FEEDING ECOLOGY AND FOOD-WEB INTERACTIONS OF THE FISH ASSEMBLAGE IN THE UPPER MISSOURI RIVER AND LOWER YELLOWSTONE RIVER WITH AN EMPHASIS ON PALLID STURGEON CONSERVATION

by

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ABSTRACT

A conservation propagation program started in the late 1990s for the endangered Pallid Sturgeon *Scaphirhynchus albus* because the species was not recruiting in the Missouri River. Stocking has been successful and several studies have suggested that the survival of stocked Pallid Sturgeon in the upper Missouri River is relatively high. Stocking of hatchery-origin Pallid Sturgeon may have created an uncharacteristic population structure, which could lead to intraspecific and interspecific competition between juvenile Pallid Sturgeon, Shovelnose Sturgeon, and other fish species in the Missouri and Yellowstone rivers. The purpose of this study was to describe the diets of Pallid Sturgeon and Shovelnose Sturgeon, determine if gape size differed between species, and assess diets of many secondary and tertiary consumers to describe the food web of the upper Missouri and lower Yellowstone rivers. Pianka’s index of diet overlap was highest in segments near Fort Peck Dam in the Missouri River. Diet overlap was low in the Missouri River below the confluence with the Yellowstone River and in the Yellowstone River. Gape size was slightly different between Pallid Sturgeon and Shovelnose Sturgeon suggesting it was not the mechanism for the shift to piscivory in Pallid Sturgeon. Chironomidae were the most abundant primary consumer in the upper Missouri River and lower Yellowstone River. Hydropsychidae were not abundant in either river system, but were frequently consumed by Goldeye, Channel Catfish, Shovelnose Sturgeon, and Stonecat in the Missouri River and Shovelnose Sturgeon in the Yellowstone River. Emerald Shiner were the most abundant secondary consumer in both rivers and the most frequently consumed secondary consumer by Pallid Sturgeon, in the Missouri River. In addition, Pallid Sturgeon in the Missouri River consumed Channel Catfish, Shovelnose Sturgeon, and either Sicklefin Chub or Sturgeon Chub. In the Yellowstone River, Pallid Sturgeon consumed Channel Catfish, *Scaphirhynchus* spp., and Stonecat. These results provide a foundation into key linkages among predators and prey to better understand the effects of stocking Pallid Sturgeon in the upper Missouri River and lower Yellowstone River.

CHAPTER ONE

INTRODUCTION TO THESIS

Pallid Sturgeon *Scaphirhynchus albus* and Shovelnose Sturgeon *Scaphirhynchus platorynchus* are sympatric species endemic to the Mississippi River basin. Pallid Sturgeon were listed as an endangered species by the United States Fish and Wildlife Service in 1990 due to several hypothesized factors including habitat fragmentation, hybridization (with Shovelnose Sturgeon), changes in water quantity and quality, overfishing, illegal harvest, and the lack of natural recruitment (USFWS 2014). A conservation propagation program began in the late 1990s as a management action to prevent extirpation of Pallid Sturgeon in the Missouri River in Montana and North Dakota (USFWS 2014). The conservation propagation program aimed to capture wild Pallid Sturgeon, maintain genetic diversity, and release hatchery-origin juvenile Pallid Sturgeon in the river. The program has been successful with 251,838 (does not include larval stocking) juvenile Pallid Sturgeon stocked from 1998 through 2017 in Recovery Priority Management Area 2 (RPMA 2), which includes the Missouri River from Fort Peck Dam downstream to the headwaters of Lake Sakakawea and the Yellowstone River from the mouth of the Tongue River downstream to the confluence with the Missouri River. Annual apparent survival rates have been estimated to be relatively high for hatchery-origin Pallid Sturgeon in RPMA 2. For example, the estimated rate for fingerling Pallid Sturgeon released in the Missouri River, three years after their initial release was 0.87 (SE [0.30]; Rotella 2015). Given such rates and the large numbers of fish that have been released, even in the face of annual attrition due to mortality, substantial numbers of fish from hatchery releases are estimated to be at large in the system, which has led to concerns among biologists about potential competition between hatchery-origin Pallid Sturgeon and sympatric Shovelnose Sturgeon.

The large number of hatchery-origin Pallid Sturgeon estimated to be alive in the river years after release has led biologists and managers to question if Pallid Sturgeon have been overstocked in RPMA 2. Historically, Pallid Sturgeon were late maturing, with low reproductive rates, and low abundance. However, the stocking program has increased the number of Pallid Sturgeon in the Missouri River, and they are probably higher in abundance now as compared to the estimated historical abundance (Braaten et al. 2009). An artificially high abundance of Pallid Sturgeon could negatively influence multiple levels of the food web.

Pallid Sturgeon less than 300 mm are insectivores feeding primarily on benthic macroinvertebrates, whereas Pallid Sturgeon greater than 300 mm begin a dietary shift to piscivory (Gerrity et al. 2006; Wanner et al. 2007; Grohs et al. 2009; French et al. 2013). Unlike Pallid Sturgeon, Shovelnose Sturgeon feed on benthic macroinvertebrate throughout their life (Modde and Schmulbach 1977; Hoover et al. 2007; Wanner et al. 2007; Gosch et al. 2018). Therefore, if food was limited, competition could occur among Pallid Sturgeon and Shovelnose Sturgeon prior to Pallid Sturgeon switching to piscivory. Furthermore, once Pallid Sturgeon switch to piscivory, there could be competition among Pallid Sturgeon and another native apex predator Sauger *Sander canadensis*. In addition, competition could occur among other secondary or tertiary consumers such as Channel Catfish *Ictalurus punctatus*, Goldeye *Hiodon alosoides*, or Stonecat *Noturus flavus*.

The linkages among primary, secondary, and tertiary consumers in RPMA 2 are currently unknown. Understanding the food-web linkages is key to better understanding the interactions among Pallid Sturgeon and other aquatic species in the Missouri River and Yellowstone River. Furthermore, it is important to understand how secondary consumers link primary and tertiary consumers throughout the food webs in both rivers. Food webs will allow biologists to better understand if Pallid Sturgeon have been overstocked in RPMA 2, which will guide future stocking efforts.

Overview of Thesis

I assessed diet overlap between Pallid Sturgeon and Shovelnose Sturgeon in Recovery Priority Management Area 2 (RPMA 2), which includes the Missouri River from Fort Peck Dam, downstream to the headwaters of Lake Sakakawea, ND and the Yellowstone River from the mouth of the Tongue River downstream to the confluence with the Missouri River near Buford, ND. In addition, I quantified the linkages among key primary, secondary, and tertiary consumers in RPMA 2 to provide a road map for future stocking and management of Pallid Sturgeon in the upper basin of the Missouri River. I also evaluated gape size between Pallid Sturgeon and Shovelnose Sturgeon as a possible mechanism behind the ontogenetic dietary shift to piscivory by Pallid Sturgeon.

In chapter two, I compared diets of Pallid Sturgeon and Shovelnose Sturgeon sampled in segments 2, 3, and 4 from the Missouri River and segments 1 and 2 from the

Yellowstone River. I used the Pianka diet overlap index to quantitatively assess diet overlap between Pallid Sturgeon and Shovelnose Sturgeon within each segment by river. I compared measurements of fork length, gape length, and gape width among Pallid Sturgeon and Shovelnose Sturgeon in segment 4 of the Missouri River and hatchery-origin Pallid Sturgeon at Garrison Dam National Fish Hatchery. The specific objectives were to: 1) quantitatively describe the diets of Pallid Sturgeon and Shovelnose Sturgeon and assess diet overlap and 2) evaluate the possibility of gape size as a mechanism for the diet shift in Pallid Sturgeon. Based on previous research, I predicted that diet overlap would be highest for Pallid Sturgeon prior to when they switch to piscivory. Furthermore, I predicted that Pallid Sturgeon diets from the Missouri River below the confluence with the Yellowstone River would be most similar to Pallid Sturgeon diets from the Yellowstone River. Given previous research on other species being gape limited prior to switching to piscivory, I predicted that gape size would be the mechanism for the shift to piscivory observed in Pallid Sturgeon.

In chapter three, I quantitatively described the diets of numerous secondary and tertiary consumers in the upper Missouri and lower Yellowstone rivers. Many of the secondary consumer feeding habits were unknown to date. These data were critical to develop the relationship of each species within the food web. I was able to describe the linkages among numerous species and relate them to Pallid Sturgeon. The specific objective of this chapter was to quantitatively describe the food-webs linkages among numerous primary, secondary, and tertiary consumers in RPMA 2. I predicted there would be differences within the Missouri and Yellowstone river food webs based on differences in habitat and species composition within the two rivers. Furthermore, I predicted that diet items in species would change along a longitudinal gradient from upstream to downstream as habitat changed from the operation of Fort Peck Dam or natural variation in the Yellowstone River.

Chapter four concludes and summarizes the major findings from chapters 2 and 3. Management implications and recommendations for future stocking of hatchery-origin Pallid Sturgeon in RPMA 2 are also discussed in chapter four.

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CHAPTER TWO

DIET OVERLAP AND GAPE SIZE OF PALLID STURGEON AND SHOVELNOSE STURGEON IN THE MISSOURI RIVER AND YELLOWSTONE RIVER

Contributions of Authors and Co-Authors

Manuscript in Chapter 2

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Contributions: Conceived and implemented the study design, collected and analyzed data, and authored the manuscript.

Co-Author: Christopher S. Guy

Contributions: Obtained funding, conceived the study design, discussed the implications of the results, and co-authored the manuscript.

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ABSTRACT

The Pallid Sturgeon conservation propagation program has been successful in the upper Missouri River and lower Yellowstone River, and several studies have suggested that the survival of stocked Pallid Sturgeon is relatively high. The high survival has prompted the question of whether too many fish have been stocked, which could result in intraspecific competition, interspecific competition, or both if food was limited. The objective of this study was to quantitatively describe the diets of Pallid Sturgeon and Shovelnose Sturgeon and determine if gape size differed between species. Diets of both species varied longitudinally in the Missouri River from segment 2 near Fort Peck Dam to segment 4 below the confluence with the Yellowstone River. Diet overlap between Pallid Sturgeon and Shovelnose Sturgeon was highest in segments 2 and 3 of the Missouri River. Pianka's index of diet overlap (± SE) was 0.81 (0.12) in segment 2 and 0.96 (0.05) in segment 3. Diet overlap was low in segment 4 of the Missouri River and both segments of the Yellowstone River. Non-tanypodinae Chironomidae was the most frequently consumed benthic macroinvertebrate by Pallid Sturgeon and Shovelnose Sturgeon in segments 2, 3, and 4 of the Missouri River and segment 2 of the Yellowstone River. In segment 1 of the Yellowstone River, Shovelnose Sturgeon fed primarily on *Cheumatopsyche* spp. and *Hydropsyche* spp. Gape size was slightly (< 9 mm) different between Pallid Sturgeon and Shovelnose Sturgeon suggesting it was not the mechanism for the shift to piscivory in Pallid Sturgeon. These results provided a foundation for future research efforts in the Missouri River and Yellowstone River. In addition, these results also provided necessary consumption data to develop bioenergetics models.

Introduction

Pallid Sturgeon *Scaphirhynchus albus* were listed as federally endangered by the United States Fish and Wildlife Service (USFWS) in 1990 due to several hypothesized factors such as habitat fragmentation, hybridization with Shovelnose Sturgeon *Scaphirhynchus platorynchus*, illegal harvest, overfishing, changes in water quantity and quality, and the lack of natural recruitment (USFWS 2014). To address the lack of natural recruitment, a conservation propagation program began in the late 1990s as a stopgap measure until the mechanism for lack of recruitment could be identified and remediated. The propagation program aimed to prevent local extirpation in areas throughout the basin where Pallid Sturgeon had recruitment failure (USFWS 2014). In Recovery Priority Management Area 2 (RPMA 2), which includes the Missouri River from Fort Peck Dam, MT downstream to the headwaters of Lake Sakakawea, ND and the Yellowstone River from the mouth of the Tongue River downstream to the confluence with the Missouri River near Buford, ND, the program has been successful with 251,838 juvenile Pallid Sturgeon stocked from 1998 through 2017. Annual apparent survival rates have been estimated to be relatively high for hatchery-origin Pallid Sturgeon in RPMA 2. For example, the estimated rate for fingerling Pallid Sturgeon released in the Missouri River, three years after their initial release was 0.87 (SE [0.30]; Rotella 2015). Given such rates and the large numbers of fish that have been released, even in the face of annual attrition due to mortality, substantial numbers of fish from hatchery releases are estimated to be at large in the system, which has led to concerns among biologists about potential competition between hatchery-origin Pallid Sturgeon and sympatric Shovelnose Sturgeon.

Numerous diet studies have assessed the degree of diet overlap between Shovelnose Sturgeon and Pallid Sturgeon in other portions of their range (Gerrity et al. 2006; Braaten et al. 2007; Wanner et al. 2007; Grohs et al. 2009; Gosch et al. 2018). Shovelnose Sturgeon feed primarily on benthic macroinvertebrates, especially taxa within the orders of Diptera, Ephemeroptera, and Trichoptera (Modde and Schmulbach 1977; Hoover et al. 2007; Wanner et al. 2007); whereas, Pallid Sturgeon primarily feed on similar benthic macroinvertebrates until they exhibit an ontogenetic diet shift to piscivory (Gerrity et al. 2006; Wanner et al. 2007; Grohs et al. 2009; French et al. 2013). In the lower and middle Mississippi River, Shovelnose Sturgeon diets were composed of 91 - 99.7% invertebrates while Pallid Sturgeon diets were composed of 4.4 - 47% invertebrates (Hoover et al. 2007). Fish were not found in Shovelnose Sturgeon diets from the middle and lower Mississippi River, but did comprise a large portion (total food volume ≥ 52.5%) in Pallid Sturgeon diets (Hoover et al. 2007). The lack of piscivory in Shovelnose Sturgeon is well documented (Held 1969; Modde and Schmulbach 1977; Gerrity et al. 2006; Hoover et al. 2007).

Most studies describing the diets of Pallid Sturgeon or Shovelnose Sturgeon identify benthic macroinvertebrates to a coarse scale such as order or family (Modde and Schmulbach 1977; Gerrity et al. 2006; Braaten et al. 2007; Hoover et al. 2007; Grohs et al. 2009; Bock et al. 2011; Seibert et al. 2011; Braaten et al. 2012; Sechler et al. 2012). I am aware of only two studies (i.e., Wanner et al. [2007]; Rapp et al. [2011]) that described macroinvertebrates in the diets of *Scaphirhynchus* spp. to genus. The finer scale of taxonomic resolution can be difficult to achieve but is important for understanding the ecology and behavior of fishes (Chipps and Garvey 2007; Rapp et al. 2011). Benthic macroinvertebrates, within order or family, can have different adaptions for diet, habitat, and reproduction (Merritt et al. 2008; Rapp et al. 2011). Thus, information about spatial or temporal foraging behavior of fishes can be lost by identifying diet items only to order or family (Rapp et al. 2011). This study is unique in that it describes the diets and assesses the degree of diet overlap for Pallid Sturgeon and Shovelnose Sturgeon at the finest taxonomic resolution and at a large spatial scale in a highly altered river (Missouri River) and an unregulated river (Yellowstone River).

There has been little research on the mechanism that causes an ontogenetic shift in Pallid Sturgeon diets but not Shovelnose Sturgeon. Two possible explanations for the shift could be the larger body size or potentially larger mouth size (gape) of Pallid Sturgeon compared to Shovelnose Sturgeon. The relationship between gape size and predator length has been well documented for numerous fish species (Michaletz et al. 1987; Magnhagen and Heibo 2001; Krebs and Turingan 2003). In addition, predator size to prey size relationships have been well documented in marine (Kneib and Stiven 1978; Schmitt and Holbrook 1984; Scharf et al. 2000) and freshwater fish species (Hambright 1991; Gill and Hart 1994; Nilsson and Brönmark 2000). Therefore, because Pallid Sturgeon obtain larger sizes than sympatric Shovelnose Sturgeon, body size and gape size may explain the switch to piscivory in Pallid Sturgeon. Thus, I evaluated the possibility of gape size as a mechanism for the diet shift in Pallid Sturgeon.

The Missouri River and Yellowstone River differ considerably with respect to flow regime. The Missouri River is highly regulated by dams and the Yellowstone River is the longest unregulated river in the contiguous USA (Galat et al. 2005b). The differences between rivers and proximity make them a good model to evaluate the effects of river regulation on diet composition of two large river obligate species. The Yellowstone River is often considered the most “natural” river occupied by Pallid Sturgeon and is used as a model for habitat construction projects and flow recommendations for other reaches in the Missouri River. Thus, studying the feeding ecology of Pallid Sturgeon and Shovelnose Sturgeon in the Missouri River and Yellowstone River will provide information that could be used to link habitat and species foraging in other portions of the Missouri River. The results from this study will also be used to develop food-web models (see Chapter 3) and bioenergetic models (concurrent study) to evaluate supply and demand of resources in the Missouri and Yellowstone rivers.

Study Area

The Missouri River is the longest named river in North America (Galat et al. 2005a). It is formed at the confluence of the Gallatin, Madison, and Jefferson rivers near Three Forks, MT. The Missouri River flows 3,768 km across the Great Plains to the confluence with the Mississippi River near St. Louis, Missouri (Galat et al. 2005a). Historically, the Missouri River was characterized by braided channels, sandbars, and unstable banks (Galat et al. 2005a). However, numerous dams (e.g., Fort Peck, Garrison, Oahe) have changed the natural flow regime and habitat of the Missouri River.

The Mississippi River basin, which includes the Missouri River, supports the most diverse freshwater fish assemblage in North America (Robison 1986). One hundred thirty-six fish species reside in the main channel of the Missouri River with 76% in seven families with Cyprinidae, Catostomidae, Centrarchidae, and Salmonidae representing the top four specious (Galat et al. 2005a). In addition to these families, the Missouri River also supports some archaic families including Acipenseridae, Polyodontidae, Hiodontidae, and Lepisosteidae (Galat et al. 2005a).

The Yellowstone River is the longest free-flowing river in the conterminous United States and one of the largest tributaries by discharge to the Missouri River (Galat et al. 2005b). The Yellowstone River originates in Yellowstone National Park and flows northeast to the confluence with the Missouri River near Buford, ND. Downriver of Billings, MT the Yellowstone River has increased water temperatures and turbidity. The Yellowstone River supports 56 fish species varying from cold-water specialists to large river obligate species. The lower Yellowstone River, which includes the reach downstream of the confluence with the Bighorn River in Bighorn, MT, supports a diverse fish assemblage with 49 species representing 15 families (Galat et al. 2005b). Cyprinidae, Catostomidae, and Ictaluridae are the most common families in the lower Yellowstone River. Similar to the Missouri River, the Yellowstone River also supports some archaic families including Acipenseridae, Polyodontidae, and Hiodontidae.

The study reach for the Missouri River was between Fort Peck Dam (river kilometer [rkm] 1771.5) and Lake Sakakawea (rkm 1568.0). The reach for the Yellowstone River was between Intake Diversion Dam (rkm 113.0) and the confluence with the Missouri River (rkm 0.0). The reach on the Missouri River was further delineated into four segments (i.e., 1-4; Figure 2.1). Annual discharge near Wolf Point, MT (segments 2 and 3) typically peaked in June or July between 354 to 566 cubic meters per second (cms). Segment 1 began at Fort Peck Dam (rkm 1774.5) and continued downstream to the confluence of the Milk River with the Missouri River (rkm 1760.0). This segment was short and characterized by hypolimnetic releases from Fort Peck Dam (Hunziker et al. 2015). Coldwater fish species were most common in this segment and many were not native to the Missouri River. Segment 2 extended from the confluence of the Missouri and Milk rivers (rkm 1760.0) downstream to Wolf Point, MT (rkm 1701.0; Figure 2.1). The segment was characterized as transitional, where turbidity was low and water temperature was influenced by the hypolimnetic release from Fort Peck Dam, but at the end of the segment, turbidity and water temperature had increased and were more representative of pre-dam conditions (Hunziker et al. 2015). The substrate in segment 2 was predominantly cobble and gravel at the upstream extent, but transitions to more sand as the distance from Fort Peck Dam increases. (Haddix et al. 2015). Segment 3 included the Missouri River from Wolf Point, MT (rkm 1701.0) downstream to the confluence with the Yellowstone River near Buford, ND (rkm 1582.0; Figure 2.1). The segment was more similar to the natural characteristics of the Missouri River with varied water temperatures, high turbidity, and sand dominated substrate (Haddix et al. 2015). Unlike the upper two reaches, segment 3 had sandbar and island formations (Haddix et al. 2015). Segment 4 was from the confluence with the Yellowstone River (rkm 1592.0) downstream to the headwaters of Lake Sakakawea, ND, (rkm 1568.0). This segment was the most similar to the natural characteristics of the Missouri River (Bramblett and White 2001). Water temperature was variable and had characteristics of a warm-water river with high turbidity and primarily sand substrate with diverse habitat features such as sand bars, islands, deep outside bends, and bluff pools (Bramblett and White 2001).

