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Ontogenetic patterns in prey use by pallid sturgeon in the Missouri River, South Dakota and Nebraska

By K. L. Grohs[1], R. A. Klumb[1], S. R. Chipps[2] and G. A. Wanner[1]

[1]*U.S. Fish and Wildlife Service, Great Plains Fish and Wildlife Conservation Office, Pierre, SD, USA;* [2]*U.S. Geological Survey, South Dakota Cooperative Fish and Wildlife Research Unit, Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, SD, USA*

Summary

The pallid sturgeon (*Scaphirhynchus albus*) is an endangered species native to the Missouri and Mississippi rivers. To date, recovery efforts have focused on stocking juvenile fish, but little is known about ontogenetic changes in diet composition. Although diet composition for pallid sturgeon is believed to change from macroinvertebrates to fish, it is unclear at what size and/or age these ontogenetic diet shifts occur. To evaluate diet composition, 29 hatchery-stocked pallid sturgeon (range 356–720 mm fork length [FL]; mean = 549; SE = 23) were collected from the Missouri River downstream of Fort Randall Dam, South Dakota and Nebraska during summer 2006. The majority of pallid sturgeon (72%) were captured within a large delta region formed by the Niobrara River in the headwaters of Lewis and Clark Lake. Predominant prey of pallid sturgeon based on percent occurrence was Ceratopogonidae (81%), Isonychiidae (67%), Chironomidae (52%), and fishes (24%). Percent composition by wet weight showed that diets were composed of fishes (68%), Ephemeroptera (23%), Decapoda (6%), and Diptera (3%). Graphical analysis of combined data showed that mayflies, particularly Isonychiidae, were an important component of pallid sturgeon diets. Nonetheless, the percent composition of fishes in the diet increased with pallid sturgeon body size; for fish > 600 mm FL (5–7 years of age) diets were composed primarily of fish prey (66%, mostly johnny darters *Etheostoma nigrum*). These findings highlight the importance of ontogenetic changes in diet composition for pallid sturgeon. Moreover, the unique habitat formed in the delta region is characterized by higher fish and invertebrate densities that may enhance foraging opportunities and thus improve recovery efforts for stocked pallid sturgeon.

Introduction

The pallid sturgeon (*Scaphirhynchus albus*) is a long-lived species native to the Missouri and lower Mississippi rivers (Forbes and Richardson, 1905; Dryer and Sandvol, 1993). The species is listed as critically endangered because of its rarity and vulnerability to extinction due to an apparent lack of natural reproduction and recruitment (Carlson et al., 1985). Sexual maturity is reached at ages 5–7 (≥ 710 mm fork length [FL]) for males and 9–12 years (≥ 850 mm FL) for females (Keenlyne and Jenkins, 1993). However, for female pallid sturgeon, first spawn does not typically occur until age 15 and spawning does not occur every year (Keenlyne and Jenkins, 1993).

The Missouri River has been modified by construction of large impoundments, dredging, and channelization (Kallemeyn, 1983; Gilbraith et al., 1988; Keenlyne, 1989; Dryer and Sandvol, 1993). About 51% of the pallid sturgeon's range has been channelized for commercial navigation. Approximately 28% has been impounded with only about 21% of the remnant, unchannelized riverine habitats located downstream of dams (Keenlyne, 1989). Six mainstem dams have blocked spawning migrations, isolated populations, reduced rearing and spawning habitats, and altered food supply (Junk et al., 1989; Hesse and Sheets, 1993). Fragmentation by dams has also altered flow, turbidity, and temperature regimes of the Missouri River (Dryer and Sandvol, 1993; Pegg et al., 2003).

Pallid sturgeon have been federally listed as an endangered species since 1990 (U.S. Fish and Wildlife Service, 1990). To benefit the pallid sturgeon population, the U.S. Fish and Wildlife Service developed a recovery plan in 1993 (Dryer and Sandvol, 1993). Four reaches of the Missouri River have been selected for recovery based on the status of pallid sturgeon and the availability of existing riverine habitat (Dryer and Sandvol, 1993). From 1992 to 2004, a total of 114,117 juvenile pallid sturgeon (JPS) have been stocked in the Missouri River (Krentz et al., 2005) and all JPS stocked are marked (Jaeger et al., 2007). Passive integrated transponder tags (PIT) were implanted in all fish ≥ 140 mm FL, with smaller fish marked with visible implant elastomer (VIE) tags (U.S. Fish and Wildlife Service, 2008). Passive integrated transponder tags allow identification of individual fish, whereas VIE tags and genetic markers identify year class (i.e., batch mark). In addition, long-term monitoring programs have been implemented to assess pallid sturgeon populations and associated fish communities in the Missouri River (Drobish, 2006).

