abundant at low values at Lisbon-Jameson compared to Miami, and whereas Miami availability decreases with increasing non-exceedance, both Lisbon-Jameson and Yellowstone increase. The peak in foraging habitat availability in the Yellowstone occurs at higher non-exceedance compared to Lisbon-Jameson (Figure 12D). This results from a

combination of channel geometry and the longer-tailed flow frequency distribution on the Yellowstone compared to the Lower Missouri River (Figure 2B).

The substantially greater availability of hypothesized foraging habitat at Lisbon-Jameson as compared to Miami (Figures 12B, D) results from the greater hydraulic variability provided by chutes and bar complexes within the main channel (Figure 13). In Miami (Figure 14), there is little foraging habitat at flows exceeding a normalized discharge of 0.4 ($\sim 1900 \text{ m}^3 \text{ s}^{-1}$), whereas availability of foraging habitat peaks at a comparable normalized discharge in Lisbon-Jameson ($\sim 2000 \text{ m}^3 \text{ s}^{-1}$). Availability of foraging habitat decreases during periods of overbank flow, reflecting the fact that depths $< 1 \text{ m}$ are not hypothesized to be supportive of foraging.

The distinct relations between discharge and habitat in each of the reaches translates into differences in the seasonal availability of hypothesized habitats (Figure 15). In general, all three reaches show little temporal variation in the availability of food-producing habitat throughout the growing season, except during very high flows (Figure 15A). This trend is especially pronounced in the Lisbon-Jameson reach where floods provide access to extensive floodplain areas contained within the adjacent wildlife refuge. Connectivity to food-producing habitat (as currently defined) is episodic in nature, with peak flows dictating annual availability of this hypothesized habitat type (Figure 16). In contrast, there is greater variability in the availability of foraging habitat depending on whether it is a wet or dry year. In all hydrologic scenarios, however, there is substantially less foraging habitat available in Miami throughout the growing season as compared to Lisbon-Jameson and Yellowstone (Figure 15B).

5. DISCUSSION

5.1. Effects of channel reconfiguration on habitat availability

Previous hydrodynamic modeling efforts to evaluate habitat in large lowland rivers of the mid-continent US have used archival hydrologic and geospatial data to compare modern channel systems with historic conditions (Jacobson and Galat, 2006; Remo and Pinter, 2007; Remo et al., 2013). More recent studies have evaluated the effects of flow control structures (i.e. dikes) and the implications for SWH (Papanicolaou et al., 2011; Remo et al., 2013), but not reach-scale channel reconfiguration. In the Upper Missouri River Basin, Bowen et al. (2003) compared

SWH-like metrics in the Yellowstone River and the Upper Missouri River. The present study represents the first effort to compare results of channel restoration to non-restored and least-altered reference reaches. This two-way comparison provides the unique opportunity to evaluate how current habitat modification projects affect hydraulic gradients in reconfigured reaches of the LMOR, and whether channel reconfiguration results in physical habitat more similar to that which existed pre-channelization in the Missouri River basin.

Our usage of two reference conditions to evaluate a restoration effort is of substantial practical importance in restoration designs. In large rivers like the Missouri it is considered impossible to return to the natural, or historically defined, system because of the expectations of society that the river will continue to produce goods and services like hydropower generation, navigation, and water supply under any restoration scenario. The multiple management objectives expected by society imply that large rivers like the Missouri cannot be restored in the holistic sense, but may instead be naturalized or rehabilitated to include some range of natural processes while still maintaining conventional goods and services (Gore and Shields, 1995; Rhoads et al., 1999). If the natural reference condition is no longer a design objective – especially recognizing the difficulties in defining a reference condition in a dynamic world (Marris, 2011) – then the value of a natural reference condition is less as a metric to gage success and more in its role as a guide for understanding processes. Conversely, existing, unrestored reaches gain importance as a reference for measuring improvement of the system. In this study we are measuring restoration of the Lisbon-Jameson reach compared to the existing condition at Miami and the least disturbed condition (LDC, Stoddard et al. (2006)) of the Yellowstone River reach. The Yellowstone condition may be unattainable for the Lower Missouri River, but an understanding of ecological processes on the Yellowstone can inform designs of restoration for the Missouri.