The Yellowstone River was delineated into two segments. Both segments were characterized by warm, turbid water. Discharge near Sidney, MT (segment 2) typically peaked in June or July between 1,982 and 2,548 cms. Segment 1 was from Intake Diversion Dam (rkm 113.0) to rkm 47.0 (Figure 2.1). Segment 1 had diverse habitat features with islands, bars, backwaters, and chutes (Kellerhals et al. 1976, cited by Bramblett and White 2001). The substrate was primarily cobble and gravel throughout the sinuous channel (Kellerhals et al. 1976, cited by Bramblett and White 2001). Segment 2 was from rkm 47.0 to the confluence with the Missouri River (rkm 0.0; Figure 2.1). This segment was dominated by sand substrate and numerous habitat features including islands, sand bars, and off channel habitat (Bramblett and White 2001).

Methods

Field

Pallid Sturgeon and Shovelnose Sturgeon (hereafter, termed *Scaphirhynchus* spp. when considered together) were sampled in the Missouri River and Yellowstone River in June, September, and October in 2013 and May through August in 2014. In addition, Pallid Sturgeon were sampled in the Missouri River from May through October in 2016. Sampling in 2013 and 2014 was conducted weekly in segments 2, 3, and 4. In 2016, sampling was conducted weekly in May and June, daily in July and August, and sporadically in September and October. Diets were collected by Montana State University (MSU), Montana Fish, Wildlife and Parks (FWP), United States Geological Survey (USGS), and the USFWS. Trammel nets, otter trawls, and angling were used to sample all *Scaphirhynchus* spp.

Trammel nets were the primary gear used to sample *Scaphirhynchus* spp. All trammel nets were 38.1-m long, 1.8-m deep, with a 22.7-kg lead line and a 12.7-mm foam core float line (Wilson et al. 2015). In addition, all inner mesh was #139 multifilament twine and all outer mesh was #9 multifilament twine (Wilson et al. 2015). Three mesh sizes were used throughout the study. The most common mesh size had an outside bar mesh of 203.2 mm and an inside bar mesh of 25.4 mm. Two larger mesh sizes were used in broodstock collection where the outside bar mesh was 254 mm and an inside bar mesh of 152.4 mm, and the other had an outside bar mesh of 203.2 mm and an inside bar mesh of 101.6 mm. All trammel nets were deployed off the bow of the boat and drifted perpendicular to flow for a minimum of 75 m and a maximum of 300 m (Wilson et al. 2015). The otter trawl sampled few (n<10) *Scaphirhynchus* spp. The otter trawl was 7.6-m long, 4.9-m wide, and 0.9-m tall. The inner mesh of the trawl was 6.35-mm bar and the outer mesh was 38.1-mm bar. The inner mesh was constructed of #18 polyethylene twine and the outer was of #9 polyethylene twine (Wilson et al. 2015). To keep the otter trawl open, a 50.8-mm sleeve was sewn along the top section to install a hoop. The trawl doors were 381-mm tall, 19.1-mm thick, 762-mm long, with 12.7-mm thick steel runners (Wilson et al. 2015). A 7.9-m long "tickler" chain was attached to the bottom of the trawl to agitate the substrate. The otter trawl was connected to the bow of the boat by two 30.5-m long, 19.1-mm thick Tenex ropes. The otter trawl was fished off the bow of the boat downstream at a rate slightly faster than river velocity (Wilson et al. 2015). The otter trawl was fished for a minimum of 75 m and a maximum of 200 m. Trotlines targeted Pallid Sturgeon and accounted for few (n<5) diet samples in the study. All trotlines were set by FWP and USFWS crews overnight for a maximum of 18 hours. Trotlines had a main line length of 32 m with 10 hooks spaced every 1.5 m and baited with Night Crawlers *Lumbricus terrestris*. Each hook was tied to a dropper that was 30.5 to 60.9 cm long and attached to the main line using hook snaps (Wilson et al. 2015). One Pallid Sturgeon diet was from a fish captured by an angler in the Missouri River.

All *Scaphirhynchus* spp. collected were measured to fork length (mm) and weighed (g). Pallid Sturgeon were scanned for passive integrated transponder tags (PIT), and checked for elastomers, radio tags, and missing scutes. *Scaphirhynchus* spp. collected by MSU in 2013 and 2014 were gastric lavaged using a modified 12-volt bilge pump. A plastic tube was inserted to the beginning of the stomach while fish were held dorsal side down. Stomach contents were washed into a 250-µm sieve and transferred into Whirl-Pak bags containing 10% buffered formalin. All other *Scaphirhynchus* spp. collected were gastric lavaged using a method similar to that described by Foster (1977) and tested by Wanner (2006). A pressurized sprayer provided a reservoir for water throughout the process. A pistol-grip garden sprayer was fitted with a flexible 5.5-mm outside diameter polyethylene tube to supply water throughout the process. *Scaphirhynchus* spp. were held dorsal side down at approximately a 45-degree angle (Wanner 2006). The tube was inserted through the esophagus to the first bend in the stomach (Wanner 2006). Once the tube was in place, water was slowly pulsated through the esophagus and stomach. At the same time, the stomach area was lightly massaged to ease regurgitation (Wanner 2006). Stomach contents were regurgitated into a large tray. The process was repeated until clean, clear water was regurgitated by the fish. All diet samples were transferred from the tray, through a 250-µm sieve, and into Whirl-Pak bags with 95% ethanol to be further processed in the laboratory.

Laboratory

All macroinvertebrates were identified to the lowest taxonomic level, if possible to genus (Merritt et al. 2008). The first 30 individuals of each genus, per stomach sample, were measured to the nearest millimeter (not including cerci or antennae; Cross et al. 2011). Length data were converted to weight using a length-weight regression and then converted into ash-free-dry-mass (AFDM) to estimate biomass (Burgherr and Meyer

1997; Benke et al. 1999). *Scaphirhynchus* spp. diets that consisted primarily of one prey item (e.g., Chironomidae) were subsampled. Subsampling was conducted on samples that contained hundreds of individual macroinvertebrates of a single genus. Samples were subsampled (1/2-1/32) using a Folsom plankton wheel to equally divide the sample each time without bias (Parker and Huryn 2006; Bertrand et al. 2009).

All fish in diet samples were identified to species, if possible. In 2016, all *Scaphirhynchus* spp. found in diet samples were identified to species using genetic methods at Southern Illinois University-Carbondale. All fish including those unidentifiable were measured to the nearest millimeter for total, standard, and fork length when possible. All fish and fish parts were dried at 60°C for a minimum of 36 hours and then burned in a muffle furnace at 500°C for approximately 6 hours to obtain AFDM (Edwards and Huryn 1995; Nakano et al. 1999).

Gape Size Measurements

Pallid Sturgeon and Shovelnose Sturgeon were sampled June-August and October 2016 in segment 4 of the Missouri River. All *Scaphirhynchus* spp. from the Missouri River were collected by trammel netting as described above. Fork length (mm), gape length, and gape width were measured on all *Scaphirhynchus* spp. sampled. Fork length was measured as described above. Gape length (mm) was measured as the inside distance of the mouth, when fully extended, from the anterior to posterior side. Gape width (mm) was measured as the inside distance of the mouth from left to right side at the mid-point of the mouth. Additionally, Pallid Sturgeon were randomly sampled from Garrison Dam

National Fish Hatchery, Coleharbor, ND in March 2017. Fork length, gape length, and gape width were measured on each Pallid Sturgeon as described above.

Data Analysis

Frequency of occurrence and percent by weight were calculated for all diet items found in *Scaphirhynchus* spp. diets (Chipps and Garvey 2007). Pianka's index of diet overlap was calculated to estimate strength of diet overlap between Shovelnose Sturgeon and Pallid Sturgeon by river segment as follows:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}},$$

where: O_{jk} = Pianka's measure of overlap, p_{ij} = proportion of diet item *i* of the total resources used by species *j*, p_{ik} = proportion of diet item *i* of the total resources used by species *k*, and *n* = total number of diet items (Pianka 1973). Pianka's index varies from 0 to 1, with 0 indicating no overlap between the species, and 1 indicating complete overlap (Pianka and Pianka 1976). Pianka values greater than 0.75 indicate high overlap; whereas, values less than 0.30 indicate limited overlap (Pianka and Pianka 1976; Matthews and Hill 1980; Matthews et al. 1982). Bootstrapping was used to provide estimates of variability for the Pianka index values. Bootstrapping included random selection of individuals with replacement and repeated 5,000 times. The mean Pianka value and standard error were calculated from the bootstrapped values (Olson et al. 2007).

Simple linear regression models were used to analyze the relationship among fork length, gape length, and gape width between Pallid Sturgeon and Shovelnose Sturgeon.

Gape length and gape width were predicted for varying fork lengths and compared by species.

Results

Diet data were collected from 159 Pallid Sturgeon in the Missouri River varying from 297 to 1167 mm fork length and 44 Shovelnose Sturgeon varying from 235 to 675 mm fork length (Table 2.1). The majority of Pallid Sturgeon sampled in the Missouri River were from segment 4 (n = 108) due to targeted sampling of large Pallid Sturgeon in 2016, which is where large Pallid Sturgeon are most common (Hunziker et al. 2017a, 2017b; Wilson et al. 2017). Shovelnose Sturgeon were more equally sampled among segments in the Missouri River (Table 2.1). Although Shovelnose Sturgeon were sampled equally among segments in the Missouri River, the abundance of Shovelnose Sturgeon decreased from upstream to downstream segments (Hunziker et al. 2017a, 2017b; Wilson et al. 2017).

Missouri River

The most frequently consumed macroinvertebrate by Pallid Sturgeon in all segments was non-tanypodinae Chironomidae ($O_i > 63\%$; Table 2.2). In all three segments, non-tanypodinae Chironomidae was also the most consumed benthic macroinvertebrate by weight, but in segment 4 the total weight of non-tanypodinae Chironomidae consumed was only 7.6%. In segment 4, unidentifiable and identifiable fishes made up the majority of the weight. Emerald Shiner *Notropis atherinoides* were the most frequently consumed diet item by weight ($W_i = 33.9\%$; Table 2.2). In segment 4, Pallid Sturgeon also consumed Channel Catfish *Ictalurus punctatus*, *Macrhybopsis* spp., *Scaphirhynchus* spp., and Cyprinidae species (Table 2.2). All *Scaphirhynchus* spp. consumed by Pallid Sturgeon in 2016 were genetically confirmed as Shovelnose Sturgeon.

The diversity of unique prey items in Pallid Sturgeon diets increased from upstream to downstream. Pallid Sturgeon consumed 15 unique diet items in segment 2, 25 in segment 3, and 37 in segment 4 (Table 2.2). Pallid Sturgeon in segment 2 had the least diverse diets and non-tanypodinae Chironomidae and *Ephemerella* spp. were the most common prey consumed. Pallid Sturgeon in segment 3 consumed a slightly higher amount of non-tanypodinae Chironomidae, but had a more diverse benthic macroinvertebrate assemblage in their diet than Pallid Sturgeon in segment 2 (Table 2.2). Diversity of genera within the order Ephemeroptera increased from upstream to downstream segments in the diets of both *Scaphirhynchus* spp. in the Missouri River. Within the order Ephemeroptera, where $O_i \geq 25\%$, there were differences observed in the diets between *Scaphirhynchus* spp. among segments in the Missouri River. For example, Pallid Sturgeon in segment 2 frequently consumed ($O_i > 25\%$) only two genera of Ephemeroptera (*Baetis* spp. and *Ephemerella* spp.); whereas, Shovelnose Sturgeon frequently consumed three genera of Ephemeroptera (*Baetis* spp., *Ephemerella* spp., and *Ephoron* spp.). However, in segment 3, Pallid Sturgeon only consumed two different genera of Ephemeroptera ($O_i > 25\%$, Cercobrachys spp. and *Ametropus* spp.); whereas, Shovelnose Sturgeon only consumed one genera of Ephemeroptera ($O_i > 25\%$, *Cercobrachys* spp.). Furthermore, in segment 4, Pallid Sturgeon only consumed two genera of Ephemeroptera ($O_i > 25\%$, *Ephoron* spp. and *Traverella* spp.). However, Shovelnose Sturgeon in segment 4 consumed five genera and one family of Ephemeroptera ($O_i > 25\%$; Table 2.2).

The diversity of unique diet items consumed by Shovelnose Sturgeon were identical for the first two segments then increased in the last segment. In segments 2 and 3, Shovelnose Sturgeon consumed 20 unique diet items and in segment 4 Shovelnose Sturgeon consumed 33 unique diet items (Table 2.2). Non-tanypodinae Chironomidae were found in all Shovelnose Sturgeon diets (i.e., $O_i = 100\%$) for all segments of the Missouri River (Table 2.2). *Hydropsyche* spp. were frequently consumed ($O_i \geq 60\%$) by Shovelnose Sturgeon in all segments of the Missouri River (Table 2.2). Although *Hydropsyche* spp. were frequently consumed in all segments of the Missouri River, the total weight of *Hydropsyche* spp. consumed was relatively small with the largest percent by weight in segment 4 ($W_i = 18.3\%$). Some prey items occurred in the diets of Shovelnose Sturgeon in all segments but varied in importance by segment. For example, *Ametropus* spp., *Traverella* spp., and *Probezzia* spp., were found in Shovelnose Sturgeon diets from all segments, but increased in percent by weight from upstream to downstream in the Missouri River (Table 2.2).

Yellowstone River

In the Yellowstone River, diets were sampled from 21 Pallid Sturgeon varying from 341 to 1003 mm fork length and 40 Shovelnose Sturgeon varying from 380 to 853 mm fork length (Table 2.1). Pallid Sturgeon were difficult to capture in both segments and abundance was lower in segment 1 than segment 2 (M. Rugg, Montana Fish, Wildlife and Parks, personal communication) leading to a small sample (n = 4). However, Shovelnose Sturgeon abundance was higher in both segments of the Yellowstone River (M. Rugg, personal communication); consequently, resulting in more data for Shovelnose Sturgeon as compared to Pallid Sturgeon (Table 2.1).

It appears that Pallid Sturgeon diets varied between segments in the Yellowstone River, but the low sample size in segment 1 makes comparing segments inappropriate. However, the number of unique prey items consumed by Pallid Sturgeon in segment 1 was 13, and 22 unique prey items were consumed by Pallid Sturgeon in segment 2 — following the same trend as noted in the Missouri River. The macroinvertebrate assemblage in Pallid Sturgeon diets from segment 2 consisted primarily of non-tanypodinae Chironomidae, *Hydropsyche* spp., *Simulium* spp., *Cercobrachys* spp., and *Isonychia* spp.; however, 35% of the total weight of all diet items consumed by Pallid Sturgeon in segment 2 of the Yellowstone River was non-tanypodinae Chironomidae and *Isonychia* spp. (Table 2.3). In both segments of the Yellowstone River, Pallid Sturgeon consumed Channel Catfish, Stonecat *Noturus flavus,* and other unidentifiable fish (Table 2.3). In addition, an unidentifiable *Scaphirhynchus* spp. was consumed by a Pallid Sturgeon in segment 2. Unidentifiable fish and identifiable fish accounted for 60% of the total weight consumed by Pallid Sturgeon in segment 2.

Unlike the Missouri River, diversity of unique prey items consumed by Shovelnose Sturgeon did not increase from upstream to downstream in the Yellowstone

River. In segment 1, Shovelnose Sturgeon consumed 25 unique prey items and in segment 2 consumed 23 unique prey items. Shovelnose Sturgeon in segment 1 consistently had *Cheumatopsyche* spp., *Hydropsyche* spp., non-tanypodinae Chironomidae, and *Simulium* spp. in their diets, but nearly 81% of the diet weight consisted of *Cheumatopsyche* spp. and *Hydropsyche* spp., which are both genera in the Hydropsychidae family (Table 2.3). This was the only segment, in both rivers, where non-tanypodinae Chironomidae was not an important prey source for Shovelnose Sturgeon. Although, non-tanypodinae Chironomidae was consumed by 90% of the Shovelnose Sturgeon sampled in segment 1, the weight was only 0.4% (Table 2.3). In contrast, all Shovelnose Sturgeon sampled in segment 2, consumed non-tanypodinae Chironomidae making up nearly 70% of the weight of all diet items (Table 2.3). Few individual Shovelnose Sturgeon consumed Copepoda and Cyclopoida (frequency of occurrence 10% and 5%, respectively), but 8.2% of the total diet weight for Shovelnose Sturgeon in segment 2 was accounted for by these prey items (Table 2.3). Opposite to Pallid Sturgeon and Shovelnose Sturgeon diets in the Missouri River, the number and frequency of Ephemeroptera families present in the diets of Shovelnose Sturgeon decreased along the longitudinal gradient in the Yellowstone River. Shovelnose Sturgeon, in segment 1, frequently ($O_i > 50\%$) consumed four genera of Ephemeroptera (*Traverella* spp., *Baetis* spp., *Rhithrogena* spp., and *Maccaffertium* spp.; Table 2.3). These four genera accounted for 11.2% of total diet weight for Shovelnose Sturgeon in segment 1. However, in segment 2, Shovelnose Sturgeon did not feed on Ephemeroptera frequently. Only two genera (*Cercobrachys* spp. and *Rhithrogena* spp.) were consumed by at least

20% of all Shovelnose Sturgeon (Table 2.3). These two genera accounted for only 8% of the total weight for all diet items consumed by Shovelnose Sturgeon in segment 2 of the Yellowstone River (Table 2.3).

Diet Overlap

Diet overlap between Pallid Sturgeon and Shovelnose Sturgeon was highest in segments 2 and 3 in the Missouri River regardless of whether the comparison included all diets or only diets that included macroinvertebrates (Table 2.4). Diet overlap between Pallid Sturgeon and Shovelnose Sturgeon was low in Missouri River segment 4 when all diet items were considered (Table 2.4) because most of the Pallid Sturgeon diets sampled contained fish (Table 2.2). Conversely, when comparing between Pallid Sturgeon that only consumed macroinvertebrates and Shovelnose Sturgeon in segment 4, diet overlap increased and indicated high overlap (Table 2.4). Diet overlap between Pallid Sturgeon and Shovelnose Sturgeon was low in both segments in the Yellowstone River (Table 2.4). In segment 1 of the Yellowstone, the sample size for Pallid Sturgeon was low, and all fish were piscivorous; thus, resulting in the lowest diet overlap value observed in the study. In segment 2, diet overlap was low when including or excluding piscivorous Pallid Sturgeon (Table 2.4). The low overlap could be a function of Pallid Sturgeon and Shovelnose Sturgeon consuming different genera of benthic macroinvertebrates (Table 2.3). For example, *Isonychia* spp. accounted for 10.8% of the total weight consumed by Pallid Sturgeon, but *Isonychia* spp. was not consumed by Shovelnose Sturgeon. Similarly, non-tanypodinae Chironomidae accounted for 24.3% of the total weight consumed by Pallid

Sturgeon, but nearly 70% of the total weight consumed by Shovelnose Sturgeon (Table 2.3).

Gape

Forty-seven Pallid Sturgeon (365 mm – 1167 mm fork length; median 464 mm) and 160 Shovelnose Sturgeon (144 mm – 861 mm fork length; median 594 mm) were sampled in segment 4 of the Missouri River, and 100 Pallid Sturgeon (151 mm – 427 mm fork length; median 321 mm) were randomly sampled from Garrison Dam National Fish Hatchery. Gape length was positively associated with fork length for Pallid Sturgeon (r^2=0.96, P<0.0001, df = 145, β_0 = -1.77 [SE = 0.51], β_1 = 0.06 [SE = 0.001]) and Shovelnose Sturgeon (r^2=0.90, P<0.0001, df = 158, β_0 = -9.59 [SE = 1.04], β_1 = 0.07 [SE = 0.002]; Figure 2.2). Gape width was also positively associated with fork length for Pallid Sturgeon (r^2=0.98, P<0.0001, df = 145, β_0 = -0.76 [SE = 0.38], β_1 = 0.08 [SE <0.0001]) and Shovelnose Sturgeon (r^2=0.94, P<0.0001, df = 158, β_0 = -1.36 [SE = 0.72], β_1 = 0.06 [SE = 0.001]; Figure 2.3). Predicted gape length at 300 mm fork length was 17.3 mm (95% CI 16.7 mm – 17.8 mm) for Pallid Sturgeon and 11.2 mm (95% CI 10.1 mm – 12.2 mm) for Shovelnose Sturgeon, and at 800 mm fork length was 49.0 mm (95% CI 48.0 mm – 50.0 mm) for Pallid Sturgeon and 45.9 mm (95% CI 44.9 mm – 46.9 mm) for Shovelnose Sturgeon. Predicted gape width at 300 mm fork length was 21.8 mm (95% CI 21.4 mm – 22.2 mm) for Pallid Sturgeon and 18.0 mm (95% CI 17.3 mm – 18.7 mm) for Shovelnose Sturgeon, and at 800 mm fork length was 59.4 mm (95% CI 58.7

mm – 60.2 mm) for Pallid Sturgeon and 50.3 mm (95% CI 49.5 mm – 51.0 mm) for Shovelnose Sturgeon.

