



Diet composition and overlap of larval pallid sturgeon and shovelnose sturgeon from the upper Missouri River, USA

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ABSTRACT: Early life stages of pallid sturgeon *Scaphirhynchus albus* are rarely collected, and thus information on their biology and ecology is extremely limited. We sampled 75 larval pallid sturgeon (25–110 mm) and 148 larval shovelnose sturgeon *S. platyrhynchus* (15–95 mm) by trawl from the upper Missouri River (USA) in 2019. Stomach contents were identified to compare food use and diet overlap between the 2 sturgeon species at the order, family, and genus levels of taxonomic prey identification. Analyses were conducted with sites pooled and with sites separated by the confluence of the Yellowstone River (upper and lower). Abundance of dominant prey in the gut (Diptera larvae) increased with fish length for both species, and regression slopes were similar. Diet overlap at pooled sites decreased from 0.94 to 0.49 when prey were identified to order and genus, respectively, and decreases in diet overlap at individual sites were more pronounced. Larval pallid sturgeon consumed a maximum of 11 unique taxa, whereas shovelnose sturgeon consumed 6 taxa that were not consumed by pallid sturgeon. These results indicate that larval diets are similar between species when evaluated at coarse taxonomic scales, but at fine taxonomic scales, notable differences exist. As information about the diets of larval pallid sturgeon captured from a riverine environment are scarce and the use of shovelnose sturgeon as an indicator of available suitable food and habitat and as a dietary surrogate for pallid sturgeon has been under consideration, our results suggest that caution be exercised in modeling efforts or management actions relating to surrogacy.

KEY WORDS: Pallid sturgeon · *Scaphirhynchus albus* · Shovelnose sturgeon · *Scaphirhynchus platyrhynchus* · Diet · Early life history

1. INTRODUCTION

The pallid sturgeon *Scaphirhynchus albus* is a long-lived fluvial fish that was designated in the USA as a federally endangered species in 1990 (US Fish and Wildlife Service 1990). Pallid sturgeon were historically distributed throughout the Missouri River,

some of its major tributaries, and in the Mississippi River downstream of the Missouri River confluence (Bailey & Cross 1954). Presently, in the Missouri River, pallid sturgeon persist upstream of Fort Peck Reservoir in Montana, in a disjunct population between Fort Peck Reservoir and Lake Sakakawea, North Dakota, and downstream from Gavins Point

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Dam, South Dakota, to the Mississippi River (Jordan et al. 2016). Missouri River dams and reservoirs have been shown as factors affecting spawning and a lack of recruitment for decades through their hypolimnetic releases, regulated flows, fragmentation, and disruption of life-stage processes (US Fish and Wildlife Service 2014, Jordan et al. 2016).

In this study, we focused on the diet composition of larval pallid sturgeon after transitioning from endogenous-feeding free embryos, settling into nursery habitat from the drifting stage of their life cycle, and beginning exogenous feeding. Laboratory studies provide some insight into this life stage (~18 mm; Rapp 2014, Deslauriers et al. 2016), but information on fish collected from a natural riverine environment is scarce. Several studies have assessed diets of larval pallid sturgeon, but because pallid sturgeon larvae are rarely captured in the wild, sample sizes in these studies were low (e.g. ≤ 10) (Braaten et al. 2012, Gosch et al. 2018, 2019)

Shovelnose sturgeon *S. platyrhynchus* are sympatric with pallid sturgeon in the Missouri River. Shovelnose sturgeon are common and are hypothesized to share many life history characteristics with pallid sturgeon (Wildhaber et al. 2007). On this basis, there is growing interest in using shovelnose sturgeon as a surrogate species for understanding pallid sturgeon early life-history characteristics such as requirements for shallow-water rearing habitat (Gemeinhardt et al. 2016) and diets (Gosch et al. 2018, 2019). Use of shovelnose sturgeon as a proxy has been suggested (Gosch et al. 2018, 2019) due to the paucity of information on larval pallid sturgeon captured from the wild, which poses an interesting dilemma. Pallid sturgeon larvae captured from the wild are exceptionally rare, and therefore shovelnose sturgeon might function as a surrogate under certain circumstances; however, to assess this hypothesis, it is necessary to have a large data set from which the comparisons can be made.