The modeling and analysis presented here highlight the geomorphic, channel engineering, and flow-regime features that create channel complexity and availability of aquatic habitat within the channelized LMOR and a relatively unaltered reach on the Yellowstone River. Typical unrestored, channelized sections of the LMOR, represented by the Miami modeling reach, are characterized by relatively uniform channel widths, morphologic variability that is controlled by river-training structures and bank revetment, and limited access to the floodplain. The results of

channelization are evident in the diversity of depths and velocities below bankfull that results from juxtaposition of the deep, fast navigation channel with lower velocities and variable depths in channel margins and wing-dike complexes. When flows exceed bankfull discharge, the diversity of depths and velocities responds in a threshold manner, wherein the distributions widen and median values decline with the addition of shallow, slow flow (Figures 5, 6). Thus, availability of foraging habitat is relatively low for discharges greater than approximately 30% of bankfull. Modest increases in foraging habitat at discharges less than 30% of bankfull indicate that lowered discharges can be effective at increasing these habitats. On the Lower Missouri River, reservoir regulation to maintain navigation flows during summer diminishes some opportunities to increase these habitats (Jacobson and Galat, 2006). Large increases in food-producing habitat during overbank flows indicates that, based on the current understanding, inundation of low-lying floodplain areas would be the primary driver of food production for age-0 sturgeon. It is important to note, however, that the notion that food might be limiting to pallid sturgeon recruitment remains an untested hypothesis.

Several features of the Lisbon-Jameson reach contribute to increased availability of food-producing and foraging habitats compared to the unrestored Miami reach. Some of the heterogeneity in the simulated distribution of velocities results from relatively shallow depths within constructed side-channel chutes. Within the main channel, the relatively large channel width, variability in channel width, and sinuosity lead to the secondary currents that drive the formation of point bars; these morphologic features in the main channel also provide the range of velocities and depths thought to support foraging. Whereas the amount of foraging habitat at the Miami channelized site decreases to near zero above 0.4 times bankfull, the amount of foraging habitat at Lisbon-Jameson increases to a peak at 0.4 times bankfull and declines to near zero only above 1.3 times bankfull, mimicking the shape of the Yellowstone foraging curve (Figure 12). The areas of foraging habitat at Lisbon-Jameson are contributed by inside-bend slopes of the point bars and by extensive areas in the chutes themselves (Figure 13).

The Lisbon-Jameson reach also displays substantial floodplain connectivity and provision of food-producing habitats in the overbank areas. The adjacent floodplain lands at Lisbon-Jameson are part of the Big Muddy National Fish and Wildlife Refuge, thus the channel is not confined by

levees to the same degree as much of the LMOR (e.g. the Miami reach) where the adjacent floodplain is used for agriculture. All three reaches show substantial increases in food-producing habitat with overbank flows, but the LMOR channelized reaches are remarkable for abrupt changes in hydraulics as flows go overbank. Both Lisbon-Jameson and Miami demonstrate substantial increases in variability of depth and velocity as navigation channel depths and velocities continue to increase whereas overbank flows are abruptly slower and shallower (Figures 5, 6). This results from the history of channelization of the LMOR that has decreased channel top widths to 1/2 to 1/3 of historical (Funk and Robinson, 1974; Hallberg et al., 1979; Hesse and Sheets, 1993). Channelization has eliminated the previously gradual lateral slopes from thalweg to the top of the bank, replacing them with an incised channel and steep banks and associated changes in hydraulic distributions (Jacobson and Galat, 2006). In contrast, the natural channel of the Yellowstone has more gradual lateral gradients of slope, depth, and velocity and thereby lacks the threshold-like increase in hydraulic complexity noted in the LMOR. The high lateral gradients in the LMOR are evident in the habitat availability curves (Figure 12) where food-producing habitat increases gradually in the Yellowstone whereas it increases rapidly at overbank flow in the Lisbon-Jameson and Miami reaches. The smaller amount of habitat availability in the Miami reach results from the levee-restricted floodplain area.