Discussion

Prior to this study, diet habits and overlap between Pallid Sturgeon and Shovelnose Sturgeon in the inter-reservoir reach of the upper Missouri River and the lower Yellowstone River were unknown. Similar to results of previous diet studies, Pallid Sturgeon initially consumed benthic macroinvertebrates and switched to piscivory when they achieved a length of 300 mm (Gerrity et al. 2006; Hoover et al. 2007; Wanner et al. 2007); whereas, Shovelnose Sturgeon fed exclusively on benthic macroinvertebrates and fish eggs at all sizes (Gerrity et al. 2006; Hoover et al. 2007; Wanner et al. 2007; Bock et al. 2010; Rapp et al. 2011). Low diet overlap between *Scaphirhynchus* spp. was observed in segment 4 of the Missouri River and segments 1 and 2 of the Yellowstone River. These results were similar to those reported for diet overlap between Pallid Sturgeon and Shovelnose Sturgeon in the Missouri River above Fort Peck Dam, MT (Gerrity et al. 2006). Gape size does not appear to be the mechanism behind the differences in diet observed for Pallid Sturgeon and Shovelnose Sturgeon in segment 4 of the Missouri River and segments 1 and 2 of the Yellowstone River. Differences in mean gape width (3.8 mm) and mean gape length (6.1 mm) between *Scaphirhynchus* spp. at 300 mm fork length is probably not biologically significant.

In segments 2 and 3 of the Missouri River, diet overlap was high between Pallid Sturgeon and Shovelnose Sturgeon. The high overlap in these segments was a function of both *Scaphirhynchus* spp. feeding primarily on similar genera of benthic macroinvertebrates. In segment 2 and 3 of the Missouri River, diet overlap slightly increased when piscivorous Pallid Sturgeon were removed from the analysis further corroborating the influence of benthic macroinvertebrates in the diet.

Pallid Sturgeon and Shovelnose Sturgeon diets differed within orders of benthic macroinvertebrates and along a longitudinal gradient from upstream to downstream in the Missouri River. Families within the order Ephemeroptera provide an example of how Fort Peck Dam may be influencing the feeding ecology of Pallid Sturgeon and Shovelnose Sturgeon. The diversity of Ephemeroptera families within Pallid Sturgeon and Shovelnose Sturgeon diets increased along the longitudinal gradient from upstream to downstream in the Missouri River. Pallid Sturgeon in segment 2 consumed five genera of Ephemeroptera; whereas, Pallid Sturgeon in segment 3 consumed seven genera of Ephemeroptera. Finally, Pallid Sturgeon in segment 4 consumed 10 genera of Ephemeroptera. A similar pattern of increased diversity in Ephemeroptera genera was observed in Shovelnose Sturgeon diets in the Missouri River. Three genera of Ephemeroptera (*Baetis* spp., *Ephemerella* spp., and *Isonychia* spp.) were consumed by Pallid Sturgeon in all three segments. However, other genera of Ephemeroptera were found in only one or two segments in the Missouri River. A few examples of genera only present in one segment of the Missouri River include *Homoneuria* spp., *Leucrocuta* spp., and *Maccaffertium* spp. Furthermore, the increase in Ephemeroptera genera along the longitudinal gradient was supported by benthic macroinvertebrate samples collected by a concurrent study (E. Scholl, Montana State University, personal communication).

The habitat in the Missouri River is affected by Fort Peck Dam and is probably influencing the occurrence of Ephemeroptera families and genera—and ultimately those consumed by *Scaphirhynchus* spp. The habitat in segment 2 of the Missouri River is more highly influenced by Fort Peck Dam than other segments in this study; therefore, non-sand habitats may be a function of the dam and ultimately contributing to the food resources for Pallid Sturgeon and Shovelnose Sturgeon. Segment 3 of the Missouri River was less influenced by Fort Peck Dam with respect to water temperature and turbidity than segment 2 (i.e., water temperature and turbidly increase with increasing distance from Fort Peck Dam) and the substrate changes from cobble-gravel to more sand patches. Changes in habitat are corroborated by the diet items sampled in Pallid Sturgeon and Shovelnose Sturgeon. For example, *Ametropus* spp. were consumed by Pallid Sturgeon and Shovelnose Sturgeon in segment 3, but not in segment 2. Unlike *Ephemerella* spp., *Ametropus* spp. are a sand and silt obligate species (Merritt and Wallace 2003). *Isonychia* spp. increased in frequency occurrence in Pallid Sturgeon and Shovelnose Sturgeon diets from segment 2 to segment 4 in the Missouri River. *Isonychia* spp. were also an important diet item for Pallid Sturgeon in the inter-reservoir reach below Fort Randall Dam, South Dakota (Wanner et al. 2007). *Isonychia* spp. are typically biovoltine and may be more readily available as a source of prey than macroinvertebrate species that are univoltine or semivoltine (Echols et al. 2010). Segment 4 of the Missouri River is furthest downstream of Fort Peck Dam and least affected relative to upstream segments. The habitat in this segment is most similar to unregulated conditions with warm water temperatures, high turbidity, sand substrate, and more diverse habitat features (e.g., sandbars). Twenty unique diet items were consumed by Pallid Sturgeon and Shovelnose Sturgeon in segment 4 of the Missouri River. The large number of unique diet items consumed by Pallid Sturgeon and Shovelnose Sturgeon in segment 4 of the Missouri River is not surprising given the distance from Fort Peck Dam. In the Colorado River, below Granby Reservoir dam (hypolimnetic release), six sites from 0.25 km to 12.0 km below the dam were sampled for macroinvertebrates (Voelz and Ward 1991). Similar to the pattern observed in *Scaphirhynchus* spp. diets in the Missouri River, macroinvertebrate taxonomic richness increased along the longitudinal gradient from Granby Dam (Voelz and Ward 1991). In addition to the unique benthic macroinvertebrate taxa, there was also unique fish species consumed by Pallid Sturgeon in segment 4. The unique fish species could be due to the increased number and size of Pallid Sturgeon sampled, but could also be related to the change in fish assemblage structure compared to segments 2 and 3. Shovelnose Sturgeon and White Sucker *Catostomus commersonii* were most common in segment 2; whereas, in segment 3 and 4 the most abundant fish species was Emerald Shiner (Haddix et al. 2015; Hunziker et al. 2015; Wilson et al. 2015). Furthermore, secondary consumers such as Channel Catfish, Sturgeon Chub, and Western Silvery Minnow *Hybognathus argyritis* increased in abundance along a longitudinal gradient from segment 2 to segment 4 (Haddix et al. 2015; Hunziker et al. 2015; Wilson et al. 2015). Other secondary consumers such as Fathead Minnow *Pimephales promelas* and Sand Shiner *Notropis stramineus* decreased in abundance along a longitudinal gradient from segment 2 to segment 4 (Haddix et al. 2015; Hunziker et al. 2015; Wilson et al. 2015).

Pallid Sturgeon consumed numerous fish species, primarily in segment 4 of the Missouri River and segments 1 and 2 of the Yellowstone River. These results are consistent with studies on Pallid Sturgeon in other reaches of the Missouri River (Gerrity et al. 2006; Wanner et al. 2007; Grohs et al. 2009). However, this was the first study to document Pallid Sturgeon consuming Shovelnose Sturgeon. Furthermore, the findings in this study are contrary to those described for Pallid Sturgeon above Fort Peck Reservoir (Gerrity et al. 2006) where piscivorous Pallid Sturgeon in RPMA 2 were more opportunistic and rarely consumed Sicklefin Chub and Sturgeon Chub. Of the 50 Pallid Sturgeon diets sampled above Fort Peck Reservoir, only 15 had stomach contents (Gerrity et al. 2006); therefore, the low sample size could have influenced the high proportion of Sicklefin Chub and Sturgeon Chub observed in the Gerrity et al. (2006) study.

Pallid Sturgeon sampled from the inter-reservoir reach in the Missouri River between Fort Randall Dam, SD and Lewis and Clark Lake, SD fed primarily on Johnny Darter *Etheostoma nigrum* (Grohs et al. 2009). In the same reach of the Missouri River, Pallid Sturgeon consumed four different fish species: Channel Catfish, Emerald Shiner, Johnny Darter, and Silver Chub *Macrhybopsis storeriana* (Wanner et al. 2007). The differences in diet of Pallid Sturgeon within the same reach could be related to sampling period or slightly younger but larger Pallid Sturgeon sampled in the second study. Although there are some minor differences between the two studies, these examples further illustrate that Pallid Sturgeon are opportunistic, feeding on available fishes in the benthic guild.

Shovelnose Sturgeon diets in this study were similar to other Shovelnose Sturgeon diet studies with taxa in the orders of Ephemeroptera, Trichoptera, and Diptera most frequently consumed (Modde and Schmulbach 1977; Hoover et al. 2007; Wanner et al. 2007; Rapp et al. 2011; Seibert et al. 2011). In the Missouri River, non-tanypodinae Chironomidae were consumed by all Shovelnose Sturgeon sampled and also accounted for at least 40% of the overall weight of diet items consumed by Shovelnose Sturgeon in segments 2, 3, and 4. These results are similar to other Shovelnose Sturgeon diet studies; for example, in the middle Wabash River all diets sampled had Chironomidae present (Bock et al. 2011), in the Missouri River above Fort Peck Reservoir Chironomidae dominated the percent occurrence and percent composition by wet weight (Gerrity et al. 2006), below Fort Randall Dam, SD the frequency of occurrence and percent composition by dry weight was dominated by Chironomidae (Wanner et al. 2007), and four genera of Chironomidae were frequently consumed by Shovelnose Sturgeon from the lower Platte River, Nebraska (Rapp et al. 2011). Similar to Shovelnose Sturgeon sampled in the Missouri River, all Shovelnose Sturgeon sampled in segment 2 of the Yellowstone River contained non-tanypodinae Chironomidae and the percent by weight was nearly 70%. However, in segment 1 of the Yellowstone River, Shovelnose Sturgeon consumed non-tanypodinae Chironomidae, but the percent by weight was less than 1%. The majority of the weight in Shovelnose Sturgeon diets in segment 1 of the Yellowstone River was a result of *Cheumatopsyche* spp. and *Hydropsyche* spp., two genera within the family Hydropsychidae. Although this differs from other segments of the Missouri and Yellowstone rivers, the high consumption of species in the Hydropsychidae family has been noted in the Mississippi River. For example, in the middle Mississippi River, 59.8% of the total volume of Shovelnose Sturgeon diets was comprised of Hydropsychidae (Hoover et al. 2007). The large amount of Hydropsychidae consumed by Pallid Sturgeon and Shovelnose Sturgeon in the middle Mississippi River indicates that gravel patches or man-made structures were foraging habitats for Pallid Sturgeon and Shovelnose Sturgeon (Hoover et al. 2007). Gravel, cobble substrate was the dominant substrate in segment 1 of the Yellowstone River (Bramblett and White 2001) and was probably the source for Hydropsychidae. Therefore, it appears that Shovelnose Sturgeon may also be opportunist and feed on a variety of macroinvertebrates in varying habitat types.

Comparing *Scaphirhynchus* spp. diets between the Missouri River and the Yellowstone River proved to be more challenging than originally expected. Due to low sample sizes of non-piscivorous Pallid Sturgeon in the Yellowstone River (n = 6), it is inappropriate to make comparisons between the feeding habits of non-piscivorous Pallid Sturgeon in the Missouri River compared to the Yellowstone River. Furthermore, due to limited sample size of piscivorous Pallid Sturgeon in segment 2 (n = 3) and segment 3 (n = 4) of the Missouri River it is also inappropriate to make comparisons of piscivorous Pallid Sturgeon in these two segments to piscivorous Pallid Sturgeon in the Yellowstone River. However, I was able to compare piscivorous Pallid Sturgeon from segment 4 of the Missouri River to piscivorous Pallid Sturgeon in segment 2 of the Yellowstone River (n = 11). Channel Catfish and *Scaphirhynchus* spp. were consumed by Pallid Sturgeon in segment 4 of the Missouri River and segment 2 of the Yellowstone River. However, these were the only similarities between piscivorous Pallid Sturgeon in the two river segments. Although Emerald Shiner were the most abundant fish species sampled in both river segments (Duncan et al. 2012; Hunziker et al. 2017a, 2017b), they were only consumed by Pallid Sturgeon in the Missouri River. Larval and juvenile Emerald Shiner inhabited backwater habitats in the upper Mississippi River (Sheaffer and Nickum 1986) and backwater and main-channel border habitats in the Kanawha River (Scott and Nielsen 1989). Therefore, Pallid Sturgeon in the Missouri River may be using backwater and main-channel border habitat more than Pallid Sturgeon in the Yellowstone River. However, telemetered Pallid Sturgeon in the upper Missouri River (Gerrity et al. 2008) and lower Yellowstone River avoided secondary channels (Bramblett and White 2001). Piscivorous Pallid Sturgeon in the Yellowstone River consumed Stonecat, a species that is commonly associated with rocky bottom riffles or boulders in deep pools (Nelson and Paetz 1992), indicating that Pallid Sturgeon may be feeding more in the main channel of the Yellowstone River. The substrate in the main channel of the Yellowstone is comprised of more rock and cobble than in segment 4 of the Missouri River. Thus, the proximity of Stonecat in the thalweg of the main channel could make them easier prey than Emerald Shiner in main-channel border habitat.

This study provides descriptive data on Pallid Sturgeon and Shovelnose Sturgeon feeding habits in the inter-reservoir reach of the upper Missouri River and the lower Yellowstone River. The variation in diet composition of *Scaphirhynchus* spp. between rivers and downstream within the Missouri River suggests that habitat varies, which directly influences macroinvertebrate composition and availability to Pallid Sturgeon and Shovelnose Sturgeon. The variability observed in the diet composition among segments indicates that Pallid Sturgeon and Shovelnose Sturgeon can consume a variety of benthic macroinvertebrate species and may be feeding in differing habitats within the same river. Similarly, piscivorous Pallid Sturgeon consumed several different fish species, providing evidence to suggest that Pallid Sturgeon are more opportunistic predators than previously described. This study provides a foundation for future research efforts in both rivers by providing the necessary consumption data to develop bioenergetics models.

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Tables

Table 2.1. Sample size (n), minimum length (all length measurements are fork length), maximum length, and median length of Pallid Sturgeon (PDSG) and Shovelnose Sturgeon (SNSG) sampled in Missouri River segments 2-4 and Yellowstone River segments 1-2 from June through October in 2013, 2014, and 2016.

River	Segment	Species	n	Minimum-Maximum (mm)	Median (mm)
Missouri	2	PDSG	27	321-468	399
Missouri	2	SNSG	15	390-675	570
Missouri	3	PDSG	24	297-828	386
Missouri	3	SNSG	15	235-628	405
Missouri	4	PDSG	108	352-1167	432
Missouri	4	SNSG	14	254-587	335
Yellowstone	1	PDSG	4	471-843	736
Yellowstone	1	SNSG	20	380-853	685
Yellowstone	2	PDSG	17	341-1003	425
Yellowstone	2	SNSG	20	426-773	605

Table 2.2. Frequency of occurrence (O_i) and percent by weight (W_i) by diet item for Pallid Sturgeon (Pallid) and Shovelnose Sturgeon (Shovelnose) sampled in Missouri River segments 2-4. Data were sorted by percent by weight for Pallid Sturgeon in segment 2. Dash marks indicate that a prey item was not present in the diet sampled. Italicized genera indicate prey were identified to genus, but not further identified to species. 2,4 Cyprinidae references species of fish found in the Cyprinidae family with pharyngeal teeth counts of 2, 4.

	Segment											
	2				3				4			
	Pallid		Shovelnose		Pallid		Shovelnose		Pallid		Shovelnose	
Diet Item	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i
Non-tanypodinae	96.3	59.3	100	72.8	91.7	69.3	100	94.6	63.6	7.6	100	43.6
Ephemerella	77.8	32.8	60.0	0.4	20.8	0.2	-	-	5.6	0.04	6.3	0.02
Baetis	44.4	5.2	86.7	16.3	12.5	0.06	-	-	14.0	0.2	43.8	0.09
Hydropsyche	40.7	1.0	60.0	3.7	41.7	5.0	60.0	1.7	34.6	6.8	93.8	18.3
Unknown Fish	11.1	0.7	-	-	16.7	12.0	-	-	68.2	17.3	-	-
Maccaffertium	7.4	0.3	-	-	-	-	-	-	-	-	-	-
Heptagenia	3.7	0.2	6.7	0.1	-	-	-	-	1.9	0.03	-	-
Dromogomphus	11.1	0.2	-	-	4.2	0.2	6.7	0.08	-	-	31.3	0.2
Fish Eggs	25.9	0.2	-	-	-	-	-	-	-	-	6.3	<0.01
Simulium	33.3	0.1	80.0	3.5	16.7	0.04	13.3	0.06	17.8	0.07	68.8	0.7
Glossosoma	3.7	0.1	6.7	<0.01	-	-	-	-	-	-	-	-
Probezzia	11.1	0.04	26.7	0.6	25.0	0.3	53.3	1.5	12.1	0.3	100	17.7

Table 2.2. Continued

	Segment											
	2				3				4			
	Pallid		Shovelnose		Pallid		Shovelnose		Pallid		Shovelnose	
Diet Item	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i
Isogenus	7.4	0.03	6.7	1.2	12.5	0.2	26.7	0.07	2.8	0.05	50.0	0.5
Isonychia	3.7	0.01	6.7	0.1	25.0	4.3	13.3	0.07	15.0	4.4	37.5	6.5
Chironomidae Pupae	22.2	<0.01	80.0	0.2	33.3	0.04	20.0	0.06	12.1	0.03	43.8	0.02
Ephemerellidae	3.7	<0.01	-	-	-	-	-	-	-	-	-	-
Nematoda	3.7	<0.01	6.7	0.02	-	-	6.7	<0.01	2.8	<0.01	31.3	<0.01
Tanypodinae	3.7	<0.01	26.7	0.01	8.3	0.01	-	-	2.8	<0.01	25.0	0.2
Cheumatopsyche	-	-	20.0	0.3	-	-	-	-	14.0	1.2	43.8	2.0
Ephoron	-	-	26.7	0.2	4.2	0.05	6.7	0.05	26.2	2.6	37.5	2.2
Heptageniidae	-	-	13.3	0.1	4.2	0.02	-	-	15.0	0.3	56.3	0.2
Muscidae	-	-	20.0	0.1	8.3	0.05	13.3	0.03	1.9	<0.01	12.5	0.01
Crambidae	-	-	6.7	0.1	-	-	-	-	-	-	-	-
Amphipoda	-	-	6.7	0.02	-	-	20.0	0.02	-	-	-	-
Brachycentrus	-	-	6.7	0.02	-	-	-	-	0.9	<0.01	-	-
Leucrocuta	-	-	6.7	0.02	-	-	-	-	3.7	0.05	-	-
Polymitarcyidae	-	-	6.7	<0.01	-	-	-	-	0.9	0.05	-	-

Table 2.2. Continued

	Segment											
	2				3				4			
	Pallid		Shovelnose		Pallid		Shovelnose		Pallid		Shovelnose	
Diet Item	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i
Araneae	-	-	6.7	<0.01	-	-	-	-	1.9	<0.01	-	-
Ametropus	-	-	-	-	33.3	5.6	20.0	0.7	12.1	0.5	37.5	1.2
Cercobrachys	-	-	-	-	33.3	0.8	33.3	0.7	3.7	<0.01	12.5	<0.01
Stylurus	-	-	-	-	4.2	0.7	-	-	2.8	0.3	25.0	1.0
Curculionidae	-	-	-	-	4.2	0.6	-	-	0.9	<0.01	6.3	0.02
Coptotomus	-	-	-	-	4.2	0.1	-	-	-	-	-	-
Traverella	-	-	-	-	16.7	0.1	20.0	0.06	43.9	2.4	37.5	1.8
Ormosia	-	-	-	-	12.5	0.1	6.7	0.01	8.4	0.05	18.8	0.01
Hagenius	-	-	-	-	4.2	0.07	-	-	-	-	-	-
Hydropsychidae	-	-	-	-	8.3	0.07	-	-	-	-	6.3	<0.01
Leptoceridae	-	-	-	-	4.2	0.04	-	-	1.9	0.01	6.3	0.02
Calanoida	-	-	-	-	4.2	0.03	-	-	0.9	<0.01	-	-
Corixidae	-	-	-	-	4.2	<0.01	6.7	0.03	6.5	0.1	31.3	0.2
Hyalella	-	-	-	-	4.2	<0.01	-	-	0.9	<0.01	-	-
Homoneuria	-	-	-	-	-	-	13.3	0.2	5.6	0.2	-	-
Tipula	-	-	-	-	-	-	6.7	0.04	1.9	0.04	25.0	0.09