In July 2019, an experimental release of nearly 1 million pallid sturgeon free embryos (1 and 5 d post hatch, dph) was conducted in the upper Missouri River of Montana (Braaten & Holley 2021, Braaten et al. 2022). A portion of the 5 dph age group transitioned from dispersing free embryos to settled benthic-feeding larvae in downstream reaches where naturally produced shovelnose sturgeon larvae also occurred. Feeding larvae of both species were captured over several weeks in summer–fall 2019 and provided the opportunity to address the following objectives: (1) quantify the diets of larval pallid sturgeon and shovelnose sturgeon from the upper Mis-

souri River; and (2) compare diets between these species to determine overlap.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in a 64 km reach of the upper Missouri River in Montana and North Dakota, between river kilometers (rkm; distance upstream from the Missouri River and Mississippi River confluence) 2499 and 2563 (Fig. 1). The Missouri River upstream of the confluence (UTC) of the Yellowstone River is primarily influenced by regulated hypolimnetic releases from Fort Peck Dam (Bowen et al. 2003), and suppressed water temperatures persist for over 300 rkm, gradually increasing downstream (Erwin et al. 2018). The Missouri River downstream of the confluence (DTC) of the Yellowstone River is also affected by releases from Fort Peck Dam, but flow and water temperature conditions are improved by the mostly natural temperature and flow additions from the Yellowstone River (Bowen et al. 2003, DeLonay et al. 2016).

2.2. Collections of sturgeon larvae

We sampled for sturgeon larvae in 8 river bends, of which 4 were located at the UTC site and 4 were located at the DTC site. Sampling for pallid sturgeon larvae at the 8 bends targeted fish that had settled as benthic larvae following the 1 July 2019 release at rkm 2739.0 of nearly 772 000 free embryos at 1 dph and 201 000 free embryos at 5 dph (Braaten et al. 2022). Sampling also targeted wild-produced shovelnose sturgeon larvae originating from spawning events in the Missouri River and Yellowstone River (Braaten & Fuller 2007). We used benthic beam trawls (Grisak 1996, Braaten et al. 2007) to sample at the 8 bends for 9 consecutive weeks from 16 July to 11 September 2019. Within each bend, we sampled 3 habitats including the inside bend, outside bend, and channel crossover (Braaten et al. 2007). The trawl was deployed for a target duration of 4 min. Following trawl deployment, detritus was rinsed from the cod end of the net into a bucket of water and sieved, and fish were placed into a separate bucket of water. If a larval *Scaphirhynchus* sturgeon was collected, additional trawls (up to 8) were conducted in the same location to potentially increase sample size. If no larval sturgeon were caught in the initial trawl,

no additional trawls were performed. Because larval *Scaphirhynchus* spp. cannot be unequivocally identified with morphometrics as pallid sturgeon or shovelnose sturgeon at small sizes, a fin clip from each fish was obtained for genetic analysis. As larval *Scaphirhynchus* spp. lack a well-defined fork in the caudal fin, total length (TL, excluding the caudal filament) was measured to the nearest 1.0 mm, and each sturgeon was preserved in 95% non-denatured ethanol. Sturgeon ≤ 50 mm were placed in individual vials and those > 50 mm were placed in individual Whirl-Pak flat wire bags.

2.3. Species identification

Single-nucleotide polymorphism (SNP) markers were initially used to screen larval *Scaphirhynchus* spp. (Eichelberger et al. 2014). Larvae with SNP genotypes consistent with pallid sturgeon were genotyped at 19 microsatellite loci (McQuown et al. 2000) and analyzed following the protocols of Jordan et al. (2019) to confidently assign each individual as pallid sturgeon or shovelnose sturgeon. For individuals identified as pallid sturgeon, a genetic parental analysis (DeHaan et al. 2008) was used to assign the pallid sturgeon larvae to parental stocks used to produce the 1 and 5 dph released free embryos (Braaten et al. 2022).

2.4. Diet processing

The pallid sturgeon larvae and a subsample of shovelnose sturgeon larvae were used for dietary analysis. Only those shovelnose sturgeon larvae caught in the same trawl or at the same macrohabitat within the same site as pallid sturgeon were used in this dietary analysis. The stomach and esophagus were extracted from each individual and placed into an individually numbered vial containing 95% non-denatured ethanol that corresponded to the field collection data. Macroinvertebrate organisms were identified to the lowest practical taxonomic level (e.g. genus) and enumerated using a binocular dissecting microscope (Nikon SMZ45). For incomplete specimens, head capsules were used to identify to the low-