Analysis of the two side-channel chutes within the Lisbon-Jameson reach shows the effects of chute age and evolutionary trajectory on hydraulic patterns and availability of hypothesized habitats. Construction of the Jameson chute began in 2007, but was delayed due to stakeholder concerns (Gosch et al., 2013), and the pilot channel for the chute extension was not completed until summer 2014. In contrast, Lisbon is a more mature chute, originally formed during the 1993 flood and period of high flows in 1993-1996, with minimum engineering intervention (Jacobson et al., 2004). At present, Lisbon is relatively wide as compared with Jameson, and hydraulic analyses presented here show greater availability of areas of slower velocities and shallow flow depths during high flows. It remains to be seen whether flood flows in Jameson will be geomorphically effective and sufficient to increase widths, decrease flow depths, and produce conditions hypothesized to be supportive of larval and juvenile pallid sturgeon.

Another factor in how these chutes function is whether they can be accessed by the targeted age-0 sturgeon, especially in the critical time at the end of their passive drifting phase. Following the period of high flows in the mid-1990s, flow from the main channel into the Lisbon chute approached 20% of the total discharge, sparking concerns about a channel avulsion. Thus, in 1999 and 2000, the USACE installed a grade-control structure approximately 450 m upstream from the chute exit, constructed a v-shaped weir 250 m downstream from the entrance, and placed notched revetment along the length of the chute entrance (Gosch et al., 2015). Our hydraulic analysis shows that Lisbon may provide more foraging and food-producing habitats as compared to Jameson, and greater hydraulic refugia during high flows. However, in a study comparing of age-0 trawl data in chutes and adjacent side channels, data revealed substantially higher catch per unit effort (CPUE) in the Jameson chute compared to the Lisbon chute (Gosch et al., 2015). The entrance control structure at the upstream end of Lisbon may be a fish barrier over much of the annual hydrograph. The hydraulic data evaluated here indicate that Lisbon may be providing environments more supportive of early life stages for pallid sturgeon, but the work of Gosch et al. (2015) highlight the fact that habitat is of little value if it is inaccessible to target species.

Transferring understanding from the Yellowstone reach to the Lower Missouri River is facilitated by scaling discharge to bankfull discharge and available habitat area to total bankfull area. The scaling accounts for differences in discharge and in channel size. The scaling does not, however, account for differences in the shape of the flood-frequency distribution between the Yellowstone River and the Lower Missouri River (Figure 2B). The growing season flow-frequency distribution on the Yellowstone is broader, with demonstrable increases in low flows and a substantially increased tail of high flows compared to the Lower Missouri River streamgages. This difference results in moderate to high flows on the Yellowstone River (greater than 2 times bankfull) being substantially more common compared to the Lower Missouri River. Consequently, the habitat types associated with those flows – especially food-producing habitats – are more prevalent over time than would be expected from channel geometry alone (Figure 12).

5.2. Ecological implications

Increasingly, habitat heterogeneity is touted as justification for channel restoration or reconfiguration projects, but few projects have demonstrated biotic responses (Palmer et al., 2010). The Missouri River is no exception to this trend and for many years the restoration program has focused on creation of riverine conditions that satisfy definition of SWH (Gemeinhardt et al., 2015; Gosch et al., 2015). Creation of SWH, largely through the construction of side-channel chutes, represents a substantial investment and the recovery program has been subject to criticism that the current management framework emphasizes the construction of features that fulfill requirements for SWH acreage, instead of focusing on measurable species outcomes and targets (Doyle et al., 2011; National Research Council, 2011). This analysis presented herein in part stems from the desire to understand what the physical implications have been of the large-scale efforts to reconfigure portions of the LMOR, beyond the simple accrual of additional area that meets the working definition of SWH.