Table 2.2. Continued

	Segment											
	2				3				4			
	Pallid		Shovelnose		Pallid		Shovelnose		Pallid		Shovelnose	
Diet Item	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i
Dolichopodidae	-	-	-	-	-	-	6.7	0.04	0.9	<0.01	37.5	0.2
Lachlania	-	-	-	-	-	-	6.7	0.03	-	-	-	-
Perlodidae	-	-	-	-	-	-	6.7	<0.01	1.9	<0.01	12.5	0.04
Tipulidae	-	-	-	-	-	-	6.7	<0.01	1.9	<0.01	12.5	0.02
Notropis atherinoides	-	-	-	-	-	-	-	-	7.5	33.9	-	-
Ictalurus punctatus	-	-	-	-	-	-	-	-	2.8	7.1	-	-
2,4 Cyprinidae	-	-	-	-	-	-	-	-	6.5	6.3	-	-
Macrhybopsis spp.	-	-	-	-	-	-	-	-	2.8	3.1	-	-
Cyprinidae	-	-	-	-	-	-	-	-	1.9	2.9	-	-
Scaphirhynchus spp.	-	-	-	-	-	-	-	-	7.5	1.6	-	-
Culicoides	-	-	-	-	-	-	-	-	2.8	0.1	62.5	2.5
Hesperocorixa	-	-	-	-	-	-	-	-	1.9	0.1	12.5	0.05
Gomphidae	-	-	-	-	-	-	-	-	0.9	0.05	12.5	0.4
Caenidae	-	-	-	-	-	-	-	-	7.5	0.03	-	-

Table 2.2. Continued

	Segment											
	2				3				4			
	Pallid		Shovelnose		Pallid		Shovelnose		Pallid		Shovelnose	
Diet Item	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i
Polycentropodidae	-	-	-	-	-	-	-	-	0.9	0.01	-	-
Dytiscidae	-	-	-	-	-	-	-	-	0.9	0.01	6.3	<0.01
Baetidae	-	-	-	-	-	-	-	-	3.7	0.01	6.3	0.04
Leptohyphidae	-	-	-	-	-	-	-	-	1.9	<0.01	-	-
Nigronia	-	-	-	-	-	-	-	-	-	-	6.3	0.07
Heteroceridae	-	-	-	-	-	-	-	-	-	-	6.3	0.03
Rhithrogena	-	-	-	-	-	-	-	-	-	-	6.3	0.02
Arctoconopa	-	-	-	-	-	-	-	-	-	-	6.3	0.01
Tricorythodes	-	-	-	-	-	-	-	-	-	-	6.3	<0.01
Branchiura	-	-	-	-	-	-	-	-	-	-	6.3	<0.01

Table 2.3. Frequency of occurrence (O_i), and percent by weight (W_i) by diet item for Pallid Sturgeon (Pallid) and Shovelnose Sturgeon (Shovelnose) sampled in Yellowstone Rivers segments 1 and 2. Data were sorted by percent by weight for Pallid Sturgeon in segment 1. Dash marks indicate that a prey item was not present in the diets sampled. Italicized genera indicate prey were identified to genus, but not further identified to species.

	Segment							
	1				2			
	Pallid		Shovelnose		Pallid		Shovelnose	
Diet Item	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i
Noturus flavus	50.0	55.7	-	-	11.8	6.3	-	-
Ictalurus punctatus	25.0	25.5	-	-	5.9	39.3	-	-
Unknown Fish	100	15.5	-	-	52.9	14.6	-	-
Isogenus	50.0	1.3	85.0	6.0	5.9	0.6	25.0	7.1
Traverella	75.0	0.6	50.0	2.9	17.6	0.4	15.0	0.3
Baetis	100	0.4	70.0	0.6	5.9	0.02	10.0	<0.01
Cheumatopsyche	75.0	0.4	95.0	65.7	5.9	0.1	30.0	1.6
Heptageniidae	25.0	0.2	5.0	0.08	11.8	0.2	15.0	0.4
Hydropsyche	50.0	0.1	95.0	15.0	29.4	1.7	20.0	0.1
Rhithrogena	25.0	0.1	85.0	6.2	17.6	0.4	20.0	5.1
Non-tanypodinae	50.0	0.05	90.0	0.4	82.4	24.3	100	69.8
Ormosia	25.0	0.01	5.0	<0.01	-	-	-	-
Fish Eggs	25.0	0.01	5.0	<0.01	17.6	0.01	25.0	0.2

Table 2.3. Continued

	Segment							
	1				2			
	Pallid		Shovelnose		Pallid		Shovelnose	
Diet Item	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i
Simulium	25.0	0.01	90.0	0.5	23.5	0.2	40.0	0.2
Dolichopodidae	25.0	<0.01	-	-	-	-	-	-
Maccaffertium	-	-	65.0	1.5	-	-	5.0	0.08
Isonychia	-	-	20.0	0.6	23.5	10.8	-	-
Tanypodinae	-	-	70.0	0.2	5.9	0.01	25.0	0.07
Perlodidae	-	-	10.0	0.09	-	-	-	-
Stenelmis	-	-	20.0	0.05	-	-	5.0	0.07
Ephoron	-	-	10.0	0.05	11.8	0.2	5.0	0.04
Cercobrachys	-	-	10.0	0.03	23.5	0.5	35.0	2.8
Probezzia	-	-	45.0	0.02	5.9	0.05	50.0	3.1
Leucrocuta	-	-	10.0	0.01	-	-	-	-
Dromogomphus	-	-	5.0	0.01	5.9	0.04	5.0	0.08
Ephemerella	-	-	5.0	0.01	-	-	-	-
Chironomidae Pupae	-	-	25.0	<0.01	17.6	0.01	40.0	0.1
Leptohyphidae	-	-	5.0	<0.01	-	-	-	-
Culicoides	-	-	15.0	<0.01	5.9	<0.01	40.0	0.5

Table 2.3. Continued

	Segment							
	1				2			
	Pallid		Shovelnose		Pallid		Shovelnose	
Diet Item	O_i	W_i	O_i	W_i	O_i	W_i	O_i	W_i
Empididae	-	-	5.0	<0.01	-	-	-	-
Leptoceridae	-	-	5.0	<0.01	-	-	-	-
Polycentropodidae	-	-	5.0	<0.01	-	-	-	-
Tipulidae	-	-	5.0	<0.01	-	-	5.0	0.01
Nematoda	-	-	5.0	<0.01	5.9	<0.01	10.0	<0.01
Scaphirhynchus spp.	-	-	-	-	5.9	0.08	-	-
Heptagenia	-	-	-	-	5.9	0.06	5.0	0.05
Hyalella	-	-	-	-	5.9	0.04	-	-
Copepoda	-	-	-	-	-	-	10.0	5.3
Cyclopoida	-	-	-	-	-	-	5.0	2.9
Planorbidae	-	-	-	-	-	-	5.0	0.06
Muscidae	-	-	-	-	-	-	5.0	0.04
Gomphidae	-	-	-	-	-	-	5.0	0.03

Table 2.4. Mean Pianka diet overlap values for Pallid Sturgeon and Shovelnose Sturgeon (standard error in parentheses) for 5,000 bootstrap runs (see methods for details) for the Missouri River and Yellowstone River by segment (1-4). Invertebrates delineates comparisons made where the data were truncated to only include macroinvertebrate data (i.e., diets containing fish were excluded). Bolded numbers indicate high overlap (i.e., values ≥ 0.75).

River	Segment	Comparison	Pianka (SE)
Missouri	2	All	**0.81 (0.12)**
Missouri	2	Invertebrates	**0.84 (0.12)**
Missouri	3	All	**0.96 (0.05)**
Missouri	3	Invertebrates	**0.99 (0.02)**
Missouri	4	All	0.24 (0.11)
Missouri	4	Invertebrates	**0.78 (0.18)**
Yellowstone	1	All	0.03 (0.08)
Yellowstone	2	All	0.40 (0.31)
Yellowstone	2	Invertebrates	0.17 (0.07)

Figure Captions

Figure 2.1. Map of the upper Missouri River, delineated into four segments, which includes the inter-reservoir reach between Fort Peck Dam, MT and the headwaters of Lake Sakakawea, ND, and the lower Yellowstone River, delineated into two segments, from Glendive, MT to the confluence with the Missouri River near Buford, ND. Bars represent segment breaks for each river.

Figure 2.2 Gape length (mm) and fork length (mm) for Pallid Sturgeon (PDSG; circles) and Shovelnose Sturgeon (SNSG; triangles) sampled from the Missouri River (segment 4) during summer 2016 and Garrison Dam National Fish Hatchery in March 2017.

Figure 2.3. Gape width (mm) and fork length (mm) for Pallid Sturgeon (PDSG; circles) and Shovelnose Sturgeon (SNSG; triangles) sampled from the Missouri River (segment 4) during summer 2016 and Garrison Dam National Fish Hatchery in March 2017.

Figures

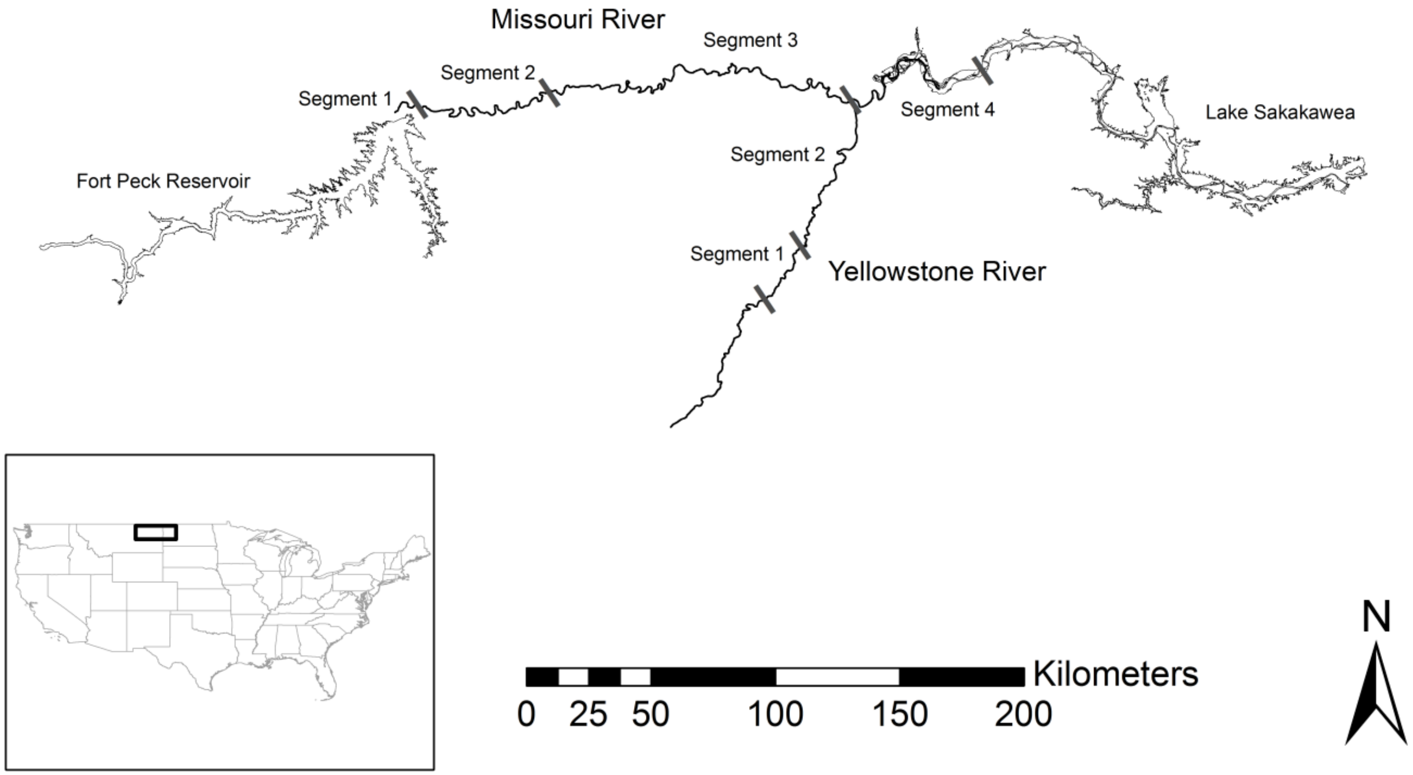

Figure 2.1.

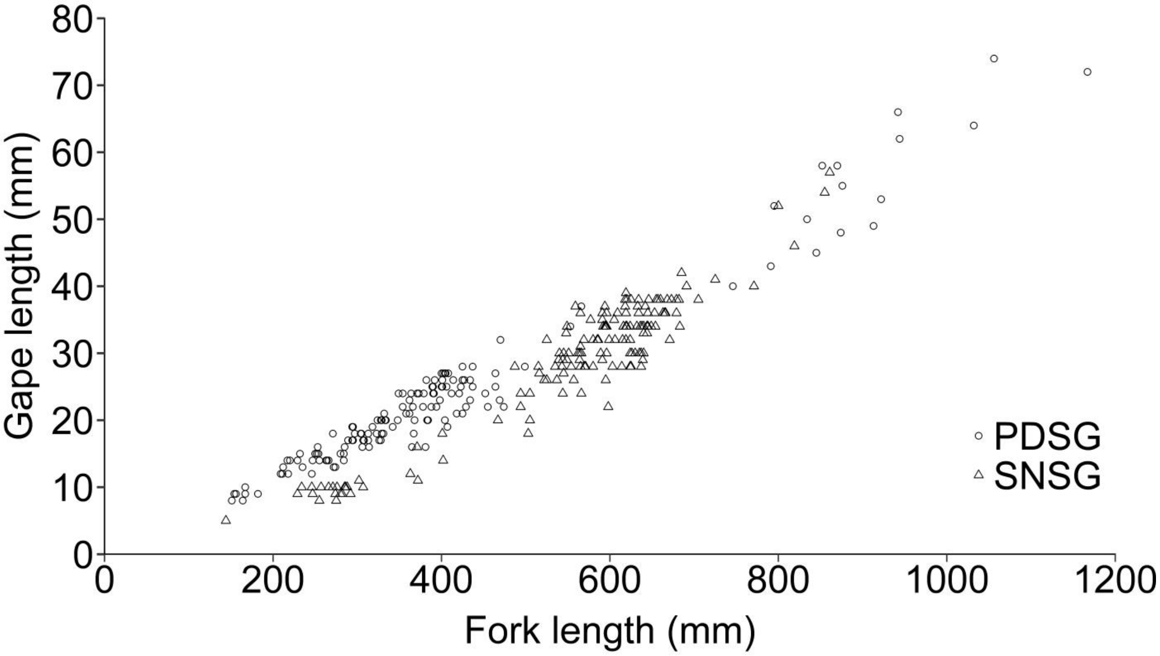
Gape length (mm)
0
10
20
30
40
50
60
70
80
Fork length (mm)
0
200
400
600
800
1000
1200
○ PDSG
△ SNSG

Figure 2.2.

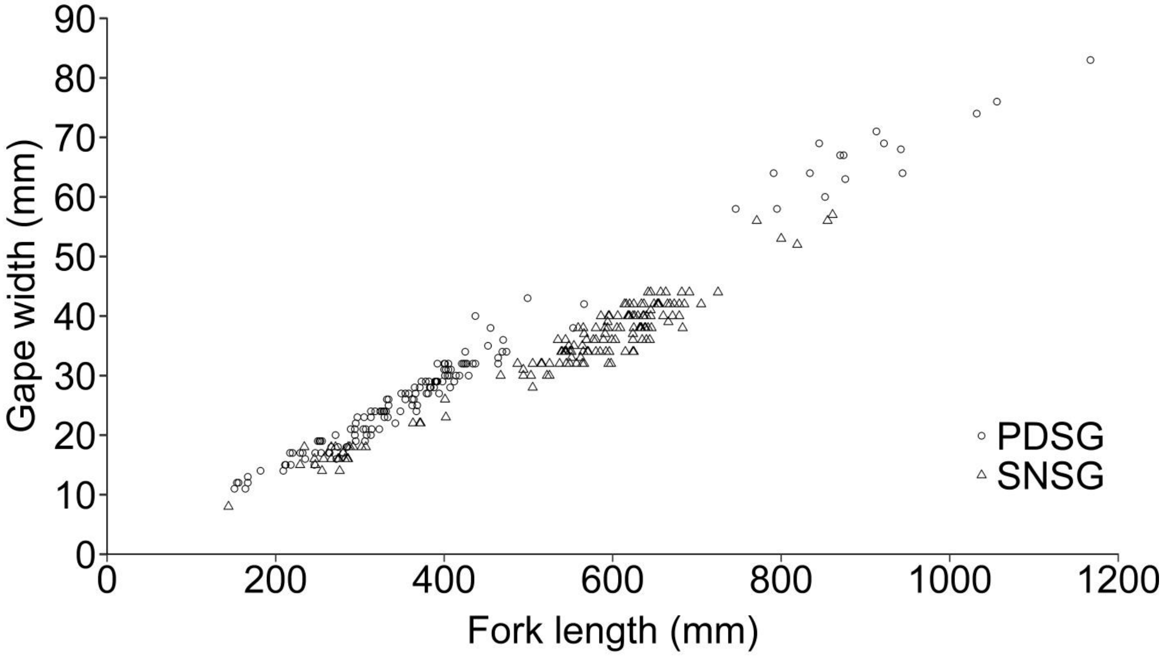
Gape width (mm)
0
10
20
30
40
50
60
70
80
90
Fork length (mm)
0
200
400
600
800
1000
1200
○ PDSG
△ SNSG

Figure 2.3.

CHAPTER THREE

QUANTITATIVE FOOD-WEB LINKAGES AMONG PRIMARY, SECONDARY, AND TERTIARY CONSUMERS IN THE UPPER MISSOURI RIVER AND LOWER YELLOWSTONE RIVER

Contributions of Authors and Co-Authors

Manuscript in Chapter 3

Author: Adeline J. Dutton

Contributions: Conceived and implemented the study design, collected and analyzed data, and authored the manuscript.

Co-Author: Christopher S. Guy

Contributions: Obtained funding, conceived the study design, discussed the implications of the results, and co-authored the manuscript.

Co-Author: Eric A. Scholl

Contributions: Collected and analyzed data

Manuscript Information Page

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ABSTRACT

A conservation propagation program started in the late 1990s for the endangered Pallid Sturgeon *Scaphirhynchus albus* because the species was not recruiting in the Missouri River. The conservation propagation program has been successful and several studies have suggested that the survival of stocked Pallid Sturgeon in the upper Missouri River is relatively high. Stocking of hatchery-origin Pallid Sturgeon may have created an uncharacteristic population structure for a long-lived species, which could lead to intraspecific and interspecific competition between juvenile Pallid Sturgeon (< 300 mm fork length), Shovelnose Sturgeon, and other fish species in the Missouri River and Yellowstone River. Thus, the purpose of this study was to quantitatively assess diets of many secondary and tertiary consumers, by gut analysis, to describe the food web of the upper Missouri River and lower Yellowstone River. Furthermore, the main focal interest of the food-web study was to better understand the effects of stocking 251,838 hatchery-origin Pallid Sturgeon on the upper Missouri River and lower Yellowstone food webs. Chironomidae were the most abundant primary consumer in the upper Missouri River (61.0% of total primary consumer abundance) and lower Yellowstone River (42.7% of total primary consumer abundance). Hydropsychidae was not abundant in either river system, but was frequently consumed by Goldeye (O_i = 75.8%), Channel Catfish (O_i = 75.0%), Shovelnose Sturgeon (O_i = 73.9%), and Stonecat (O_i = 63.3%) in the Missouri River and Shovelnose Sturgeon (O_i = 67.5%) in the Yellowstone River. Emerald Shiner were the most abundant secondary consumer in both rivers. In the Missouri River, Emerald Shiner were the most frequently consumed secondary consumer by Pallid Sturgeon. Other secondary consumers consumed by Pallid Sturgeon in the Missouri River included Channel Catfish, Shovelnose Sturgeon, and either Sicklefin Chub or Sturgeon Chub. Sauger, a tertiary consumer, consumed Channel Catfish, Emerald Shiner, Freshwater Drum, *Hybognathus* spp., Stonecat, and Sicklefin Chub or Sturgeon Chub in the Missouri River. In the Yellowstone River, Pallid Sturgeon consumed Channel Catfish, *Scaphirhynchus* spp., and Stonecat. The food-web models presented here provide the foundation into key linkages among predators and prey for better understanding the effects of stocking Pallid Sturgeon in the upper Missouri River and lower Yellowstone River.