Although recovery efforts have focused on stocking juvenile fish, little is known about ontogeny of diet composition or food availability for pallid sturgeon once they are stocked into the river. Aquatic insect larvae (Diptera and Ephemeroptera) represented important (35–60%) food items for pallid sturgeon in the Missouri (Carlson et al., 1985; Wanner et al., 2007a), and in the middle and lower Mississippi rivers (Hoover et al., 2007). However, in the upper Missouri River basin, fish prey occurred in 54% of pallid sturgeon diets and represented over 90% of the diets based on wet weight (Gerrity et al., 2006).

Because the relative importance of prey items can be assessed using a variety of different diet measures, selecting an appropriate index is often dependent on the questions being asked. When summarized using a single diet index, such as percent by weight, diet data are usually presented in tabulated format; thus, the relative importance of different prey items is often based on subjective interpretation (Chipps and Garvey, 2007). Graphical techniques for diet analysis are generally easier to interpret than tabulated data and can simultaneously incorporate more than one diet measure. The objectives of this study were to assess summer diets of pallid sturgeon downstream of Fort Randall Dam, one of the recovery areas listed in the recovery plan to: (i) identify patterns of prey use using a graphical approach, (ii) explore changes in prey use as a function of pallid sturgeon length and age, and (iii) compare pallid sturgeon diet composition to other areas of the Missouri River.

Materials and methods

Study Area

Our study area was located on the Missouri River downstream of Fort Randall Dam (river kilometer [rkm] 1,416) and extended to Lewis and Clark Lake (rkm 1,305), herein referred to as the Fort Randall reach (Fig. 1). The Fort Randall reach retains riverine characteristics and habitat types that include a meandering river channel with inside bends, outside bends, secondary connected channels, channel crossovers, and braided areas. Since the closure of Gavins Point Dam in 1957, a braided delta has formed from the Niobrara River confluence (rkm 1,358), the largest tributary of the Missouri River in this reach. Currently, sedimentation has extended the delta downstream of Santee, Nebraska (rkm 1,332) into Lewis and Clark Lake (Kaemingk et al., 2007). Flows from Fort Randall Dam are regulated for power generation and navigation downstream in the channelized section of the Missouri River. Because Fort Randall Dam regulates discharge, it has caused alterations from the historical hydrograph in the riverine section including daily and seasonal water level fluctuations (Pegg et al., 2003; Jordan et al., 2006). In addition, hypolimnetic water releases from Lake Francis Case through Fort Randall Dam cause reduced downstream water temperatures upstream of the Niobrara River confluence (Klumb, 2007).

Pallid sturgeon diets

Pallid sturgeon were sampled monthly from 10 randomly selected bends in the Fort Randall reach as part of a long-term pallid sturgeon assessment for the Missouri River (Drobish, 2006). Pallid sturgeon used in this study for diet analysis were sampled from June through September 2006 (i.e. summer). All sturgeon collected were measured for FL (mm), weighed to the nearest gram (g), scanned for PIT tags, checked for VIE tags, and underwent gastric lavage before being released (Hyslop, 1980; Wanner, 2006).