As shown in this analysis, heterogeneity by itself may be a misleading metric of restoration success. Channelization of the LMOR has actually created a very heterogeneous hydraulic environment, with the deep, fast navigation channel juxtaposed adjacent to wingdike fields with deep, slow scour holes and bar complexes with variable hydraulics. When flows flood overbank areas, shallow, slow areas are added to the population. By most measures of variability, these are diverse environments, but it is unclear how much of the available environment is actually supportive habitat for target species and life stages. Adding SWH moved the complex toward the historical reference but without strong evidence that the historical SWH metric is supportive of the management objective of increasing recruitment of age-0 pallid sturgeon. Moreover, recent data indicate a lack of association between SWH and catch of age-0 sturgeon (Gemeinhardt et al., 2015). The challenge to restoration efforts – especially in systems where funding is limited and other objectives compete with restoration – is to provide exactly those elements of hydraulic habitat that are limiting to the target population. This approach is firmly in the realm of “designer ecosystems” (Ross et al., 2015) in the sense that the design is to optimize population growth of pallid sturgeon while accommodating conventional river services (e.g., navigation and flood-risk reduction).

594 These restoration activities are also taking place in an explicit adaptive-management
595 environment in which uncertainties are acknowledged and learning is designed into the
596 management program (U.S. Army Corps of Engineers, in draft). The dominant uncertainty in
597 LMOR restoration activities is whether specific habitats are limiting to pallid sturgeon
598 population growth. The LMOR management effort has included a focused effort to define key
599 hypotheses for population limitation and to design management actions that will address them.
600 This “effects analysis” (Jacobson et al., 2016a) included an expert-opinion process to develop
601 and rank hypotheses. The definitions of food-producing and foraging habitat criteria emerged
602 from this effort. In the context of the current study, these definitions are considered working
603 hypotheses based on the current state of understanding of functional requirements of pallid
604 sturgeon. We anticipate these definitions will be further refined with the collection of additional
605 data, or subsequent research may determine different habitat classes or processes which are of
606 greater importance for the successful recruitment of pallid sturgeon. Nevertheless, the present
607 definitions provide ecologically based metrics that can be used to measure restoration progress
608 and to define testable hypotheses.

609
610 There are numerous areas of ongoing research related to pallid sturgeon ecology, reproductive
611 biology, and habitat requirements. For example, food-producing habitat under the current
612 definition is comparable in abundance in Miami and Lisbon-Jameson. In Miami, areas below the
613 0.8-ms^{-1} threshold are present along channel margins during periods where discharge is less than
614 bankfull and present on floodplains during overbank flows. Similar patterns are observed for the
615 Lisbon-Jameson reach. Yet, it remains undetermined whether low velocities are equally
616 supportive of food production when located in the active channel or on inundated floodplain
617 surfaces. The current working definition of food-producing habitat was based on the notion that
618 the diet of age-0 pallid sturgeon larvae consist predominantly of Chironomidae larvae which
619 reside in fine sand. The velocity criteria used here may be appropriate for identifying areas of
620 fine sand within the channel, but may not be on the floodplain. Additionally, timing, frequency,
621 and duration of availability of channel habitats will differ from that of floodplain habitats. One
622 implication of the threshold of large increases in food-producing habitat in overbank flows in the
623 channelized river compared to the gradual increase in the natural river (Yellowstone) is that the
624 food-production associated with overbank flows is likely to be more episodic and irregular in the

channelized river. Further, flow regulation and channel incision have decreased frequencies of overbank flows in much of the LMOR (Jacobson et al., 2011), thereby decreasing frequency of large, food-producing events.

Substrate is often included as a key variable in habitat models (Ahmadi-Nedushan et al., 2006; Tonina and Jorde, 2013), and substrate is thought to be very important to benthic rheophilic fish such as the pallid sturgeon. A shortcoming of the habitat modeling efforts for pallid sturgeon to date is that none incorporate substrate explicitly. Pallid sturgeon are found dominantly over sand substrate, and in proportion to sand availability in the Missouri River (Bramblett and White, 2001) except during spawning, when they select coarse, hard substrate (DeLonay et al., 2016a). However, it is not clear that previous work on characterizing substrate size distributions is adequate to evaluate habitat selection, particularly as it relates to age-0 sturgeon. At present, there is limited technology available for widespread mapping of substrate at fine scales of resolution in a large turbid river such as the Missouri River. Discrete bed samples, near-bed imagery, and high-resolution multi-beam bathymetry reveal the LMOR is composed of dunes and fine to coarse sand with patches of gravel and exposed bedrock (DeLonay et al., 2016b); dunes up to 1.5-m amplitude are common in the navigation channel (Reuter et al., 2009; Elliott and Jacobson, 2016). Acoustic imagery suggests that adult sturgeon interact with dunes to exploit flow-field hydraulics to minimize energy expenditures (DeLonay, pers comm, 2016) and thus resolution of current 2D hydrodynamic models may not be adequate to capture relevant hydraulics, especially for age-0 and juvenile sturgeon. There is an increasing need for advances in technologies to map substrate and flow fields to quantify hydraulics at scales most relevant to fish.