Introduction

Eighty-five percent of species in the family Acipenseridae are at risk of extinction, making the family of sturgeon the most threatened group of animals on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2010). Numerous anthropogenic factors such as water pollution, habitat degradation, and overfishing have led to the imperilment of sturgeon throughout the world (Williams et al. 1987; Birnstein 1993; Boreman 1997; Pikitch et al. 2005). Given the difficulty in reversing the factors that negatively influence sturgeon populations, conservation propagation is the primary management tool to maintain many sturgeon populations (Doroshov 1985; Secor et al. 2002; Chebanov and Billard 2001; George et al. 2009). Sturgeon propagation began in the mid-1800s in Russia with Sterlet *Acipenser ruthenus* (Milshtein 1969) and methods were developed for Pallid Sturgeon *Scaphirhynchus albus* in the mid-1990s (United States Fish and Wildlife Service [USFWS] 1993).

In North America, Pallid Sturgeon are one of four endangered species in the Acipenseridae family. Similar to other sturgeon species, numerous anthropogenic factors such as habitat fragmentation, illegal harvest, and changes in water quality and quantity led to the range-wide decline of Pallid Sturgeon and subsequent listing as an endangered species by the USFWS in 1990 (USFWS 1990). In parallel with these factors, Pallid Sturgeon have numerous reproductive characteristics that can compound the effects for successful recruitment in altered environments (Guy et al. 2015), such as late age-atmaturity, spawning periodicity of two years for females, and long drift distances (245-530 km depending on water velocity) for larvae (Braaten et al. 2008, 2012).

To prevent extirpation of Pallid Sturgeon, a conservation propagation program was created by the USFWS in 1992 (USFWS 2014). The conservation propagation program was one of five key steps in the strategy plan for recovery of Pallid Sturgeon (USFWS 2014). Supplemental stocking to artificially augment the Pallid Sturgeon population began in 1998 in Recovery Priority Management Area 2 (RPMA 2), which encompasses the Missouri River from Fort Peck Dam (MT) downstream to the headwaters of Lake Sakakawea (ND) and the Yellowstone River between the mouth of the Tongue River and the confluence with the Missouri River (near Buford, ND). Since 1998, 251,838 hatchery-origin juvenile Pallid Sturgeon have been stocked in the upper basin of the Missouri River.

The reintroduction of threatened and endangered species to enhance population abundance is often unsuccessful because the underlying mechanisms for reduced survival are not addressed (Beck et al. 1994; Snyder et al. 1996). Interestingly, this was not the case for Pallid Sturgeon stocked in RPMA 2. Estimates of survival rates were high for hatchery-origin Pallid Sturgeon in RPMA 2; for example, interval survival rates for fingerlings released in the Missouri River, three years after release was 0.87 (SE [0.30]; Rotella 2015). The large number of fish estimated to remain alive years after release suggest that there might be an artificially large population of Pallid Sturgeon. For example, Pallid Sturgeon were characterized as a large, slow-growing, late-maturing species that were believed to be in low abundance (Jordan et al. 2016).

In addition to the possibility that stocking might have created an uncharacteristic population structure for a long-lived species, the increase in Pallid Sturgeon population abundance could lead to intraspecific and interspecific competition between juvenile Pallid Sturgeon (< 300 mm fork length; see Chapter 2) and Shovelnose Sturgeon. Furthermore, competition could occur between Sauger *Sander canadensis*, which is another native benthic apex predator. Assessing food limitation and potential competition in a large-river ecosystem requires knowledge of the food web; however, linking food-web research back to fisheries management is a relatively new concept and is often coined ecosystem-based fisheries management (Pikitch et al. 2004). Food-web research in freshwater ecosystems began gaining attention in the early 1990s, but still today less than three percent of all publications in 12 key journals with high impact factors (e.g., Science, Nature, Trends in Ecology and Evolution) are on traditional food webs (i.e., not mutualistic or host-parasitoid webs; Ings et al. 2009). The research presented here bridges the gap between food-webs and fisheries management by describing linkages between primary, secondary, and tertiary consumers in the Missouri and Yellowstone rivers and provides baseline information on food availability.

Study Site

The Missouri River is the longest named river in North America (Galat et al. 2005a). It is formed at the confluence of the Gallatin, Madison, and Jefferson rivers near Three Forks, MT and flows 3,768 km across the Great Plains to the confluence with the Mississippi River near St. Louis, Missouri (Galat et al. 2005a). Historically, the Missouri

River was characterized by braided channels, sandbars, and unstable banks (Galat et al. 2005a). However, numerous dams (e.g., Fort Peck, Garrison, Oahe) have changed the natural flow regime and habitat of the Missouri River.

The Mississippi River basin, which includes the Missouri River, supports the most diverse freshwater fish assemblage in North America (Robison 1986). One hundred thirty-six fish species reside in the main channel of the Missouri River with 76% in seven families with Cyprinidae, Catostomidae, Centrarchidae, and Salmonidae representing the top four specious (Galat et al. 2005a). In addition to these families, the Missouri River also supports numerous archaic families including Acipenseridae, Polyodontidae, Hiodontidae, and Lepisosteidae (Galat et al. 2005a).

The Yellowstone River is the longest free-flowing river in the conterminous United States and one of the largest tributaries by discharge to the Missouri River (Galat et al. 2005b). The Yellowstone River originates in Yellowstone National Park and flows northeast to the confluence with the Missouri River near Buford, ND. Downriver of Billings, MT the Yellowstone River has increased water temperatures and turbidity. The Yellowstone River has 56 fish species varying from cold-water specialists to large river obligate species. The lower Yellowstone River, which includes the reach downstream of the confluence with the Bighorn River in Bighorn, MT, supports a diverse fish assemblage with 49 species representing 15 families (Galat et al. 2005b). Cyprinidae, Catostomidae, and Ictaluridae are the most common families in the lower Yellowstone River. Similar to the Missouri River, the Yellowstone River also supports numerous archaic families including Acipenseridae, Polyodontidae, and Hiodontidae.

The study reach for the Missouri River was between Fort Peck Dam (river kilometer [rkm] 1771.5) and Lake Sakakawea (rkm 1568.0). The reach for the Yellowstone River was between Intake Diversion Dam (rkm 113.0) and the confluence with the Missouri River (rkm 0.0). The reach on the Missouri River was further delineated into four segments (i.e., 1-4; Figure 3.1). Annual discharge near Wolf Point, MT (segment 2 and 3) typically peaked in June or July between 354 to 566 cubic meters per second (cms). Segment 1 began at Fort Peck Dam (rkm 1774.5) and continued downstream to the confluence of the Milk River with the Missouri River (rkm 1760.0). This segment was short and characterized by hypolimentic releases from Fort Peck Dam (Hunziker et al. 2015). Coldwater fish species were most common in this segment and many were not native to the Missouri River. Segment 2 extended from the confluence of the Missouri and Milk rivers (rkm 1760.0) downstream to Wolf Point, MT (rkm 1701.0; Figure 3.1). The segment was characterized as transitional, where turbidity was low and water temperature was influenced by the hypolimentic release from Fort Peck Dam, but at the end of the segment turbidity and water temperature had increased and were more representative of pre-dam conditions (Hunziker et al. 2015). The substrate in segment 2 was predominantly cobble and gravel at the upstream extent, but transitions to more sand as the distance from Fort Peck Dam increases. (Haddix et al. 2015). Segment 3 included the Missouri River from Wolf Point, MT (rkm 1701.0) downstream to the confluence with the Yellowstone River near Buford, ND (rkm 1582.0; Figure 3.1). The segment was more similar to the natural characteristics of the Missouri River with varied water temperatures, high turbidity, and sand dominated substrate (Haddix et al. 2015). Unlike the upper two reaches, segment 3 had sandbar and island formations (Haddix et al. 2015). Segment 4 was from the confluence with the Yellowstone River (rkm 1592.0) downstream to the headwaters of Lake Sakakawea, ND, (rkm 1568.0). This segment was the most similar to the natural characteristics of the Missouri River (Bramblett and White 2001). Water temperature was variable and had characteristics of a warm-water river with high turbidity and primarily sand substrate with diverse habitat features such as sand bars, islands, deep outside bends, and bluff pools (Bramblett and White 2001).

The Yellowstone River was delineated into two segments. Both segments were characterized by warm, turbid water. Discharge near Sidney, MT (segment 2) typically peaked in June or July between 1,982 and 2,548 cms. Segment 1 was from Intake Diversion Dam (rkm 113.0) to rkm 40.0 (Figure 3.1). Segment 1 had diverse habitat features with islands, bars, backwaters, and chutes (Kellerhals et al. 1976, cited by Bramblett and White 2001). The substrate was primarily cobble and gravel throughout the sinuous channel (Kellerhals et al. 1976, cited by Bramblett and White 2001). Segment 2 was from rkm 40.0 to the confluence with the Missouri River (rkm 0.0; Figure 3.1). This segment was dominated by sand substrate and numerous habitat features including islands, sand bars, and off channel habitat (Bramblett and White 2001).

Methods

Selection Criteria

The Missouri River, in Montana, has 64 fish species (Galat et al. 2005a). However, many species are in low abundance (e.g., White Crappie *Pomoxis annularis*, Northern Pike *Esox lucius*, Burbot *Lota lota*) or only found immediately below Fort Peck Dam because of the hypolimnetic release (e.g., Rainbow Trout *Oncorhynchus mykiss*). Because of monetary and logistic constraints, I had to truncate the number of fish species included in the food web. Fish species incorporated in the food-web analysis were selected based on four criteria: 1) high in abundance (CPUE > 5.0 fish/gear units), 2) potential prey for Pallid Sturgeon, 3) potential predator on juvenile Pallid Sturgeon, or 4) potential competitor with Pallid Sturgeon. In the Missouri River, the following species were targeted for the food web: Channel Catfish *Ictalurus punctatus*, Emerald Shiner *Notropis atherinoides*, Flathead Chub *Platygobio gracilis*, Freshwater Drum *Aplodinotus grunniens*, Goldeye *Hiodon alosoides*, Pallid Sturgeon, Sauger, Shovelnose Sturgeon, Sicklefin Chub *Macrhybopsis meeki*, Stonecat *Noturus flavus*, and Sturgeon Chub *Macrhybopsis gelida*. These species were targeted in the Missouri River based on the selection criteria and supported by data from peer-reviewed scientific literature, taxonomic keys containing life-history information, and grey-literature reports (e.g., Pflieger 1997; Gerrity et al. 2006; Hoover et al. 2007; Wanner et al. 2007; Hunziker et al. 2017a, 2017b, Wilson et al. 2017). The same species were also targeted in the Yellowstone River with the exception of Freshwater Drum, Sauger, Sicklefin Chub, Stonecat, and Sturgeon Chub. In addition, *Hybognathus* spp. (including Brassy Minnow, Plains Minnow, and Western Silvery Minnow) were targeted in the Yellowstone River, but not the Missouri River. Similar to the Missouri River, these species were targeted based on the selection criteria and supported by data from peer-reviewed scientific literature, taxonomic keys containing life-history information, and grey-literature reports (e.g., Pflieger 1997; Gerrity et al. 2006; Hoover et al. 2007; Wanner et al. 2007; Duncan et al. 2012).

Field

Fish. Pallid Sturgeon and Shovelnose Sturgeon were sampled in the Missouri River and Yellowstone River in June, September, and October 2013 and May through August 2014. In addition, Pallid Sturgeon were sampled in the Missouri River from May through October 2016. All other fish species were collected in the summer and autumn months of 2013 through 2015. Diet samples were collected by Montana State University (MSU), Montana Fish, Wildlife and Parks (FWP), United States Geological Survey (USGS), and the USFWS. Trammel netting, otter trawling, trotlining, angling, beam trawling, seining, and backpack electrofishing were used to sample fish.

Trammel netting targeted large-bodied benthic fish species including Channel Catfish Goldeye, Pallid Sturgeon, Sauger, and Shovelnose Sturgeon. All trammel nets were 38.1-m long, 1.8-m deep, with a 22.7-kg lead line and a 12.7-mm foam core float line (Wilson et al. 2015). In addition, all inner mesh was #139 multifilament twine and all outer mesh was #9 multifilament twine (Wilson et al. 2015). Three mesh sizes were deployed throughout the study. The most common mesh size had an outside bar mesh of 203.2 mm and an inside bar mesh of 25.4 mm. Two larger mesh sizes were used in broodstock collection; one had an outside bar mesh of 254 mm and an inside bar mesh of 152.4 mm, and the other had an outside bar mesh of 203.2 mm and an inside bar mesh of 101.6 mm. All trammel nets were deployed off the bow of the boat and drifted perpendicular to flow for a minimum of 75 m and a maximum of 300 m (Wilson et al. 2015). Otter trawling was used to target small-bodied benthic species including Flathead Chub, Freshwater Drum, *Hybognathus* spp., Sicklefin Chub, Stonecat, and Sturgeon Chub. The otter trawl was 7.6-m long, 4.9-m wide, and 0.9-m tall. The inner mesh of the trawl was 6.35-mm bar and the outer mesh was 38.1-mm bar. The inner mesh was constructed of #18 polyethylene twine and the outer was of #9 polyethylene twine (Wilson et al. 2015). In order to keep the net open, a 50.8-mm sleeve was sewn along the top section to install a hoop. The trawl doors were 381-mm tall, 19.1-mm thick, 762-mm long, with 12.7-mm thick steel runners (Wilson et al. 2015). A 7.9-m long tickler chain was attached to the bottom of the trawl to agitate the substrate. The otter trawl was connected to the bow of the boat by two 30.5-m long, 19.1-mm thick Tenex ropes. The otter trawl was fished off the bow of the boat downstream at a rate slightly faster than river velocity (Wilson et al. 2015). The otter trawl was fished for a minimum of 75 m and a maximum of 200 m. Trotlines targeted Pallid Sturgeon and accounted for few diet samples in the study. All trotlines were set by FWP and USFWS crews overnight for a maximum of 18 h. Trotlines had a main line length of 32 m with 10 hooks spaced every 1.5 m and baited with night crawlers *Lumbricus terrestris*. Each hook was tied to a dropper that was 30.5 - 60.9-cm long and attached to the main line using hook snaps (Wilson et al. 2015). Beam trawling was conducted by USFWS and FWP personnel. Beam trawling targeted small bodied benthic species including Freshwater Drum, Sicklefin Chub, and Sturgeon Chub. Beam trawls were 2-m wide, 0.5-m tall, and 5.5-m long with an inner mesh of 0.32 cm and an outer mesh of 3.81 cm (Braaten et al. 2007).

The cod end opening was 16.5 cm with the bottom line a 0.95-cm chain. The beam trawl was fished off the bow of the boat downstream at rate slightly faster than the current (Braaten et al. 2007). Beam trawls were fished for a minimum of 75 m and a maximum of 200 m. Seining was conducted in backwater habitat areas, shallow riffles, and point bars in the main channel to target small cyprinids (e.g., Emerald Shiners and Flathead Chub). The seine was 6.1-m long and 1.2-m deep with 6.35-mm square. Backpack electrofishing was conducted in near-shore habitats with woody debris and was used to target Stonecat. A Halltech backpack electrofisher was operated from shallow (< 1 m depth) water (Halltech Environmental Inc., Guelph, ON, Canada). One Pallid Sturgeon diet was from a fish captured by an angler in the Missouri River.

All *Scaphirhynchus* spp. collected were measured to fork length (mm) and weighed (g). Pallid Sturgeon were scanned for passive integrated transponder tags (PIT), and checked for elastomers, radio tags, and missing scutes. *Scaphirhynchus* spp. collected by MSU in 2013 and 2014 were gastric lavaged using a modified 12-volt bilge pump. A hard-plastic tube was inserted to the beginning of the stomach while fish were held dorsal side down. Stomach contents were washed into a 250-µm sieve and transferred into Whirl Pak bags preserved in 10% buffered formalin. All other *Scaphirhynchus* spp. collected were gastric lavaged using a method similar to that described by Foster (1977) and tested by Wanner (2006). A pressurized weed sprayer provided a reservoir for water throughout the process. A pistol-grip garden sprayer was fitted with a flexible 5.5-mm outside diameter polyethylene tube to supply water throughout the process. *Scaphirhynchus* spp. were held dorsal side down at approximately a 45° angle (Wanner 2006). The tube was inserted through the esophagus to the first bend in the stomach (Wanner 2006). Once the tube was in place, water was slowly pulsated through the esophagus and stomach. At the same time, the stomach area was lightly massaged to ease regurgitation (Wanner 2006). Stomach contents were regurgitated into a large tray. The process was repeated until clean, clear water was regurgitated by the fish. All diet samples were transferred from the tray, through a 500-µm sieve, and into whirl-pak bags with 95% ethanol to be further processed in the laboratory.

Total length (mm) was measured on all other fish species. Large-bodied fishes (Channel Catfish, Goldeye, and Sauger) were gastric lavaged. Diets collected from fish prior to 2016 were lavaged by placing a plastic tube into the esophagus to the beginning of the stomach (Quist et al. 2002). A modified 12 V bilge pump flushed water into the stomach and initiated regurgitation of stomach contents into a 250-µm sieve (Quist et al. 2002). All stomach contents were transferred to a Whirl Pak bag and preserved in either 95% ethanol or 10% buffered formalin. In 2016, only Sauger were gastric lavaged following methods similar to those described by Foster (1977). A pistol-grip garden sprayer was fitted with a flexible 5.5-mm outside diameter polyethylene tube to supply water throughout the process. Sauger were held dorsal side down at approximately a 45° angle. The tube was inserted to the beginning of the stomach. Once the tube was in place, water was slowly pulsated through the esophagus and stomach. Stomach contents were regurgitated into a large tray. The process was repeated until clean, clear water was regurgitated by the fish. All diet items were transferred through a 250 µm sieve and preserved in 95% ethanol. Fishes too small to lavage were euthanized and preserved in either 95% ethanol or 10% buffered formalin (these included Emerald Shiner, Flathead Chub, *Hybognathus* spp., Sicklefin Chub, and Sturgeon Chub and small individuals of Channel Catfish, Freshwater Drum, Goldeye, Sauger, Shovelnose Sturgeon, and Stonecat).

Benthic macroinvertebrates. Benthic habitats were quantified in 2013 and 2014 using side-scan sonar. Side-scan sonar is an active remote sensing system that produces two-dimensional imagery of the riverbed by transmitting and receiving high frequency (455-800 kHz) sound waves that are reflected from underwater objects (Kaeser and Litts 2010). Continuous large-scale swaths of sound waves produce “echograms” containing spatially explicit information of riverbed texture (Buscombe et al. 2015). These textures are then geo-referenced and delineated as different habitat types based on an *a priori* classification scheme and displayed on maps with dimensional accuracy (Kaeser and Litts 2010).

Benthic habitat data were collected using side-scan sonar from August to November 2013 from all segments in the Missouri and Yellowstone rivers. Data were analyzed with raster layers and then exported to ArcGIS to create a substrate classification scheme. After classifying substrate, benthic habitat locations were ground truthed for accuracy. For further details on the transformation from field to classification of habitat type (E. Scholl, unpublished).

Macroinvertebrates were sampled five times between October 2014 and October 2015 to estimate community abundance on major habitat types in the Missouri and Yellowstone rivers. At each sampling event, a stratified sampling design was used based on aerial proportions of major benthic habitats to allocate between 25-30 samples per reach. Different habitats were sampled with varying gear types. Sand habitat was sampled with a Ponar dredge sampler (0.052 m^2) attached to a sounding reel on the boat. Cobble and gravel substrate was sampled with a Hess sampler (0.086 m^2). Woody debris was sampled by placing a 250-μm mesh bag and scrubbing off all macroinvertebrates. Large rocks were collected into bucks and scrubbed and depositional backwater habitats were sampled with a stovepipe core (0.031 m^2). For further details on macroinvertebrate collection see (Scholl, unpublished).

Lab

Pallid Sturgeon and Shovelnose Sturgeon. All macroinvertebrates were identified to the lowest taxonomic level, if possible to genus (Merritt et al. 2008). The first 30 individuals of each genus, per stomach sample, were measured to the nearest millimeter (not including cerci or antennae; Cross et al. 2011). Length data was converted to weight using a length-weight regression and then converted into ash-free-dry-mass (AFDM) to estimate biomass (Burgherr and Meyer 1997; Benke et al. 1999). *Scaphirhynchus* spp. diets that consisted primarily of one prey item (e.g., Chironomidae) were subsampled. Subsampling was conducted on samples that contained hundreds of individual macroinvertebrates of a single genus. Samples were subsampled (1/2-1/32) using a Folsom plankton wheel to equally divide the sample each time without bias (Parker and Huryn 2006; Bertrand et al. 2009).