Pallid sturgeon in 2006 were collected using drifted trammel nets or an otter trawl (Wanner et al., 2007b). Multifilament trammel nets were drifted perpendicular to the current at least 75 m for a targeted maximum distance of 300 m. Trammel nets were 38 m in length, 1.8 m in depth, with outside wall panels of 15.2 cm bar mesh (number 9 nylon twine), and inside wall panels of 2.5 cm bar mesh (number 139 nylon twine). Float lines were constructed of 1.3 cm poly-foamcore and leadlines were 22.7 kg leadcore. The otter trawl was towed downstream for at least 75 m up to a targeted maximum distance of 300 m. The otter trawl was a 4.9 m wide by 0.9 m high skate trawl. Otter boards were 38.1 cm high, 76.2 cm long, and weighed 13.6 kg each. The outer chafing mesh was a sapphire twine with a 1.9 cm bar mesh, the inner netting was 0.6 cm bar mesh, and the codend opening was 0.4 m. The footrope was 4.9 m long having a 4.8 mm diameter chain attached to help maintain contact with the substrate. The headrope was 4.6 m long with floats spaced every 0.9 m. Typical duration was 5–15 min for trammel drifts and 2–3 min for each trawl depending on water velocity and presence of snags. Distance of trammel net drifts and otter trawl hauls was measured with a global positioning system (GPS).

Stomach contents were collected non-lethally from each pallid sturgeon captured using pulsed gastric lavage (Haley, 1998; Brosse et al., 2002; Wanner, 2006; Shuman and Peters, 2007). Gastric lavage entailed inserting a tube down the esophagus into the stomach where water was flushed to induce regurgitation (Hyslop, 1980). After stomach contents were flushed, the fish were then placed in a recovery tank and monitored (Wanner, 2006). Gastric lavage has been shown to have no effects on sturgeon mortality (Brosse et al., 2002; Shuman and Peters, 2007) or short-term growth and condition (Wanner, 2006) with food recovery rates $> 70\%$ (Brosse et al., 2002; Wanner, 2006; Shuman and Peters, 2007). Stomach contents were collected in a 500 μm mesh sieve and preserved in a 10% formalin solution. In the laboratory, prey items were identified to at least the family level and fishes were identified to species, when possible, using dichotomous keys (Merrit and Cummins, 1996; Pflieger, 1997; Wiggins, 2000; Thorp and Covich, 2001; Voshell, 2002). After prey items were identified and counted, wet weight of each taxonomic group from each sample was measured, then dried at 65°C for 24–48 h and

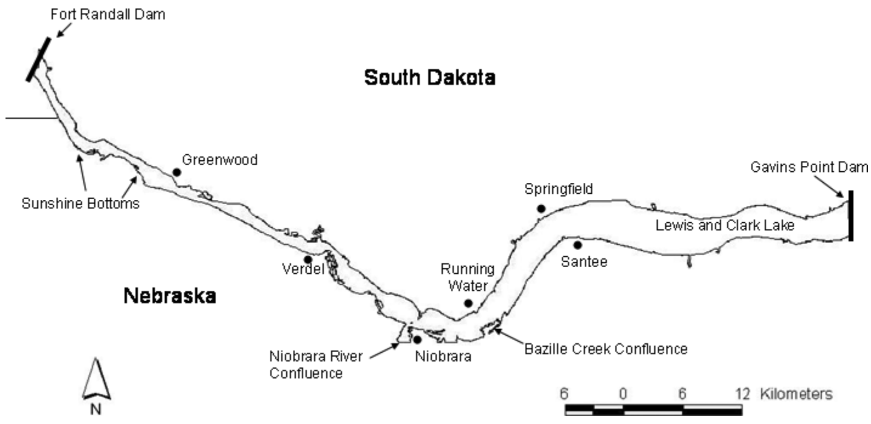

Fig. 1. Missouri River downstream of Fort Randall Dam (rkm 1,416), South Dakota to Niobrara River confluence (rkm 1,358) and Gavins Point Dam (rkm 1,305), South Dakota and Nebraska, USA. A delta has formed downstream of the Niobrara River confluence extending downstream of Santee, Nebraska, USA (rkm 1,332)

weighed to the nearest 0.01 g. For each prey type, stomach contents were expressed as frequency of occurrence, percent composition by number (Bowen, 1996), and percent composition by dry weight.