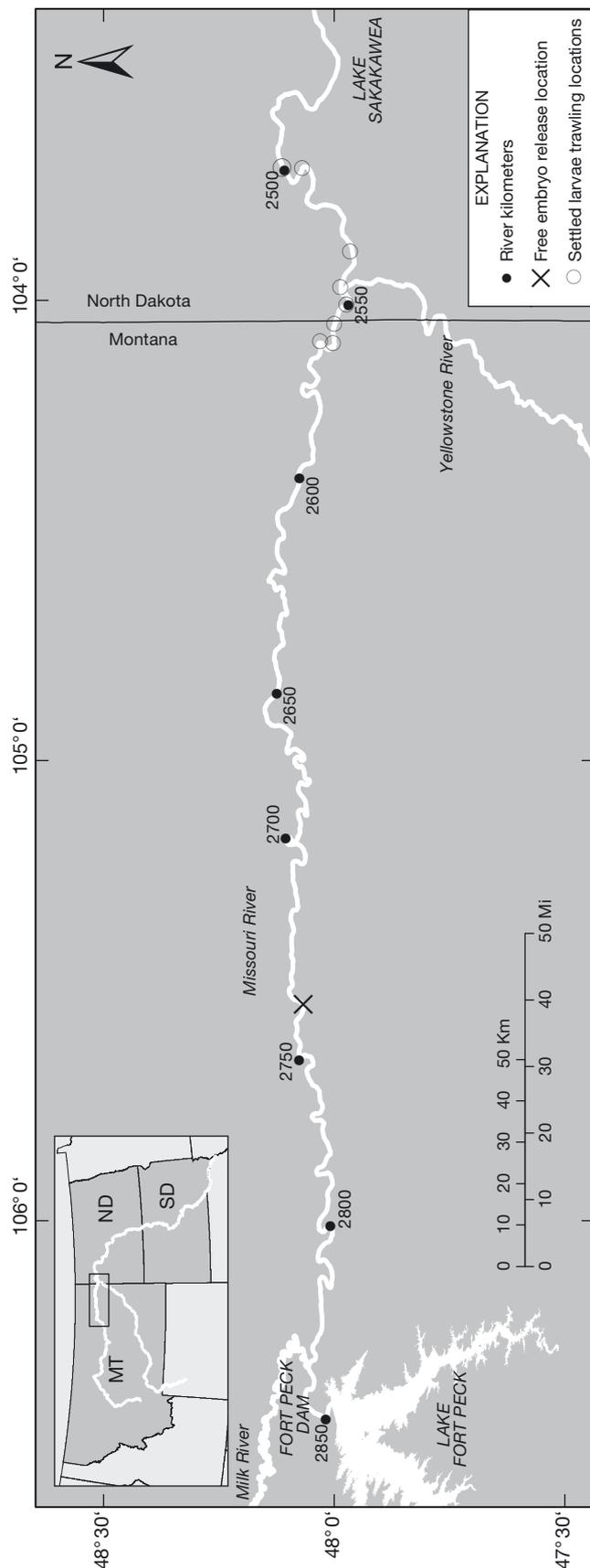


Fig. 1. Study area on the Missouri River in Montana (MT) and North Dakota (ND), USA, with pallid sturgeon *Scaphirhynchus albus* free embryo release location and trawl sampling locations shown. SD: South Dakota

est practical taxonomic level. Standard taxonomic references were used for insect identification (Merritt et al. 2008). Larval midge specimens (Diptera: Chironomidae) were mounted on labeled glass slides with CMCP-10 mounting media (Masters Chemical) and allowed to cure for 1 mo before identification with the use of a compound microscope (Nikon SMZ1270).

2.5. Statistical analysis

We used ANCOVAs to compare the number of numerically dominant macroinvertebrates consumed by order (i.e. Diptera and Ephemeroptera) between pallid sturgeon and shovelnose sturgeon, using length as a covariate to control for fish size. Three ANCOVAs were conducted. The first tested for differences between pallid sturgeon and shovelnose sturgeon across all sites (i.e. pooled sites), whereas the other 2 ANCOVAs tested for diet differences within only the UTC site or the DTC site (i.e. site analysis). The site analysis was conducted because of the disparity in numbers of pallid sturgeon and shovelnose sturgeon captured at sites on the Missouri River upstream and downstream of the Yellowstone River confluence. Numbers of macroinvertebrates were natural log-transformed prior to ANCOVAs. Pearson's correlation coefficient was calculated on the most abundant prey taxa by fish length for each fish species.

Diet overlap between pallid and shovelnose sturgeon was calculated using Morisita's overlap index (Morisita 1959). Morisita's index was calculated for pooled sites, the UTC site, and the DTC site for each level of taxonomic macroinvertebrate prey identification (i.e. order, family, and genus). We evaluated diet composition at multiple taxonomic scales because processes such as niche partitioning or competition between species may occur at the different scales (Shuai et al. 2019). Because not every diet item could be identified to the lowest taxonomic levels, analyses at family and genus scales include unidentified prey of higher taxonomic scales. Morisita's index was calculated using the 'dietOverlap' function of the 'FSAmisc' package in R (Ogle 2015). The formula for Morisita's index is:

$$M = \frac{2 \sum_i^n p_{ij} p_{ik}}{\sum_i^n p_{ij} \left[\frac{(n_{ij} - 1)}{(N_j - 1)} \right] + \sum_i^n p_{ik} \left[\frac{(n_{ik} - 1)}{(N_k - 1)} \right]} \quad (1)$$

where M is Morisita's index of niche overlap between species j and k , p_{ij} (p_{ik}) is the proportion that

resource i represents of the total resources used by species j (k), n_{ij} (n_{ik}) is the number of individuals of species j (k) that used resource category i , and N_j (N_k) is the total number of individuals of species j (k) in the sample. Values range from 0 (no overlap) to 1.0 (complete overlap). We selected the Morisita's index because of its general lack of bias and ability to handle low sample sizes (Smith & Zaret 1982, Krebs 1999).