An additional perspective on the utility of existing hydrodynamic modeling relates to the first 9-12 days of pallid sturgeon life when the newly hatched free embryos drift downstream for potentially hundreds of km in a quasi-passive state. In addition to hypotheses bearing on food production and foraging habitats to support age-0 sturgeon, a related hypothesis states that hydraulic conditions may be a primary constraint on the ability of these free embryos to exit the highly engineered navigation channel and enter parts of the channel supportive of foraging and transition to benthic orientation where they can initiate exogenous feeding (Braaten et al., 2008;

Braaten et al., 2012; Erwin and Jacobson, 2014). The concept of hydraulics that allow drifting free embryos to exit the navigation channel when they need to begin feeding in supportive habitats has been described as interception hydraulics, a complement to food-producing and foraging habitats. Current 2D hydrodynamic models are insufficient to quantify the complex hydraulics associated with interception; hence there is a need to move beyond simple depth-averaged velocity magnitude, or scalars, and evaluate flow vectors and transport of drifting free embryos.

6. CONCLUSIONS

Cost-effective and successful recovery of endangered species requires quantitative tools to evaluate the effects of management actions on target species. To date, much of the restoration effort and resources in the LMOR have focused on the construction of shallow-water habitat (SWH), but it remains unclear whether these activities have benefited the endangered pallid sturgeon. Recent criticisms of the recovery program have resulted in a shift from emphasis on SWH to employing best-available research to identify habitats types more explicitly linked with functional requirements of pallid sturgeon. Here, we focused on physical conditions thought to be supportive of food-production and foraging for age-0 pallid sturgeon. These habitat metrics provide a framework for conducting a two-way comparison, where the effects of channel restoration (Lisbon-Jameson) are compared to both a typical channelized reach (Miami) and a relatively natural reach (Yellowstone). The least-disturbed reference condition (Yellowstone) may be impossible to achieve on the LMOR, but understanding the hydraulic patterns in this setting helps inform the design of better-functioning restoration projects in the lower basin.

The analysis presented here indicates that construction of side-channel chutes in the LMOR and increased floodplain connectivity increases the availability of foraging habitat as compared to typical channelized conditions. Whereas foraging habitat (as currently defined) appears limited in the typical channelized LMOR (Miami), the availability of foraging habitat in the Lisbon-Jameson reach is more comparable to the relatively unaltered reach of the Yellowstone River. The availability of food-producing habitat is low in all reaches at flows less than bankfull, but reaches in the LMOR display a threshold-like response as flows overtop channel banks, reflecting the effects of channelization on hydraulics in the main channel. These high lateral

gradients result in punctuated ecological events corresponding to flows that go over bank. This threshold effect in the restored Lisbon-James reach remains distinct from that of the Yellowstone reference reach, where hydraulic changes are less abrupt and overbank flows are both more frequent and more gradually inundate the adjacent floodplain.

The design objectives for channel reconfigurations on the LMOR began in the early 2000s with a focus on restoring SWH as a measure of some of the lost natural channel morphology. Without evidence to support its biological function it became evident that restoration investments were not providing the anticipated results and costs became difficult to justify. As evidence failed to support SWH as a useful metric, scientists refined the habitat definitions and design objectives by considering specific ecological functions of channel morphology (food production, foraging, and interception) to support recruitment from age-0. Our present assessment of limiting habitat on the LMOR is based on these hypothesized ecological functions (Jacobson et al., 2016a) but within an adaptive management framework wherein the definitions are expected to be tested and to evolve. The present definitions provide indicators for measuring performance relative to reference reaches, metrics that are indicative of ecological processes that should inform restoration designs, and a framework to test and improve the hypotheses. Ongoing, structured field experiments will provide data to evaluate model performance and further refine our understanding of habitat requirements.