The relative importance of prey in pallid sturgeon diets was assessed by plotting prey-specific abundance (PSA_i) against percent occurrence (PO_i) (Amundsen et al., 1996). In a technique developed by Costello (1990) and later modified by Amundsen et al. (1996), prey-specific abundance is plotted against frequency of occurrence to interpret general feeding patterns of fishes. Prey-specific abundance is defined as the proportional abundance of prey *i* in predators that contain prey *i* and calculated as

$$PSA_i = \left(\sum S_i / \sum S_{ti}\right) 100,$$

where PSA_i equals prey-specific abundance of prey *i*, S_i equals the dry weight of prey *i* in stomachs, and S_{ti} equals the total dry weight of prey in predators that contain prey *i*. Although largely qualitative, graphical techniques are useful for evaluating important aspects of the fishes diet that include feeding strategy (specialized vs general) and prey importance (dominant vs rare taxa). To explore patterns of prey use, we constructed bivariate plots of PSA_i vs PO_i (Chipps and Garvey, 2007). Opportunistic feeding is represented for prey items that have low PO in the diets and a high PSA. Dominant prey items have high PO in the diets and high PSA values. Generalized feeding is characterized by prey items that have a high PO and low PSA. Rare prey items have both a low PO and low PSA value. When plotted in this fashion, graphical techniques can be used to evaluate relative prey dominance and the degree of homogeneity of the diet (Costello, 1990; Amundsen et al., 1996; Strand et al., 2008).

Ontogenetic patterns in diet composition were evaluated by plotting diet composition as a function of pallid sturgeon length and age. Known age of pallid sturgeon was determined from PIT and VIE tags. Percent composition based on dry weight of Diptera, Ephemeroptera, Trichoptera, and fish was plotted by 100 mm FL categories and age in years. To increase our sample size and size-distribution of pallids, we included summer diet data from 16 pallid sturgeon reported by Wanner et al. (2007a). These fish were collected in the Fort Randall reach from June to September 2003 and 2004.

Results

Pallid sturgeon diets

Twenty-nine pallid sturgeon (ages 2–9) were collected for diet analysis from June through September 2006, of which 21 had prey items in their stomachs. All fish were of hatchery-origin and represented six year-classes. These 21 pallid sturgeon ranged from 356 to 720 mm FL (mean = 494; SE = 25). The eight pallid sturgeon from which prey items were not recovered ranged from 495 to 711 mm FL (mean = 603, SE = 30). Based on age and length, pallid sturgeon in our study consisted of juveniles and sub-adults. The predominant prey items, based on percent occurrence, were Ceratopogonidae (81.0%), Isonychiidae (66.7%), Chironomidae (52.4%), and fishes (24.0%; Table 1). Based on percent composition by dry weight, diets were composed of fishes (65.8%), Ephemeroptera (24.2%), Decapoda (7.3%), and Diptera (2.0%; Table 1).

Table 1
Number (N), frequency of occurrence, mean percent composition by number, and mean percent composition by dry weight for prey items recovered from 21 pallid sturgeon (*S. albus*) stomachs in summer of 2006 in the Missouri River downstream of Fort Randall Dam, South Dakota and Nebraska, USA

Prey item	*N*	Frequency of occurrence (%)	Percent composition by number (%)	Percent composition by dry weight (%)
Diptera	309	81.0	36.8	2.05
Chironomidae	29	52.4	3.5	0.42
Simulidae	1	5.0	0.1	0.02
Ceratopogonidae	279	81.0	33.2	1.61
Ephemeroptera	499	90.5	59.3	24.24
Isonychiidae	371	66.7	44.1	19.93
Caenidae	116	33.3	13.8	2.24
Pseudironidae	11	23.8	1.3	1.89
Polymitarcyidae	1	4.8	0.1	0.17
Trichoptera	4	19.0	0.5	0.31
Hydropsychidae	4	19.0	0.5	0.31
Plecoptera	1	4.8	0.1	0.17
Perlodidae	1	5.0	0.1	0.17
Decapoda	1	5.0	0.1	7.32
Astacidae	1	5.0	0.1	7.32
Hymenoptera	1	5.0	0.1	0.03
Formicidae	1	5.0	0.1	0.03
Fish	26	24.0	3.1	65.87
Johnny Darter	24	19.1	2.9	65.65
Channel Catfish	1	4.8	0.1	0.21
Unidentified Fish	1	4.8	0.1	0.01