All fish in the diet samples were identified to species, if possible. All fish including those unidentifiable were measured to the nearest millimeter for total, standard, and fork length when applicable. All fish and fish parts were dried at 60° C for a minimum of 36 h and then burned in a muffle furnace at 500° C for approximately 6 h to obtain AFDM (Edwards and Huryn 1995, Nakano et al. 1999).

Non-*Scaphirhynchus* spp. fish. All benthic macroinvertebrates were identified to family (Merritt et al. 2008) and recorded as presence data. All terrestrial insects were identified to order (Merritt et al. 2008) and recorded as presence data. All fish in the diet samples were identified to species, if possible, and recorded as presence data.

Benthic Macroinvertebrates. All macroinvertebrate samples were rinsed through 1-mm and 250-µm sieves stacked to separate into coarse (> 1 mm) and fine (< 1 mm > 250 µm) size classes. Fine samples with a large number of invertebrates (> 200) were subsampled using a Folsom plankton wheel. Macroinvertebrates were identified to the lowest possible taxonomic level, in most cases genus, using Merritt et al. (2008) and Smith (2001). All macroinvertebrates were measured to the nearest millimeter (excluding tail appendages and antennae). The first 30 individuals in each taxon were measured, individuals counted but not measured were assumed to have the same size distribution (Cross et al. 2013).

Food-web structure

Frequency of occurrence was calculated for all diet items in fish stomachs (Chipps and Garvey 2007). Food webs were constructed from abundance of primary consumers, catch per unit effort (CPUE) for secondary and tertiary consumers, and frequency of occurrence of prey in diets to weight linkages among primary, secondary, and tertiary consumers. Primary consumer abundance was binned into quantiles to represent availability. Each quantile was represented by a different line type, estimates of primary consumer abundance by family are in Appendix (Table A.1). The 10.0% - 24.9% (total primary consumer abundance) quantile was represented by a grey dotted line, 25.0% - 49.9% thin dark grey line, 50.0% - 74.9% medium weight black line, and > 74.9% thick black line. Catch per unit effort of fishes was obtained for the Missouri River from the Pallid Sturgeon Population Assessment Program (Hunziker et al. 2017a; 2017b; Wilson et al. 2017) and for the Yellowstone River from Duncan et al. (2012). In each river, CPUE was averaged among segments for the most efficient gear type for the species (e.g., Pallid Sturgeon sampled using trammel nets had the highest CPUE). Catch per unit effort of secondary consumers was delineated into three categories: low (0 - 0.99), medium (1.0 - 4.99), and high (≥ 5.0). Each category was represented by a different line type in the food web. If CPUE data were not available, an ellipse was used to delineate the missing information in the food web. Estimates of fish species CPUE is in Appendix (Table A.2; A.3). Linkages among primary, secondary, and tertiary consumers were categorized by four quantiles from 0-100. The number of macroinvertebrate families included in the food-web model was truncated to improve readability and comprehension. A linkage in the food web was included in the food web if the linkage between a primary consumer and secondary consumer was present in ≥ 10% of all diets sampled from one species. The first quantile (10% - 24.9% frequency of occurrence of all diets sampled from one fish species included the prey item) was represented by a dotted grey line, 25.0% - 49.9% (frequency of occurrence) solid thin grey line, 50.0% - 74.9% (frequency of occurrence) solid black line, and > 74.9% (frequency of occurrence) thick black line. All linkages between secondary and tertiary consumers were represented in the food web and all linkages were represented in the direction from prey to predator. Food webs are visual representations of the complexity, connectivity, and broad relationships among trophic levels in the Missouri River and Yellowstone River. Due to the complexity of the food webs, it can be difficult to follow individual lines from prey to predator; however, data used to construct the food web are presented in tabular format.

Results

Missouri River

In the Missouri River, diets were sampled from 11 fish species: Channel Catfish, Emerald Shiner, Flathead Chub, Freshwater Drum, Goldeye, Pallid Sturgeon, Sauger, Shovelnose Sturgeon, Sicklefin Chub, Stonecat, and Sturgeon Chub (Table 3.1). Fish sampling was evenly targeted among segments 2, 3, and 4; however, the majority of fish were sampled in segment 4 and few fish were sampled in segment 1 (Table 3.1).

Thirty-four benthic macroinvertebrate families, eight additional aquatic taxa, 10 terrestrial orders, and two additional terrestrial classes were consumed by the secondary and tertiary consumers in the Missouri River (Appendix Table A.4; A.5). Chironomidae was the most abundant benthic macroinvertebrate sampled in the Missouri River accounting for approximately 61% of all benthic macroinvertebrate abundance (Figure 3.2). Correspondingly, Chironomidae was frequently consumed by Freshwater Drum ([frequency of occurrence] $O_i = 100\%$), Shovelnose Sturgeon ($O_i = 100\%$), Sturgeon Chub ($O_i = 76.5\%$), Pallid Sturgeon ($O_i = 73.0\%$), Flathead Chub ($O_i = 70.0\%$), Channel Catfish ($O_i = 52.3\%$), and Goldeye ($O_i = 51.5\%$; Figure 3.2; Table 3.3). Hydropsychidae was much lower in abundance than Chironomidae accounting for only 2.6% of the total benthic macroinvertebrate abundance (Figure 3.2; Table 3.3). However, Hydropsychidae was frequently consumed by Goldeye ($O_i = 75.8\%$), Channel Catfish ($O_i = 75.0\%$), Shovelnose Sturgeon ($O_i = 73.9\%$), and Stonecat ($O_i = 63.3\%$; Figure 3.2). Terrestrial Coleoptera were the most frequently consumed diet item by Sicklefin Chub ($O_i = 78.9\%$) and Emerald Shiner ($O_i = 70.0\%$; Figure 3.2; Table 3.3). Frequency of occurrence was also ≥ 10 % for Araneae, Diptera, Hymenoptera, Orthoptera, Rodents, and Thysanoptera. Leptophlebiidae was rare in benthic macroinvertebrate samples; however, they were consumed by eight of the species and frequently (e.g., [$O_i > 50.0\%$]) by Channel Catfish, Pallid Sturgeon, and Stonecat (Figure 3.2; Table 3.3). Similarly, Ceratopogonidae were rare in benthic macroinvertebrate samples; however, they were frequently consumed by Pallid Sturgeon (at the secondary consumer level, which is not represented in the cumulative table value) and Shovelnose Sturgeon ($O_i = 60.9\%$). Simuliidae were only frequently consumed by Shovelnose Sturgeon (O_i = 54.3%), but were also consumed at a lesser frequency by Channel Catfish, Emerald Shiner, Goldeye, Pallid Sturgeon, Sicklefin Chub, and Stonecat (Figure 3.2; Table 3.3). Oligochaeta were relatively common in the benthic macroinvertebrate samples accounting for 28.3% of the total benthic macroinvertebrate abundance; however, they were not consumed by any fishes sampled in the Missouri River (Figure 3.2).

Ten different Ephemeroptera families were consumed by at least two fish species in the Missouri River (number of fish species in parentheses): Ametropidae (2), Baetidae (7), Caenidae (3), Ephemerellidae (6), Heptageniidae (7), Isonychiidae (5), Leptohyphidae (4), Leptophlebiidae (8), Oligoneuriidae (2), and Polymitarcyidae (4). The consumption of Ephemeroptera families was high, but abundance for the ten families accounted for less than 13% of the total abundance of all benthic macroinvertebrates.

Emerald Shiner were the most abundant fish species in the Missouri River of the fishes sampled, followed by Shovelnose Sturgeon and Channel Catfish (Hunkizer et al. 2017a, 2017b; Wilson et al. 2017). Sicklefin Chub and Sturgeon Chub were the least common species of the fish species sampled. Channel Catfish, Flathead Chub, Goldeye, Pallid Sturgeon, Shovelnose Sturgeon, and Stonecat fed on at least 10 taxa at a frequency of occurrence ≥ 10%. Emerald Shiner, Freshwater Drum, Sauger, Sicklefin Chub, and Sturgeon Chub fed on nine or fewer taxa at a frequency of occurrence ≥ 10%. Pallid Sturgeon (at the tertiary level) and Sauger consumed a variety of secondary and primary consumers (Figure 3.2). Pallid Sturgeon consumed Channel Catfish, Emerald Shiner, Shovelnose Sturgeon, and either Sicklefin Chub or Sturgeon Chub (Sicklefin Chub and

Sturgeon Chub have the same pharyngeal arch count [14, 41]). Pharyngeal arches with the count of 24, 42 were also found in stomach contents, but this count is common among many Cyprinidae species. As with Pallid Sturgeon at the secondary consumer level, Chironomidae were the most common benthic macroinvertebrate in Pallid Sturgeon diets. However, Chironomidae may have been in the diets of secondary consumers consumed by Pallid Sturgeon. Sauger consumed Channel Catfish, Emerald Shiner, Freshwater Drum, *Hybognathus* spp., Stonecat, and Sicklefin Chub or Sturgeon Chub (Figure 3.2; Table 3.3). In addition to the identifiable fish species, Pallid Sturgeon and Sauger diets contained many unidentifiable fish parts.

Yellowstone River

Channel Catfish, Emerald Shiner, Flathead Chub, Goldeye, *Hybognathus* spp., Pallid Sturgeon, and Shovelnose Sturgeon were sampled for diets in the Yellowstone River. Most fishes were sampled in segment 2 of the Yellowstone River (Table 3.2).

Twenty-six benthic macroinvertebrate families, six additional aquatic taxa, six terrestrial orders, and one additional terrestrial taxon were consumed by secondary and tertiary consumers in the Yellowstone River. Chironomidae was the most abundant benthic macroinvertebrate in the Yellowstone River representing 42.7% of the benthic macroinvertebrate abundance and it was also the most frequently consumed macroinvertebrate by Shovelnose Sturgeon (O_i = 100%), Pallid Sturgeon (O_i = 76.2%), and Channel Catfish (O_i = 73.9%; Figure 3.3; Table 3.4). Hirudinea was relatively low in abundance, but was the most frequently consumed benthic macroinvertebrate by Emerald

Shiners (O_i = 51.6%; Figure 3.3; Table 3.4) — Emerald Shiners were the most abundant fish species in the lower Yellowstone River (Duncan et al. 2012). Pallid Sturgeon were the only tertiary consumer sampled in the Yellowstone River. Unlike piscivorous Pallid Sturgeon in the Missouri River, piscivorous Pallid Sturgeon in the Yellowstone River fed primarily on Stonecat but also consumed Channel Catfish and *Scaphirhynchus* spp. (Figure 3.3; Table 3.4).

Channel Catfish, Pallid Sturgeon, and Shovelnose Sturgeon fed on at least 10 diet items at a frequency of occurrence ≥ 10% — similar to observations in the Missouri River (Figure 3.3). Emerald Shiner, Flathead Chub, Goldeye, and *Hybognathus* spp. fed on nine or fewer diet items at a frequency of occurrence ≥ 10% (Figure 3.3).

River comparison

Food webs for the Missouri River and Yellowstone River illustrated the dynamic linkages among primary, secondary, and tertiary consumers. Chironomidae and Hydropsychidae were the most linked primary consumer in both food webs. Chironomidae was the most abundant benthic macroinvertebrate in both rivers (Appendix A.1). Simuliidae was connected to 63% of fish species sampled in the Missouri River and 83% of fish species sampled in the Yellowstone River. Similar to Hydropsychidae, Simuliidae was low in abundance in both rivers (Appendix A.1). The second most abundant benthic macroinvertebrate in the Missouri River, Oligochaeta, was not consumed by any fish species.

Channel Catfish, Emerald Shiner, Flathead Chub, Goldeye, Pallid Sturgeon, and Shovelnose Sturgeon were sampled in both rivers. Channel Catfish in the Missouri River frequently ($O_i \geq 50\%$) consumed three diet items Hydropsychidae, Leptophlebiidae, and Chironomidae; however, in the Yellowstone River Channel Catfish only frequently consumed Chironomidae (Tables 3.3 and 3.4). In the Missouri River, terrestrial inputs especially Coleoptera were consumed by Emerald Shiners, but Emerald Shiners in the Yellowstone River consumed more benthic macroinvertebrates (Table 3.3; 3.4). Regardless of the differences in diet items between rivers, Emerald Shiners consumed few diet items in the Missouri River and Yellowstone River. Goldeye had highly varying diets between the Missouri River and Yellowstone River. In the Missouri River, Goldeye fed on 32 prey taxa, whereas they fed on 13 prey items in the Yellowstone River. Pallid Sturgeon were the only tertiary consumer sampled in both food webs. Piscivorous Pallid Sturgeon in the Missouri River consumed Channel Catfish, Emerald Shiner, *Macrhybopsis* spp., and Shovelnose Sturgeon. In the Yellowstone River, piscivorous Pallid Sturgeon consumed Channel Catfish, *Scaphirhynchus* spp., and Stonecat.

Discussion

This was the first study to develop food webs for the Missouri River and Yellowstone River based on diet analyses of secondary and tertiary consumers. The linkages presented here among primary, secondary, and tertiary consumers in the upper Missouri River and lower Yellowstone River provide better insight into the complexity of species interactions in large-river ecosystems. Prior to this study, primary consumer abundance, diets of many fishes, and potential effects of stocking 251,838 hatchery-origin Pallid Sturgeon in Recovery Priority Management Area 2 (RPMA 2) were unknown.

A large diversity of aquatic and terrestrial primary consumers was consumed by secondary and tertiary consumers in the Missouri River and Yellowstone River. However, the diversity of benthic macroinvertebrate families consumed by secondary and tertiary consumers was higher in the Missouri River than the Yellowstone River. Despite the subtle differences between rivers, Chironomidae was the dominate family represented in the diets of most fishes. The high abundance of Chironomidae in large rivers has been documented in other systems. For example, larval Chironomidae contributed 46% of the total production of benthic macroinvertebrates at control sites and 85% of the total production of benthic macroinvertebrates at sewage exposed sites in the St. Lawrence River (deBruyn et al. 2003). In the Mississippi River, Chironomidae, Nematodes, and sand dwelling Oligochaetes were the primary organisms sampled in the main channel (Dettmers et al. 2001). Oligochaetes were also in relative high abundance in the Missouri River in this study but were not a prey source for the fishes used in this study. Most Oligochaetes feed in sediments (Govedich et al. 2010); potentially concealing them from many predators in the Missouri River.

Terrestrial invertebrates contributed to the diversity of prey in fish diets in the Missouri River and Yellowstone River. Similar to the pattern with benthic macroinvertebrates, there was a higher diversity of terrestrial inputs observed in the diets of fish from the Missouri River compared to the Yellowstone River. The river continuum concept described the aquatic-terrestrial linkage along a longitudinal gradient. The river continuum concept suggests that the linkage between aquatic and terrestrial systems weakens as stream size increases, especially in large, turbid warm water rivers (Vannote et al. 1980). However, the results of my study did not support such a pattern. The strength of the linkage between the terrestrial and aquatic systems is stronger in the larger Missouri River compared to the smaller Yellowstone River. Furthermore, large rivers, in unaltered systems, receive fine particulate organic matter from upstream reaches through the processing of organic debris (Vannote et al. 1980), but in regulated rivers dams trap fine particulate matter and highly alter river process. The Missouri River is highly regulated by dams, which undoubtedly alter natural river dynamics and food webs. Additionally, the altered flow and sediment regime in the Missouri River could reduce the nutrient cycling within the littoral zone compared to the Yellowstone River (Bowen et al. 2003).

Eighty-eight percent of secondary and tertiary consumers sampled in both rivers were linked to Chironomidae and Hydropsychidae. Linkages to Chironomidae were expected given the high abundance of Chironomidae in the benthic macroinvertebrate samples and diversity of habitats Chironomidae occupy (Hudson et al.1990; Pinder 1995; Ferrington Jr. 2008). However, the high number of linkages to Hydropsychidae was unexpected because Hydropsychidae are often associated with patches of solid (e.g., rock or wood) habitat (Hauer and Stanford 1982). Diverse habitat, including rock and wood, is often underrepresented in altered large river systems (Gore and Shields Jr. 1995).

Hydropsychidae frequently occur in the drift of smaller streams (Cloud and Stewart 1974; Bird and Hynes 1981; Bergey and Ward 1989). Thus, fishes in the upper Missouri River and lower Yellowstone River are either feeding in habitat other than sand, feeding on the drift, or both. Regardless of how fish are feeding on Hydropsychidae, many fishes are obtaining food resources that are produced in non-sand habitats — which is often represented by small patches in large, warmwater rivers.

Although some differences (e.g., terrestrial inputs) were noted between the food webs of the upper Missouri River and lower Yellowstone River, overall the food webs were similar. The similarity of the food webs may be related to sampling. Sampling effort was equal among segments 2, 3, and 4 in the Missouri River, but the majority of fish diet samples were from segment 4. Segment 4 was below the confluence with the Yellowstone River; therefore, the two habitats would be most similar to that in segment 2 of the Yellowstone River. Segment 2 of the Yellowstone River and segment 4 of the Missouri River have warm, turbid water and more complex habitat features (e.g., backwaters and islands). Similar to the Missouri River, sampling effort was equal in both segments of the Yellowstone River, but the majority of fish sampled were from segment 2. The similarities between the Missouri River and the Yellowstone River could be attributed to the influence of the Yellowstone River as a large tributary to the Missouri River. In smaller systems, physical, chemical, and biological attributes all peaked at or below tributary junctions in the mainstem (Kiffney et al. 2006). Therefore, the similarities between segment 2 of the Yellowstone River and segment 4 of the Missouri

River could be attributed to the Yellowstone River funneling detritus, nutrients, and macroinvertebrates from the Yellowstone River in to the Missouri River.

Diverse fish assemblages are common in many large river systems; thus, understanding the linkages among fishes within large-river ecosystems are challenging. Some challenges include one gear type is not efficient for sampling the diverse fish assemblage in large rivers and access to large rivers may be problematic (Lapointe et al. 2006). Thus, many large-river food web papers assess linkages using stable isotope signatures (Peterson et al. 1985; Jepsen and Winemiller 2002; Hoeinghaus et al. 2007; Pingram et al. 2014). Stable isotope signatures determine the trophic level of a diet item; however, it can be difficult to identify the diet item to species. Stable isotopes are useful for integrating diet information over a longer temporal scale than diet studies. Therefore, most large river food-web research methodology uses stable isotopic signatures. However, I was interested in explicitly identifying linkages among taxa for the Missouri River and Yellowstone River; therefore, diet analyses were needed. Here, some fish species (e.g., Emerald Shiner and Sicklefin Chub) were more closely linked to the terrestrial ecosystem than other fishes. There are few studies that demonstrate a clear link between terrestrial inputs and aquatic food webs in large, warm-water rivers (Cloe III and Garman 1996). The research regarding terrestrial inputs has focused on salmonid species (Rondorf et al. 1990; Wipfli 1997; Baxter et al. 2007; Pingram et al. 2014).

Most aquatic food-web studies have focused on the base of the food web at the primary producer or primary consumer level in small streams (Power 1990; Schoenly et al. 1991; Elser et al. 2000; Cheshire et al. 2005) or specific interactions between trophic levels that can lead to trophic cascades (Stein et al. 1995; Stibor et al. 2004). In addition to these food-web studies, the remaining body of literature on aquatic food webs has stable isotope methodology. Studies on the explicit linkages in aquatic ecosystems are lacking from the aquatic food-web literature. Therefore, this study provides a unique case history of food-web linkages in two large, warm-water rivers.

Historically, Pallid Sturgeon, an apex predator in both rivers, were low in abundance (Braaten et al. 2009). However, stocking of hatchery-origin Pallid Sturgeon has increased the abundance of one of the few apex predators in the system. Similar to other apex predators (e.g., Northern Pike *Esox Lucius*, Muskellunge *Esox masquinongy*), Pallid Sturgeon exhibit opportunistic or adaptive foraging strategies. Adaptive foraging strategies are critical to food web-dynamics (Abrams 1996; Kondoh 2003; Beckerman et al. 2006) and food-web stability (Kondoh 2003; Heckmann et al. 2012). For example, a complex system with biological parameters that change intermittently over long-time intervals would have a few strong adaptive links and many weaker adaptive links (Kondoh 2003). The linkages present in the Missouri River and Yellowstone River appear to follow a similar trend to that described above with Pallid Sturgeon as a strong adaptive forager in both river systems.

Intraspecific competition among Pallid Sturgeon could be possible because of the artificially high number of Pallid Sturgeon compared to historical estimates (Braaten et al. 2009). Describing patterns through the entire food web were challenging, but one pattern emerged similar to what was found in the Layman et al. (2005) study. The wide range of secondary consumer body sizes (e.g., Sicklefin Chub, Shovelnose Sturgeon) and opportunistic piscivores resulted in no relationship between body size and trophic position. This corroborates the complexity and structure of the Cinaruco River food web, where the link between primary consumer body size and trophic position was also weak (Layman et al. 2005).