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923

924 Table 1. Summary data for modeling reaches. Average bankfull width reported for Lisbon-
 925 Jameson is the average width measured along the main channel, excluding side-channel chutes.
 926 River miles (RM) are the standard metric for reporting location on the Missouri River.

Reach	River	Nearest stream gage (gage no.)	River miles (RM)	Reach length (km)	Mean bankfull width (m)	Reach slope (m/m)	Steady	Area model domain (km ²)	No. cells	Min. cell area (m ²)	Max. cell area (m ²)
							state model runs (m ³ /s)				
Fairview, MT	Yellow- stone	Sidney, MT (06329500)	4.6- 8.9	10.0	350	0.00012	150-3000	21.43	433654	4.08	1598
Miami, MO	LMOR	Waverly, MO (06895500)	259.2- 264.4	10.5	345	0.00015	550-6550	7.62	248021	6.42	1826
Lisbon- Jameson, MO	LMOR	Glasgow, MO (06906500)	210.0- 219.1	15.0	442	0.00018	600-7000	37.01	855942	3.37	3744

930 Table 2. Water surface elevation data used for model calibration and selected channel roughness
 931 values.

Model reach	Survey date	Measured discharge (m ³ /s)	Approximate flow exceedance (%)	Downstream stage (m)	Calibrated channel roughness	Water surface prediction root mean square error (m)
Fairview	6/24/2014	827	7.5	569.61	0.028	0.021
Fairview	6/27/2015	835	7.4	569.59	0.025	0.028
Fairview	6/23/2015	1082	4.4	570.26	0.025	0.026
Fairview	6/17/2015	1266	2.8	570.67	0.026	0.013
mean					0.026	
Miami	11/27/2007	743	91.1	190.11	0.027	0.036
Miami	8/15/2007	1384	50.5	191.63	0.026	0.038
Miami	3/26/2007	1473	46.0	191.88	0.027	0.032
Miami	4/30/2007	2472	16.4	193.29	0.023	0.042
Miami	5/18/2007	3136	9.1	194.85	0.026	0.039
mean					0.026	
Lis-Jam	5/7/2014	1,135	76.7	178.05	0.029	0.097
Lis-Jam	5/16/2014	2,162	32.5	179.59	0.029	0.058
Lis-Jam	6/27/2014	3,564	12.5	181.30	0.028	0.055
Lis-Jam	7/9/2014	3,860	9.8	181.83	0.030	0.044
Lis-Jam	6/8/2014	4,613	6.6	182.18	0.029	0.038
Lis-Jam	9/13/2014	5,974	2.7	183.04	0.028	0.046
mean					0.029	

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Figure captions

Figure 1. Hydrodynamic modeling reaches in the Missouri River Basin (A): (B) the Fairview reach of the Yellowstone River, ND; (C) the Miami reach of the Lower Missouri River, MO; and (D) the Lisbon-Jameson reach of the Lower Missouri River, MO.

Figure 2. (A) Hydrograph for the three study reaches for the period 1967 to 2015. The solid lines represents the median daily flow and shaded regions represents the interquartile range of flows. The Boonville (USGS 06909000 Missouri River at Boonville, MO), Waverly (06895500 Missouri River at Waverly, MO), and Sidney (06329500 Yellowstone River near Sidney, MT) stream gages correspond to the Lisbon-Jameson, Miami, and Fairview/Yellowstone modeling reaches, respectively. (B) Cumulative distribution frequency of discharge in each of the three reaches, for discharges measured during the post-spawn growing season, May through October. Discharge are normalized by bankfull discharge for each reach.

Figure 3. Calibrated roughness values for three modeling reaches. Range in discharge at each site represent range in discharge for which water surface data were available.

Figure 4. Simulated velocities for a range of discharges at the Fairview reach of the Yellowstone River, MT. Subplots correspond to (A) minimum modeled discharge, (B) approximate mean annual flow, (C) approximate bankfull flow, and (D) maximum modeled flow (~99th percentile of daily discharge for period from 1967 to 2015).