Relative prey importance

Pallid sturgeon diets were primarily composed (% dry weight) of fishes and Ephemeroptera, especially johnny darters *Etheostoma nigrum* and Isonychiidae. Graphical analysis based on dry weights, showed that Isonychiidae was the dominant prey item in the diets. Johnny darters, Decapoda (Astacidae), and Polymitarcyidae were opportunistically consumed, whereas pallid sturgeon showed generalized feeding patterns on Ceratopogonidae and Chironomidae. Johnny darters represented a high proportion of consumed prey but occurred in only 20% of pallid sturgeon diets, while Diptera occurred in > 50% of the diets but represented a small proportion of consumed prey. Rare prey items included Caenidae, Pseudironidae, Hydropsychidae, Perlodidae, Simulidae, channel catfish *Ictalurus punctatus*, unidentifiable fish, and Formicidae. Graphical analysis of diet composition showed that mayflies, particularly Isonychiidae, were an important component of pallid sturgeon diets (Fig. 2). In general, the percent of fishes in pallid sturgeon diets (mostly johnny darters) increased with body size, whereas the proportion of mayflies (Ephemeroptera) decreased especially for pallid sturgeon ≥ 600 mm FL (Fig. 3) and fish ≥ 5 years of age (Fig. 4). In pallid sturgeon > 600 mm FL and > age 7, one of the two fish sampled had a decapod in its diet, consequently biasing the percent composition (> 88%) by dry weight towards the other category which included Decapoda, Plecoptera, and Hymenoptera (Figs 3 and 4).

Discussion

In 2006, fishes and Ephemeroptera, especially johnny darters and *Isonychia* spp. were predominant prey items in pallid sturgeon diets. Even though pallid sturgeon in this study consumed more macroinvertebrates in terms of numbers of

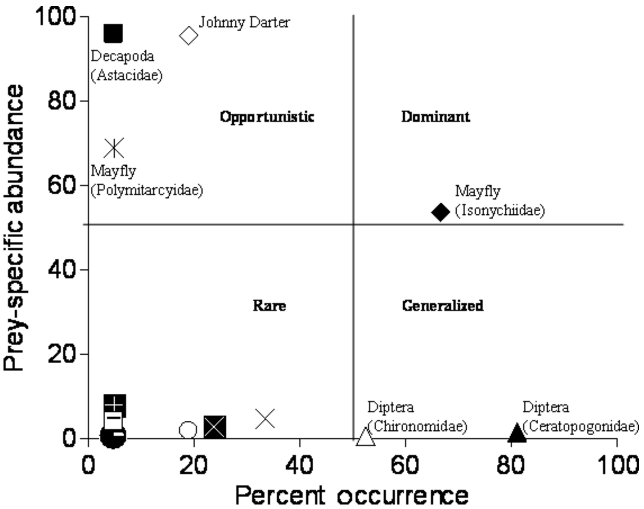

Fig. 2. Graphical representation of prey-specific abundance (% dry wt) vs percent occurrence from diets of 21 pallid sturgeon (*S. albus*), Missouri River downstream of Fort Randall Dam, South Dakota and Nebraska, USA, June – September 2006. The four quadrants represent feeding strategy (generalized and opportunistically consumed) and prey importance (dominant and rare taxa). Rare prey items included Caenidae (X), Pseudironidae (☒), Hydropsychidae (O), Perlodidae (☐), Simulidae (⊟), channel catfish (•), unidentifiable fish (⊞), and Formicidae (–) (adapted from Amundsen et al., 1996)

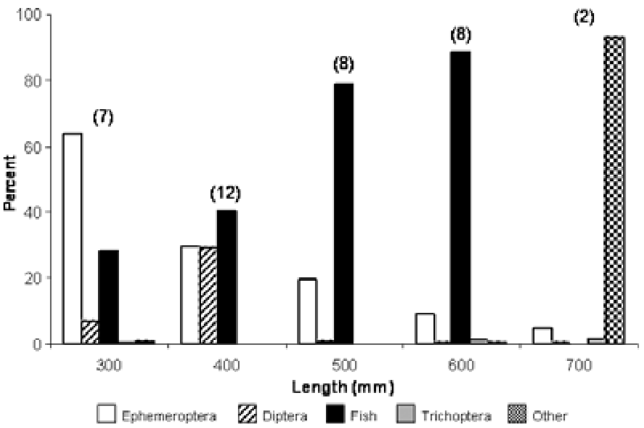

Fig. 3. Percent composition by dry weight from diets of 37 pallid sturgeon (*S. albus*), Missouri River downstream of Fort Randall Dam, South Dakota and Nebraska, USA, June – September 2003, 2004, and 2006 by 100 mm fork length category (numbers of fish in parentheses). Other taxa included Plecoptera, Hymenoptera, and Decapoda