This study provided descriptive data on the estimated abundance of many primary consumers and feeding habits of many secondary and tertiary consumers in the inter-reservoir reach of the upper Missouri River and lower Yellowstone River. The primary consumer assemblage in both rivers was dominated by Chironomidae which supports similar studies in other large river systems. The variability in different taxa consumed by fish species indicates that the food webs of each river system are complex and highly connected. Linkages among the terrestrial ecosystem and the aquatic ecosystem were higher in the Missouri River compared to the Yellowstone River. The food webs described here provide the necessary consumption data to develop bioenergetics models and direct future research needs to inform the guidelines for stocking hatchery-origin Pallid Sturgeon. Although my research addresses many data gaps in the conservation of Pallid Sturgeon in RPMA 2, I acknowledge the potential shortcomings of this work. I tried to sample evenly among segments of both river systems; however, the food webs primarily describe the linkages among fish assemblages present in segment 4 of the Missouri River and segment 2 of the Yellowstone River. In addition, sample sizes were not large enough to develop food webs at varying temporal scales. Instead, I aimed to focus on the large-scale linkages, and regardless of the shortcomings, this research provides invaluable insight to the linkages among primary, secondary, and tertiary consumers in the Missouri River and Yellowstone River.

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Tables

Table 3.1. Sample size by segment for species sampled in the Missouri River segments 1-4 from May through October 2013-2016.

	Segment				
Fish Species	1	2	3	4	Total
Channel Catfish	1	5	14	24	44
Emerald Shiner	3	6	8	13	30
Flathead Chub	0	6	5	19	30
Freshwater Drum	0	0	0	26	26
Goldeye	2	12	12	7	33
Pallid Sturgeon	0	27	24	108	159
Sauger	0	2	4	23	29
Shovelnose Sturgeon	0	15	15	14	44
Sicklefin Chub	0	0	0	19	19
Stonecat	0	0	5	25	30
Sturgeon Chub	0	0	0	17	17

Table 3.2. Sample size by segment for species sampled in the Yellowstone River segments 1 and 2 from May through October 2013-2015.

Fish Species	Segment 1	Segment 2	Total
Channel Catfish	2	21	23
Emerald Shiner	12	19	31
Flathead Chub	5	25	30
Goldeye	16	13	29
Hybognathus spp.	9	22	31
Pallid Sturgeon	4	17	21
Shovelnose Sturgeon	20	20	40

Table 3.3. Frequency of occurrence (O_i) by diet item for fishes sampled in Missouri River segments 1-4. Data were sorted first by common name of fish species and then within a fish species by highest frequency of occurrence. Sample size (n) represents the number of individual diets examined for each species.

Species	Diet Item	O_i
Channel Catfish	Hydropsychidae	75.0
Ictalurus punctatus	Leptophlebiidae	61.4
n=40	Chironomidae	52.3
	Baetidae	36.4
	Amorphous Detritus	29.5
	Corixidae	29.5
	Polymitarcyidae	27.3
	Unknown Terrestrial Insecta	22.7
	Arachnida	22.7
	Ceratopogonidae	20.5
	Unknown Fish Parts	18.2
	Perlodidae	15.9
	Terrestrial Coleoptera	15.9
	Simuliidae	15.9
	Muscidae	11.4
	Tipulidae	11.4
	Orthoptera	9.1
	Curculionidae	9.1
	Aquatic Coleoptera	9.1
	Terrestrial Diptera	6.8
	Brachycentridae	6.8
	Isonychiidae	6.8
	Terrestrial Hymenoptera	6.8
	Elmidae	6.8
	Pupating Diptera	6.8
	Carabidae	4.5
	Chironomidae Pupae	4.5
	Rodents	4.5
	Leptoceridae	4.5
	Ephemerellidae	4.5
	Glossosomatidae	4.5
	Heptageniidae	4.5
	Parasitic Worm	4.5

Species	Diet Item	O_i
	Leptohyphidae	2.3
	Insect Eggs	2.3
	Aquatic Plecoptera	2.3
	Zygoptera	2.3
	Terrestrial Insecta Pupae	2.3
	Birds	2.3
	Haliplidae	2.3
	Aquatic Diptera	2.3
	Dolichopodidae	2.3
	Tabanidae	2.3
	Coenagrionidae	2.3
	Caenidae	2.3
	Hirudinea	2.3
	Aquatic Ephemeroptera	2.3
Emerald Shiner *Notropis atherinoides* n=30	Terrestrial Coleoptera	70.0
	Terrestrial Diptera	30.0
	Chironomidae	20.0
	Hirudinea	13.3
	Insect Eggs	13.3
	Hydropsychidae	10.0
	Diptera Pupae	10.0
	Corixidae	6.7
	Baetidae	6.7
	Aquatic Plecoptera	6.7
	Arachnida	3.3
	Terrestrial Trichoptera	3.3
	Terrestrial Insecta	3.3
	Amorphous Detritus	3.3
	Simuliidae	3.3
	Terrestrial Homoptera	3.3
	Terrestrial Plecoptera	3.3
	Heptageniidae	3.3
	Terrestrial Hymenoptera	3.3
Flathead Chub *Platygobio gracilis* n=30	Chironomidae	70.0
	Tipulidae	26.7
	Terrestrial Thysanoptera	20.0
	Hydropsychidae	20.0
	Amorphous Detritus	20.0

Species	Diet Item	O_i
	Terrestrial Diptera	16.7
	Terrestrial Homoptera	16.7
	Nematoda	13.3
	Terrestrial Hymenoptera	10.0
	Corixidae	10.0
	Terrestrial Coleoptera	10.0
	Unknown Fish Parts	6.7
	Ceratopogonidae	6.7
	Arachnida	3.3
	Isonychiidae	3.3
	Leptophlebiidae	3.3
	Insect Eggs	3.3
	Heptageniidae	3.3
	Ostracoda	3.3
Freshwater Drum	Chironomidae	100.0
Aplodinotus grunniens	Amorphous Detritus	26.9
n=26	Hydropsychidae	26.9
	Pupating Diptera	15.4
	Baetidae	15.4
	Corixidae	11.5
	Caenidae	7.7
	Ceratopogonidae	7.7
	Heptageniidae	7.7
	Leptophlebiidae	7.7
	Ephemerellidae	3.8
	Terrestrial Diptera	3.8
Goldeye	Hydropsychidae	75.8
Hiodon alosoides	Chironomidae	51.5
n=30	Terrestrial Coleoptera	48.5
	Corixidae	39.4
	Amorphous Detritus	36.4
	Perlodidae	33.3
	Ephemerellidae	33.3
	Ceratopogonidae	21.2
	Leptophlebiidae	15.2
	Rodents	12.1
	Parasitic Worm	12.1
	Terrestrial Hymenoptera	9.1

Species	Diet Item	O_i
	Heptageniidae	9.1
	Unknown Fish Parts	9.1
	Arachnida	6.1
	Tipulidae	6.1
	Baetidae	6.1
	Unknown Terrestrial Insecta	6.1
	Aquatic Coleoptera	6.1
	Muscidae	6.1
	Terrestrial Orthoptera	6.1
	Simuliidae	3.0
	Fish Eggs	3.0
	Melyridae	3.0
	Carabidae	3.0
	Aquatic Diptera	3.0
	Terrestrial Diptera	3.0
	Emerald Shiner	3.0
	Terrestrial Homoptera	3.0
	Polydesmida	3.0
	Polymitarcyidae	3.0
	Crawfish	3.0
	Cladocera	3.0
	Copepoda	3.0
Pallid Sturgeon *Scaphirhynchus albus* n=159	Chironomidae	73.0
	Unknown Fish Parts	50.3
	Hydropsychidae	38.4
	Leptophlebiidae	32.1
	Baetidae	21.4
	Ephemerellidae	20.8
	Simuliidae	20.1
	Polymitarcyidae	18.9
	Isonychiidae	15.1
	Ceratopogonidae	14.5
	Ametropidae	13.2
	Heptageniidae	12.6
	Caenidae	12.6
	Tipulidae	8.2
	Perlodidae	6.3
	Corixidae	6.3

Species	Diet Item	O_i
	Emerald Shiner	5.0
	Gomphidae	5.0
	Sturgeon	5.0
	24 Pharyngeal arch	4.4
	Fish Eggs	4.4
	Oligoneuriidae	3.8
	Muscidae	2.5
	Nematoda	2.5
	Channel Catfish	2.5
	Sturgeon or Sicklefin Chub	1.9
	Leptoceridae	1.9
	Calanoida	1.3
	Leptohyphidae	1.3
	Curculionidae	1.3
	Arachnida	1.3
	Amphipoda	1.3
	Cyprinidae	1.3
	Dytiscidae	1.3
	Brachycentridae	0.6
	Glossosomatidae	0.6
	Dolichopodidae	0.6
Sauger	Unknown Fish Parts	51.7
Sander canadensis	Chironomidae	31.0
n=29	Fish with 2,4 Pharyngeal Arch	24.1
	Freshwater Drum	13.8
	Channel Catfish	6.9
	Emerald Shiner	6.9
	Terrestrial Diptera	6.9
	Terrestrial Coleoptera	6.9
	Leptohyphidae	3.4
	Stonecat	3.4
	Terrestrial Hemiptera	3.4
	Diptera Pupae	3.4
	Hybognathus spp.	3.4
	Cyprinidae	3.4
	Sturgeon or Sicklefin Chub	3.4
Shovelnose Sturgeon	Chironomidae	100
Scaphirhynchus platorynchus	Hydropsychidae	73.9

Species	Diet Item	O_i
n=46	Ceratopogonidae	60.9
	Simuliidae	54.3
	Baetidae	45.7
	Perlodidae	30.4
	Polymitarcyidae	26.1
	Heptageniidae	26.1
	Ephemerellidae	21.7
	Ametropidae	19.6
	Leptophlebiidae	19.6
	Gomphidae	19.6
	Tipulidae	19.6
	Isonychiidae	19.6
	Nematoda	15.2
	Dolichopodidae	15.2
	Caenidae	15.2
	Muscidae	15.2
	Corixidae	15.2
	Amphipoda	8.7
	Oligoneuriidae	6.5
	Arachnida	2.2
	Leptoceridae	2.2
	Branchiura	2.2
	Leptohyphidae	2.2
	Glossosomatidae	2.2
	Dytiscidae	2.2
	Heteroceridae	2.2
	Brachycentridae	2.2
	Curculionidae	2.2
	Crambidae	2.2
	Corydalidae	2.2
Sicklefin Chub	Terrestrial Coleoptera	78.9
Macrhybopsis meeki	Leptoceridae	36.8
n=19	Hydropsychidae	36.8
	Chironomidae	21.1
	Carabidae	5.3
	Unknown Terrestrial Insecta	5.3
	Brachycentridae	5.3
	Amorphous Detritus	5.3

Species	Diet Item	O_i
	Simuliidae	5.3
	Corixidae	5.3
	Hirudinea	5.3
Stonecat *Noturus flavus* n=30	Hydropsychidae	63.3
	Leptophlebiidae	33.3
	Perlodidae	30.0
	Simuliidae	30.0
	Chironomidae	26.7
	Isonychiidae	23.3
	Amorphous Detritus	20.0
	Heptageniidae	16.7
	Parasitic Worm	13.3
	Baetidae	10.0
	Pupating Simuliidae	6.7
	Terrestrial Homoptera	3.3
	Crawfish	3.3
	Ephemerellidae	3.3
	Glossosomatidae	3.3
	Brachycentridae	3.3
Sturgeon Chub *Macrhybopsis gelida* n=17	Chironomidae	76.5
	Hirudinea	17.6
	Hydropsychidae	17.6
	Pupating Diptera	17.6
	Terrestrial Coleoptera	5.9
	Leptophlebiidae	5.9
	Amorphous Detritus	5.9

Table 3.4. Frequency of occurrence (O_i) by diet item for fishes sampled in the Yellowstone River segments 1 and 2. Data were sorted first by common name of fish species and then within a fish species by highest frequency of occurrence. Sample size (n) represents the number of individual diets examined for each species.

Species	Diet Item	O_i
Channel Catfish	Chironomidae	73.9
Ictalurus punctatus	Hydropsychidae	39.1
n=30	Amorphous Detritus	39.1
	Unknown Fish Parts	30.4
	Tipulidae	26.1
	Curculionidae	26.1
	Terrestrial Hymenoptera	17.4
	Terrestrial Coleoptera	17.4
	Elmidae	17.4
	Aquatic Coleoptera	17.4
	Muscidae	17.4
	Terrestrial Insecta	17.4
	Leptophlebiidae	13.0
	Trichoptera	13.0
	Simuliidae	13.0
	Heptageniidae	13.0
	Chrysomelidae	13.0
	Corixidae	8.7
	Perlodidae	8.7
	Pupating Insecta	8.7
	Polycentropodidae	4.3
	Carabidae	4.3
	Fish Eggs	4.3
	Ceratopogonidae	4.3
	Aquatic Diptera	4.3
	Pupating Diptera	4.3
	Aquatic Odonata	4.3
	Insecta	4.3
	Nematoda	4.3
Emerald Shiner	Hirudinea	51.6
Notropis atherinoides	Terrestrial Coleoptera	25.8
n=31	Chironomidae	22.6
	Terrestrial Diptera	16.1

Species	Diet Item	O_i
	Simuliidae	12.9
	Terrestrial Insecta	6.5
	Hydropsychidae	3.2
	Terrestrial Odonata	3.2
	Amorphous Detritus	3.2
	Diptera Pupae	3.2
	Insect Eggs	3.2
	Terrestrial Hymenoptera	3.2
Flathead Chub	Amorphous Detritus	60.0
Platygobio gracilis	Chironomidae	46.7
n=30	Ostracoda	20.0
	Terrestrial Diptera	20.0
	Heptageniidae	20.0
	Baetidae	16.7
	Parasitic Worm	16.7
	Filamentous Algae	10.0
	Terrestrial Coleoptera	10.0
	Hydropsychidae	6.7
	Arachnida	3.3
	Simuliidae	3.3
	Insect Eggs	3.3
	Leptoceridae	3.3
	Terrestrial Hymenoptera	3.3
	Hirudinea	3.3
	Terrestrial Homoptera	3.3
	Ceratopogonidae	3.3
Goldeye	Amorphous Detritus	62.1
Hiodon alosoides	Unknown Fish Parts	34.5
n=32	Terrestrial Orthoptera	31.0
	Terrestrial Coleoptera	24.1
	Hydropsychidae	10.3
	Terrestrial Hymenoptera	10.3
	Chironomidae	6.9
	Corixidae	6.9
	Cyprinidae	6.9
	Carabidae	3.4
	Tipulidae	3.4
	Emerald Shiner	3.4

Species	Diet Item	O_i
Pallid Sturgeon	Chironomidae	76.2
Scaphirhynchus albus	Unknown Fish Parts	61.9
n=21	Hydropsychidae	47.6
	Leptophlebiidae	28.6
	Heptageniidae	28.6
	Simuliidae	23.8
	Baetidae	23.8
	Caenidae	19.0
	Stonecat	19.0
	Isonychiidae	19.0
	Fish Eggs	19.0
	Perlodidae	14.3
	Channel Catfish	9.5
	Polymitarcyidae	9.5
	Ceratopogonidae	9.5
	Nematoda	4.8
	Tipulidae	4.8
	Sturgeon	4.8
	Gomphidae	4.8
	Dolichopodidae	4.8
	Amphipoda	4.8
Shovelnose Sturgeon	Chironomidae	100
Scaphirhynchus platorynchus	Hydropsychidae	67.5
n=40	Simuliidae	65.0
	Heptageniidae	60.0
	Perlodidae	55.0
	Ceratopogonidae	52.5
	Baetidae	40.0
	Leptophlebiidae	32.5
	Caenidae	22.5
	Fish Eggs	16.3
	Elmidae	12.5
	Isonychiidae	10.0
	Nematoda	10.0
	Gomphidae	7.5
	Ephemerellidae	7.5
	Tipulidae	7.5
	Polymitarcyidae	7.5

Species	Diet Item	O_i
	Copepoda	5.0
	Planorbidae	2.5
	Leptoceridae	2.5
	Empididae	2.5
	Leptohyphidae	2.5
	Polycentropodidae	2.5
	Muscidae	2.5
	Cyclopoida	2.5

Figure Captions

3.1. Map of the upper Missouri River, delineated into four segments, which includes the inter-reservoir reach between Fort Peck Dam, MT and the headwaters of Lake Sakakawea, ND, and the lower Yellowstone River, delineated into two segments, from Glendive, MT to the confluence with the Missouri River near Buford, ND. Bars represent segment breaks for each river.

3.2. Food web in the upper Missouri River including fish from segments 1-4. The width of the boxes for primary consumers represents the proportion of the primary consumer relative to the total abundance of primary consumers. The width of boxes for secondary and tertiary consumer represents the proportion of the catch per unit effort (CPUE) of that fish species in relation to all fish species. Arrows between two consumers represent the frequency of occurrence of a diet item in all diets sampled per species. The thicker the arrow the more frequent that diet item was found in the diets of a specific species. For detailed descriptions and estimates of abundance, CPUE, and linkages refer to methods, tables, and appendix tables.

3.3. Food web in the lower Yellowstone River including fish from segments 1 and 2. The width of the boxes for primary consumers represents the proportion of the primary consumer relative to the total abundance of primary consumers. The width of boxes for secondary and tertiary consumer represents the proportion of the catch per unit effort (CPUE) of that fish species in relation to all fish species. The ellipse boxes indicate a species without a known CPUE for the Yellowstone River. Arrows between two consumers represent the frequency of occurrence of a diet item in all diets sampled per species. The thicker the arrow the more frequent that diet item was found in the diets of a specific species. For detailed descriptions and estimates of abundance, CPUE, and linkages refer to methods, tables, and appendix tables.