Figure 5. Distribution of modeled velocities for the (A) Lisbon-Jameson, (B) Miami, and (C) Yellowstone reaches. Statistics were calculated for each reach on a 2-m grid. The black dashed line corresponds to the median velocity and shaded region corresponds to the interquartile range. The dashed and dotted lines correspond to the 5th, 10th, 90th, and 95th percentiles as indicated in the legend.

Figure 6. Distribution of modeled flow depths for the (A) Lisbon-Jameson, (B) Miami, and (C) Yellowstone reaches. Statistics were calculated for each reach on a 2-m grid. The black dashed line corresponds to the median velocity and shaded region corresponds to the interquartile range. The dashed and dotted lines correspond to the 5th, 10th, 90th, and 95th percentiles as indicated in the legend.

Figure 7. Simulated velocities for a range of discharges for the Miami reach of the Lower Missouri River, MO. Subplots correspond to (A) minimum modeled discharge, (B) approximate mean annual flow, (C) approximate bankfull flow, and (D) maximum modeled flow (~99th percentile of daily discharge for period from 1967 to 2015).

Figure 8. Simulated velocities for a range of discharges for the Lisbon-Jameson reach of the Lower Missouri River, MO. Subplots correspond to (A) minimum modeled discharge, (B) approximate mean annual flow, (C) approximate bankfull flow, and (D) maximum modeled flow (~98th percentile of daily discharge for period from 1967 to 2015).

Figure 9. Distribution of modeled velocities for the three in-channel settings in the Lisbon-Jameson reach: (A) the main channel, (B) the Lisbon Chute, and (C) the Jameson chute. Statistics were calculated for each section on a 2-m grid. The black dashed line corresponds to the median velocity and shaded region corresponds to the interquartile range. The dashed and dotted lines correspond to the 5th, 10th, 90th, and 95th percentiles as indicated in the legend.

Figure 10. Distribution of modeled flow depths for the three in-channel settings in the Lisbon-Jameson reach: (A) the main channel, (B) the Lisbon Chute, and (C) the Jameson chute. Statistics were calculated for each section on a 2-m grid. The black dashed line corresponds to the median velocity and shaded region corresponds to the interquartile range. The dashed and dotted lines correspond to the 5th, 10th, 90th, and 95th percentiles as indicated in the legend.

Figure 11. Modeled availability of foraging and food-producing habitats for a subset of discharges simulated for the Fairview reach of the Yellowstone River, MT.

Figure 12. Modeled habitat availability for simulated range of flows in Lisbon-Jameson (LJ), Miami (MI), and Yellowstone reaches for hypothesized habitat types: food producing and foraging. In (A) and (B), discharge is normalized by bankfull discharge; (C) and (D) show the same habitat data, but with discharge represented by the corresponding flow non-exceedance percentile.

Figure 13. Modeled availability of foraging and food-producing habitats for a subset of discharges simulated for the Lisbon-Jameson reach of the Lower Missouri River, MO.

990 Figure 14. Modeled availability of foraging and food-producing habitats for a subset of
991 discharges simulated for the Miami reach of the Lower Missouri River, MO.

992 Figure 15. Median habitat availability by month during the post-spawn growing season (May –
993 Oct) for Lisbon-Jameson (LJ), Miami (MI), and Yellowstone reaches for hypothesized habitat
994 types: (A) food producing and (B) foraging.

995 Figure 16. Normalized food-producing habitat calculated using the peak daily discharge for each
996 year from 1967-2015 for (A) Lisbon-Jameson, (B) Miami, and (C) Yellowstone reaches. Dashed
997 grey horizontal line represents the median normalized food-producing habitat calculated for the
998 period of record.

999

Figure1

Waterbody data from the U.S. Geological Survey National Hydrography Dataset, 2006.

Imagery from National Agricultural Imagery Program (NAIP)
Fairview imagery 2015; Miami and Lisbon-Jameson from 2014

Figure2A

Figure2B

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Figure8

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Figure10

Figure11

Figure12A

Figure12B

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Figure14

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Figure16