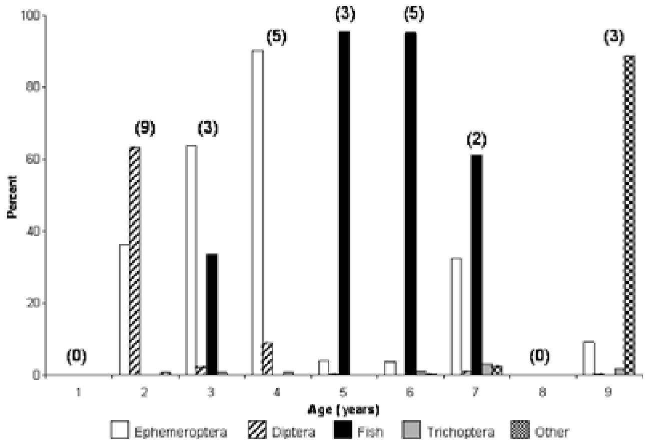

Fig. 4. Percent composition by dry weight from diets of 30 pallid sturgeon, Missouri River downstream of Fort Randall Dam, South Dakota and Nebraska, USA, June–September 2003, 2004, and 2006 by age in years (numbers of fish in parentheses). Other taxa included Plecoptera, Hymenoptera, and Decapoda

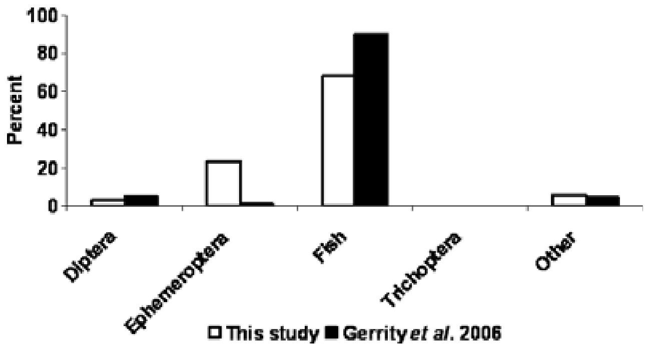

Fig. 5. Percent composition by wet weight of Diptera, Ephemeroptera, fish, Trichoptera, and other prey in diets of pallid sturgeon (*S. albus*) sampled in Missouri River upstream of Fort Peck Reservoir, Montana, USA, 2003 – 2004 (Gerrity et al., 2006; $N = 50$) and downstream of Fort Randall Dam, South Dakota, USA, 2006 (this study; $N = 21$). Other taxa included Plecoptera, Hymenoptera, and Decapoda

prey, fishes (mostly johnny darters) generally made up a larger proportion of the diet by weight as shown in previous studies (Gerrity et al., 2006; Wanner et al., 2007a). However, based on our graphical analysis, Ephemeroptera (mostly Isonychiidae) represented a dominant prey item, occurring in a high proportion of the diets sampled and representing an appreciable amount of consumed prey. These patterns are difficult to discern from simple diet measures (i.e., % by number or mass) and illustrate the importance of macroinvertebrates as a food source for pallid sturgeon, especially for fish < 600 mm FL.

Diet composition of pallid sturgeon, like other fishes, can vary seasonally (Wanner et al., 2007a) or among locations (Carlson et al., 1985; Gerrity et al., 2006; Hoover et al., 2007). In this study, we found that fish composed the greatest portion of the diets (66%), followed by Ephemeroptera (24%). In a similar study on the Missouri River, downstream of Fort Randall Dam, Wanner et al. (2007a) showed that fish composed 38% of pallid sturgeon diets, followed by Diptera (29%) and Ephemeroptera (28%). In a relatively unaltered stretch of the Missouri River above Fort Peck Reservoir, Montana, USA, native benthic cyprinids, especially sturgeon chub *Macrhybopsis gelida* and sicklefin chub *M. meeki*, were important in pallid sturgeon diets, composing 90% of the diets by wet weight (Fig. 5; Gerrity et al., 2006). Additionally, in a study in the Mississippi River, the primary prey for pallid sturgeon was larval Hydropsychidae followed by Ephemeroptera, Diptera, speckled chub *M. aestivalis*, and silver chub *M. storeriana* (Hoover et al., 2007). In terms of wet weight, pallid sturgeon in the Fort Randall reach of the Missouri River relied less on fishes as a prey source than fish in the upper Missouri River in Montana (Fig. 5).