Figures

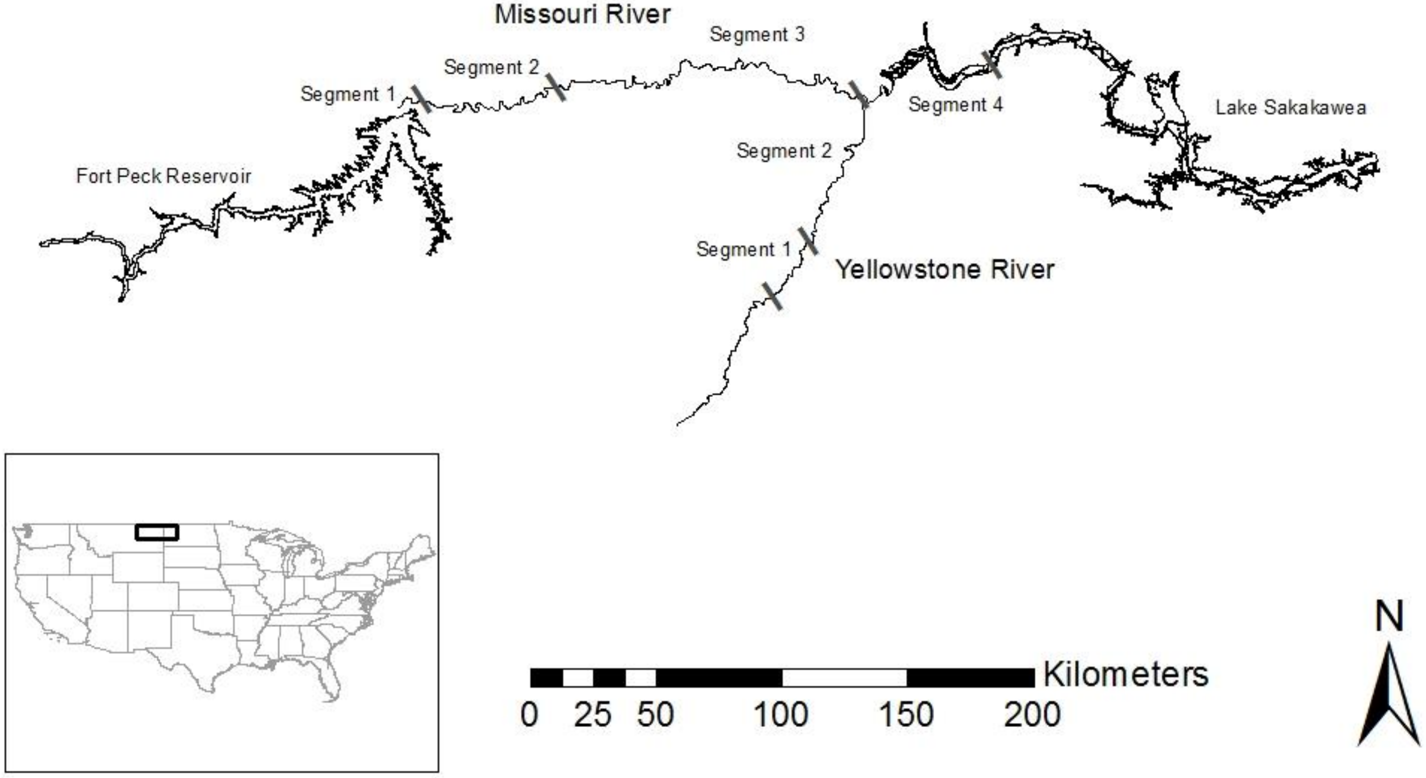

Figure 3.1

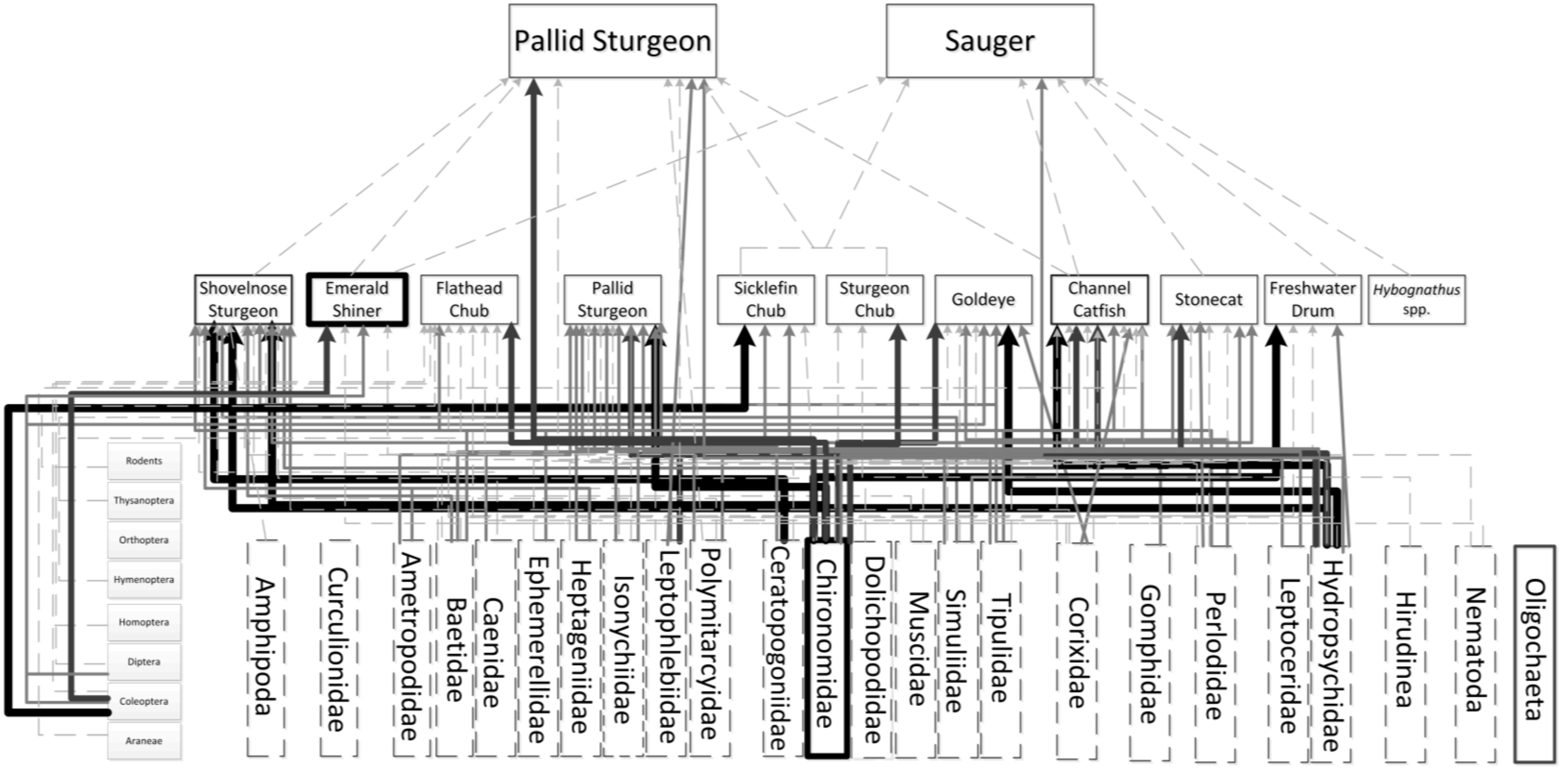
Pallid Sturgeon
Sauger
Shovelnose Sturgeon
Emerald Shiner
Flathead Chub
Pallid Sturgeon
Sicklefin Chub
Sturgeon Chub
Goldeye
Channel Catfish
Stonecat
Freshwater Drum
Hybognathus spp.
Rodents
Thysanoptera
Orthoptera
Hymenoptera
Homoptera
Diptera
Coleoptera
Araneae
Amphipoda
Curculionidae
Ametropodidae
Baetidae
Caenidae
Ephemerellidae
Heptageniidae
Isonychiidae
Leptophlebiidae
Polymitarcyidae
Ceratopogoniidae
Chironomidae
Dolichopodidae
Muscidae
Simuliidae
Tipulidae
Corixidae
Gomphidae
Perlodidae
Leptoceridae
Hydropsychidae
Hirudinea
Nematoda
Oligochaeta

Figure 3.2.

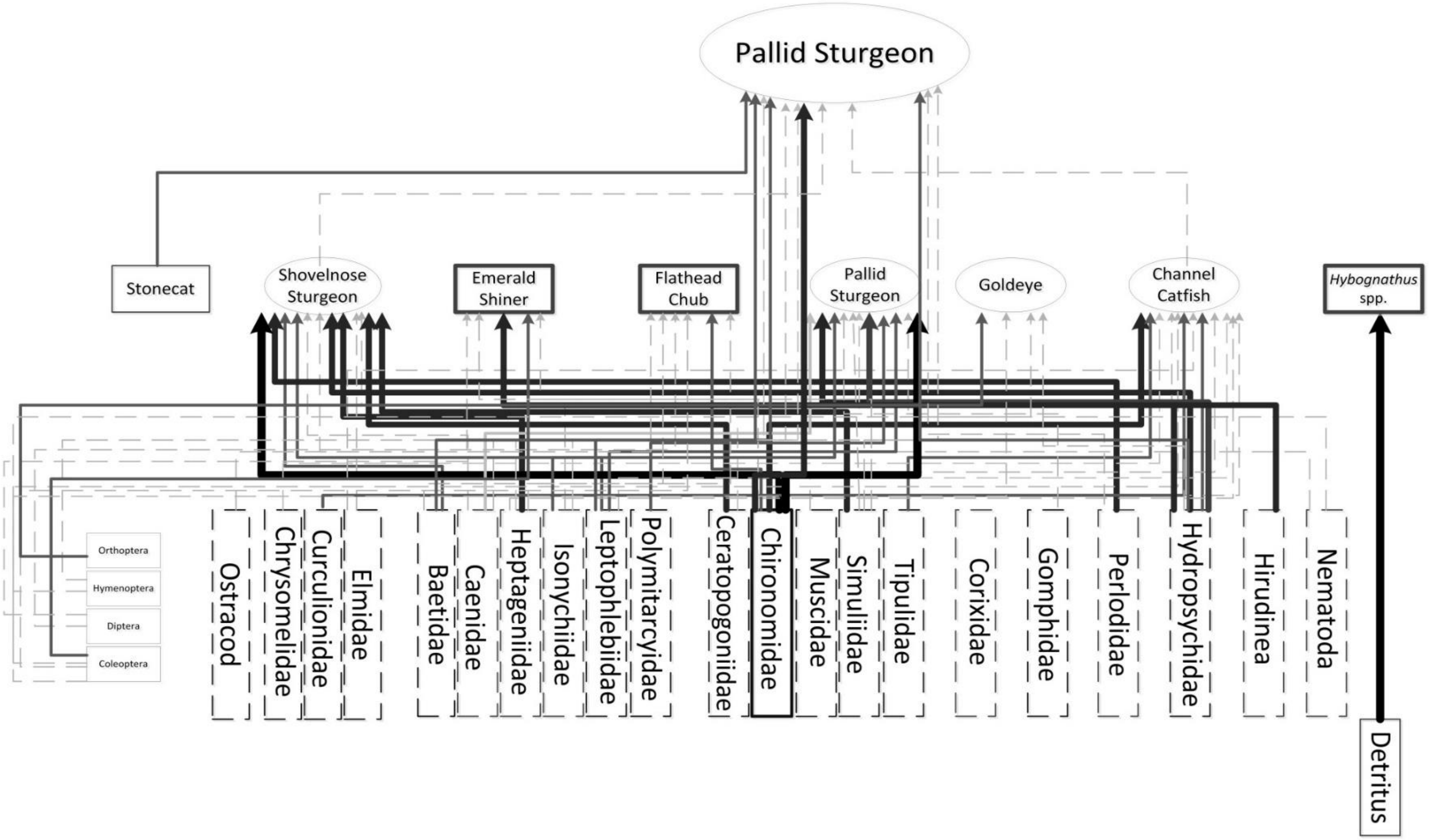
Pallid Sturgeon
Stonecat
Shovelnose Sturgeon
Emerald Shiner
Flathead Chub
Pallid Sturgeon
Goldeye
Channel Catfish
Hybognathus spp.
Orthoptera
Hymenoptera
Diptera
Coleoptera
Ostracod
Chrysomelidae
Curculionidae
Elmidae
Baetidae
Caenidae
Heptageniidae
Isonychiidae
Leptophlebiidae
Polymitarcyidae
Ceratopogoniidae
Chironomidae
Muscidae
Simuliidae
Tipulidae
Corixidae
Gomphidae
Perlodidae
Hydropsychidae
Hirudinea
Nematoda
Detritus

Figure 3.3

CHAPTER FOUR

CONCLUSIONS

The objectives of this research were: 1) to quantitatively describe the diets and assess diet overlap of Pallid Sturgeon and Shovelnose Sturgeon, 2) to evaluate the possibility of gape size as a mechanism for the ontogenetic diet shift in Pallid Sturgeon, and 3) to assess the linkages among primary, secondary, and tertiary consumers within the upper Missouri River and lower Yellowstone River. In chapter two, I compared the diets of Pallid Sturgeon and Shovelnose Sturgeon in the upper Missouri River and the lower Yellowstone River and investigated if gape size was the mechanism behind Pallid Sturgeon exhibiting an ontogenetic dietary shift. In chapter three, I described the diets of numerous fish species and developed food webs to better understand how benthic macroinvertebrates and fish species are linked in the upper Missouri River and lower Yellowstone River.

In chapter two, I found evidence in support of my hypothesis that diet overlap between Pallid Sturgeon and Shovelnose Sturgeon would be highest prior to switching to piscivory. I did not find evidence that gape size was the mechanism for the shift to piscivory by Pallid Sturgeon. In chapter three, I found evidence that diet items consumed by species changed from upstream to downstream as habitat changed from the operation of Fort Peck Dam or natural variation in the Yellowstone River. However, I did not find much support that the food webs were vastly different between the upper Missouri River and the lower Yellowstone River. However, the Missouri River did have more terrestrial inputs into the food web compared to the Yellowstone River food web.

This study was the first to quantify the diets of Pallid Sturgeon and Shovelnose Sturgeon in RPMA 2 which encompasses the area in the Missouri River from Fort Peck Dam downstream to the headwaters of Lake Sakakawea and the Yellowstone River from the mouth of the Tongue River downstream to the confluence with the Missouri River. Prior to this study, the diet patterns and diet overlap of Pallid Sturgeon and Shovelnose Sturgeon in RPMA 2 were unknown. Similar to other diet studies, Pallid Sturgeon initially consumed benthic macroinvertebrates and switched to piscivory once they reached 300 mm (Gerrity et al. 2006; Hoover et al. 2007; Wanner et al. 2007); whereas, Shovelnose Sturgeon fed primarily on benthic macroinvertebrates at all sizes (Gerrity et al. 2006; Hoover et al. 2007; Wanner et al. 2007; Bock et al. 2010; Rapp et al. 2011). Low diet overlap between the two *Scaphirhynchus* spp. was observed in segment 4 of the Missouri River and segments 1 and 2 of the Yellowstone River. These results were similar to those reported for diet overlap between Pallid Sturgeon and Shovelnose Sturgeon in the Missouri River above Fort Peck Dam, MT (Gerrity et al. 2006). In segments 2 and 3 of the Missouri River, diet overlap was high between Pallid Sturgeon and Shovelnose Sturgeon. The high overlap in these two segments is a function of both *Scaphirhynchus* spp. feeding primarily on similar genera of benthic macroinvertebrates.

This was the first study to develop food webs for the Missouri River and Yellowstone River based on diet analyses of secondary and tertiary consumers. The linkages presented here provide better insight into the complexity of species interactions in large-river ecosystems. Prior to this study, primary consumer abundance, diets of many fishes, and potential effects of stocking 251,838 hatchery-origin Pallid Sturgeon in Recovery Priority Management Area 2 (RPMA 2) were unknown.

The diversity of benthic macroinvertebrate families consumed by secondary and tertiary consumers was higher in the Missouri River than the Yellowstone River. Despite the subtle differences between rivers, Chironomidae was the dominate family represented in the diets of most fishes.

Terrestrial invertebrates contributed to the diversity of prey in fish diets in the Missouri River and Yellowstone River. Similar to the pattern with benthic macroinvertebrates, there was a higher diversity of terrestrial inputs observed in the diets of fish from the Missouri River compared to the Yellowstone River. Although some differences (e.g., terrestrial inputs) were noted between the food webs of the upper Missouri River and the lower Yellowstone River, overall the webs were similar. The similarity of the food webs may be related to sampling proximity — segment 4 in the Missouri River and segment 2 in the Yellowstone River. Thus, the similarities between the two river food webs should not be surprising given the similarity of habitat, water temperature and clarity, and species composition in these two segments of the Missouri River and Yellowstone River.

These two chapters filled data gaps on the feeding ecology of several fishes in the upper Missouri River and lower Yellowstone River. By better understanding how primary, secondary, and tertiary consumers are linked in both rivers systems, a concurrent study will develop bioenergetic models to compare and contrast the food availability and demand in the upper Missouri River with the lower Yellowstone River.

The outcomes of these models will ultimately guide future stocking of hatchery-origin Pallid Sturgeon. Finally, these chapters will provide a necessary road map for future research on Pallid Sturgeon throughout the Mississippi River basin.

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APPENDIX

Table A.1. Availability, in percent, for primary consumers in the Missouri River (Missouri) segments 2-4 and Yellowstone River (Yellowstone) segments 1 and 2. Primary consumers are ordered from left to right as they appear in the food web (Figure 3.2 and 3.3) of the Missouri River and Yellowstone River. If a value was not included on the food web, it is represented by N/A.

	Missouri	Yellowstone
Primary Consumer	Abundance	
Amphipoda	<1.0	N/A
Chrysomelidae	N/A	<1.0
Curculionidae	<1.0	<1.0
Elmidae	N/A	<1.0
Ametropidae	<1.0	N/A
Baetidae	1.7	5.2
Caenidae	<1.0	<1.0
Ephemerellidae	<1.0	N/A
Heptageniidae	2.2	7.8
Isonychiidae	<1.0	<1.0
Leptophlebiidae	<1.0	10.9
Polymitarcyidae	<1.0	1.2
Ceratopogonidae	2.8	<1.0
Chironomidae	60.8	42.7
Dolichopodidae	<1.0	N/A
Muscidae	<1.0	<1.0
Simuliidae	<1.0	5.1
Tipulidae	<1.0	<1.0
Corixidae	1.3	<1.0
Gomphidae	<1.0	<1.0
Perlodidae	<1.0	2.5
Leptoceridae	<1.0	N/A
Hydropsychidae	2.6	12.7
Hirudinea	<1.0	<1.0
Nematoda	<1.0	<1.0
Oligochaeta	28.3	N/A

Table A.2. Mean catch per unit effort (CPUE) of secondary and tertiary consumers in the Missouri River food web. Units differ based on gear type used to sample each species. If CPUE was not reported for a segment, then N/A was used in the table. Catch-per-unit-effort data can be found in Hunziker et al. (2017a), (2017b), and Wilson (2017).

Species	Segment 2	Segment 3	Segment 4
Channel Catfish	1.3 fish/net night	0.83 fish/net night	2.8 fish/100 m
Emerald Shiner	N/A	N/A	46.4 fish/net night
Flathead Chub	0.079 fish/100 m	0.19 fish/net night	0.036 fish/net night
Freshwater Drum	N/A	0.031 fish/net night	0.57 fish/100 m
Goldeye	0.29 fish/100 m	0.27 fish/100 m	0.18 fish/100 m
Hybognathus spp.	N/A	N/A	0.42 fish/100 m
Pallid Sturgeon	0.086 fish/100 m	0.19 fish/net night	0.48 fish/net night
Sauger	0.40 fish/100 m	0.38 fish/100 m	0.51 fish/100 m
Shovelnose Sturgeon	3.9 fish/net night	0.96 fish/net night	0.72 fish/100 m
Sicklefin Chub	N/A	N/A	0.25 fish/100 m
Stonecat	N/A	0.18 fish/net night	0.067 fish/100 m
Sturgeon Chub	N/A	N/A	0.11 fish/100 m

Table A.3. Mean catch per unit effort (CPUE) of secondary and tertiary consumers in the Yellowstone River food web. Units differ based on gear type used to sample each species. If CPUE was not reported for a segment, then N/A was used in the table. Catch-per-unit-effort data can be found in Duncan et al. (2012).

Species	Segment 1	Segment 2
Channel Catfish	N/A	N/A
Emerald Shiner	123.5 fish/net night	35.4 fish/net night
Flathead Chub	10.7 fish/net night	1.2 fish/net night
Goldeye	N/A	N/A
Hybognathus spp.	23.9 fish/net night	1.8 fish/net night
Pallid Sturgeon	N/A	N/A
Shovelnose Sturgeon	N/A	N/A
Stonecat	0.4 fish/net night	<0.1 fish/net night

Table A.4. All diet items consumed by Channel Catfish, Emerald Shiner, Flathead Chub, Freshwater Drum, Goldeye, Pallid Sturgeon, Sauger, Sicklefin Chub, Shovelnose Sturgeon, Stonecat, and Sturgeon Chub sampled in the Missouri River segments 1-4.

Aquatic Invertebrate	Fish	Terrestrial Inputs
Hydropsychidae	Stonecat	Coleoptera
Leptophlebiidae	*Hybognathus* spp.	Diptera
Chironomidae	Channel Catfish	Hymenoptera
Baetidae	Sturgeon Chub or Sicklefin Chub	Rodents
Corixidae	Emerald Shiner	Birds
Polymitarcyidae	Crawfish	Trichoptera
Ceratopogonidae	Unknown Fish	Homoptera
Perlodidae	Shovelnose Sturgeon	Plecoptera
Simuliidae	*Scaphirhynchus* spp.	Thysanoptera
Muscidae	2,4 Cyprinidae pharyngeal arch	Arachnida
Tipulidae	Cyprinidae	Orthoptera
Curculionidae		Polydesmida
Brachycentridae		
Isonychiidae		
Elmidae		
Carabidae		
Leptoceridae		
Ephemerellidae		
Glossosomatidae		
Heptageniidae		
Leptohyphidae		
Haliplidae		
Dolichopodidae		
Tabanidae		
Coenagrionidae		
Caenidae		
Hirudinea		
Nematoda		
Ostracoda		
Melyridae		
Cladocera		
Copepoda		
Ametropidae		
Gomphidae		
Oligoneuriidae		
Calanoida		
Dytiscidae		
Amphipoda		
Branchiura		

Table A.4. Continued

Aquatic Invertebrate	Fish	Terrestrial Inputs
Heteroceridae		
Crambidae		
Corydalidae		

Table A.5. All diet items consumed by Channel Catfish, Emerald Shiner, Flathead Chub, Goldeye, *Hybognathus* spp., Pallid Sturgeon, and Shovelnose Sturgeon sampled in the Yellowstone River segments 1 and 2.

Aquatic Invertebrate	Fish	Terrestrial Inputs
Chironomidae	*Scaphirhynchus* spp.	Coleoptera
Hydropsychidae	Channel Catfish	Hymneoptera
Tipulidae	Stonecat	Diptera
Curculionidae	Emerald Shiner	Odonata
Elmidae	Unknown fish parts	Arachnida
Muscidae	Cyprinidae	Homoptera
Leptophlebiidae		Orthoptera
Simuliidae		
Heptageniidae		
Chrysomelidae		
Corixidae		
Perlodidae		
Polycentropodidae		
Carabidae		
Ceratopogonidae		
Nematoda		
Hirudinea		
Ostracoda		
Baetidae		
Leptoceridae		
Caenidae		
Isonychiidae		
Polymitarcyidae		
Gomphidae		
Dolichopodidae		
Amphipoda		
Ephemerellidae		
Copepoda		
Planorbidae		
Empididae		
Leptohyphidae		
Cyclopoida		