Prey fish assemblages for pallid sturgeon in the Missouri River differ between Montana and South Dakota. Downstream of Fort Randall Dam, johnny darters and channel catfish are present; however, no sturgeon chubs or sicklefin chubs were collected from 2003 to 2006 in this reach of the Missouri River (Shuman et al., 2005, 2006, 2007; Hoagstrom et al., 2006; Kaemingk et al., 2007). In the upper Missouri River, Montana and North Dakota, native cyprinids such as sturgeon chubs and sicklefin chubs are moderately abundant in main channel habitats (Gardner, 2004; Welker and Scarnecchia, 2004). However, johnny darters are absent in the upper Missouri River, Montana (Brown, 1971). Throughout the Missouri River, declines of sturgeon chubs and sicklefin chubs have occurred (Galat et al., 2005). Pallid sturgeon can opportunistically forage on other species, such as johnny darters and channel catfish that are present in the Fort Randall reach. The lack of native cyprinids available to pallid sturgeon in the Fort Randall reach may be reflected in the high proportions of macroinvertebrates in the diet.

Macroinvertebrates frequently consumed by pallid sturgeon such as Chironomidae, Ceratopogonidae, Isonychiidae, Caenidae, and Hydropsychidae are relatively abundant in the Fort Randall reach, especially in the delta formed downstream of the Niobrara and Missouri river confluence (Grohs, 2008). In this study, 72% of pallid sturgeon sampled were collected in the delta. All of the major prey items collected in the pallid sturgeon diets except Chironomidae have been found to be generally more abundant in the delta area (Grohs, 2008). Jordan et al. (2006) reported that pallid sturgeon were primarily located in the main channel, although 14 pallid sturgeon were located in the delta in 2002. In the delta downstream of Fort Randall Dam, Shuman et al. (2005, 2006) collected five pallid sturgeon in 2004 – 2005 and 27 pallid sturgeon from 2005 - 2006. Spindler (2008) found that pallid sturgeon capture areas had higher densities of drifting Ephemeroptera and Diptera compared to non-capture areas, with most capture areas located in the delta of the Missouri River downstream of Fort Randall Dam. Sediment transport and habitat formation is dynamic in the delta, which has increased habitat diversity and has the potential to enhance production of macroinvertebrates and be key feeding areas for fish (Kaemingk et al., 2007), including pallid sturgeon.

Although pallid sturgeon have been hypothesized to undergo an ontogenetic diet shift to piscivory, information on the size and ⁄ or age at which this occurs has been lacking. In the Fort Randall reach, we found that pallid sturgeon < 600 mm FL relied on macroinvertebrates as their primary prey, but increased their reliance on fishes substantially when they exceeded 600 mm FL. This reliance on fishes was also apparent in the diets of pallid sturgeon ≥ 5 years of age, which suggested that pallid sturgeon undergo an ontogenetic diet shift to piscivory between 5 to 7 years of age. Similarly, Gerrity et al. (2006) found that sub-adult and adult pallid sturgeon (≥ age 6) were piscivorous and preyed upon native riverine cyprinid species; however, the size range (and subsequently age range) of fish in their study was likely too narrow to assess presence of an ontogenetic diet shift. Our study supports the notion that pallid sturgeon undergo an ontogenetic diet shift by switching from macroinvertebrates to fish prey at sizes > 600 mm (or approximately 5–7 years of age). These observations lend support to the current pallid sturgeon stocking plan (U.S. Fish and Wildlife Service, 2008) that piscivory becomes important for pallid sturgeon and, hence, should be considered in recovery efforts.

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Author's address: Kristen L. Grohs, U.S. Fish and Wildlife Service, Great Plains Fish and Wildlife Conservation Office, Pierre, SD 57501, USA.
E-mail: Kristen_Grohs@fws.gov