To further compare the diets between pallid and shovelnose sturgeon, we calculated 2 additional diet measures which were performed on each species without site consideration to increase sample size. Frequency of occurrence (O) provides information on rare versus dominant prey by evaluating how often a prey type is consumed; however, it does not provide any information about the relative importance of that prey in the overall diet (Chipps & Garvey 2007). Mathematically, frequency of occurrence is expressed as:

$$O_i = \frac{n_i}{T} \quad (2)$$

where O_i is the frequency of occurrence of prey taxon i , n_i is the number of fish that consumed prey taxon i , and T is the total number of fish with any prey items in their stomachs. Two types of diet item abundance were used: (1) abundance, where all specimens of a given taxon were summed within each species, and (2) prey-specific abundance based on the percentage a prey taxon comprises of all prey taxa in only the predators that consumed that prey (Amundsen et al. 1996). The equation for prey-specific abundance is:

$$A_i = \left(\frac{\sum S_i}{\sum S_t} \right) 100 \quad (3)$$

where A_i is the prey-specific abundance for prey i , S_i is the total number of prey i in stomach contents, and S_t is the total number of prey i in only predators that consumed prey i .

Prey-specific abundance was plotted by frequency of occurrence in a bivariate plot to visualize the diet composition of pallid and shovelnose sturgeon diets (see Fig. 3). Interpretations about diet composition from the bivariate plot of prey-specific abundance and frequency of occurrence can be made along 3 axes, including feeding strategy, prey importance, and niche width (Amundsen et al. 1996, Chipps & Garvey 2007). All analyses were performed in the statistical software R (version 4.1.0; R Core Team 2021) using the 'tidyverse' package (version 1.3.1; Wickham et al. 2019) for data manipulation and figure creation.

3. RESULTS

3.1. Fish collection

During the course of this study, we conducted 625 trawls across the 8 sites during the 9 wk sampling period. Trawling captured 705 larval *Scaphirhynchus* spp., of which 83 larvae were genetically confirmed as pallid sturgeon that survived from the original release of 5 dph free embryos. No larvae from the 1 dph free embryos were captured during trawling. The water temperature during the sampling period was 13.8–22.2°C (mean = 18.6°C) at UTC sites and 15.4–24.9°C (mean = 21.0°C) at DTC sites (Braaten & Holley 2021). Eight pallid sturgeon larvae stored in Whirl-Pak bags became desiccated, and stomach contents could not be extracted. Therefore, stomach and esophagus contents were extracted and identified for 75 of the pallid sturgeon captured. In addition, 622 shovelnose sturgeon larvae were captured during the sampling period, of which 148 were subsampled for use in the diet analysis contingent on the fish being captured concurrently with pallid sturgeon or in the same macrohabitats within a site. Only 5 of the 75 larval pallid sturgeon were collected at DTC sites. Conversely, only 10 of the 148 larval shovelnose sturgeon were captured at UTC sites. Pallid sturgeon TL ranged from 25 to 110 mm, and shovelnose sturgeon TL ranged from 15 to 95 mm (Table 1).

3.2. Diet analysis

We identified 4445 prey items from larval pallid and shovelnose sturgeon (Table 2; Holley et al. 2022). All *Scaphirhynchus* spp. examined had consumed at least 1 prey item; none had totally empty stomachs. Three orders of aquatic macroinvertebrates were identified: Diptera, Ephemeroptera, and Odonata. At all sites, pallid sturgeon larvae consumed 2602 Diptera (UTC: 1371, DTC: 1231), 44 Ephemeroptera (UTC: 35, DTC: 9), and 1 Odonata (UTC: 0, DTC: 1; Table 2). Shovelnose sturgeon consumed 1651 Diptera (UTC: 221, DTC: 1430), 147 Ephemeroptera (UTC: 6, DTC: 141), and 0 Odonata. At finer taxonomic scales, the dominant prey items were *Dasyhelea* (Diptera: Ceratopogonidae), Chironomidae (Diptera), and *Stictochironomus* (Diptera: Chironomidae). The ceratopogonids in this study were identified to the subfamily Dasyheleinae, which contains only a single genus (Merritt et al. 2008). For this rea-

son, all of these specimens were recorded as *Dasyhelea*. Of these major prey items, pallid sturgeon consumed a total of 1486 *Dasyhelea*, 829 Chironomidae excluding *Stictochironomus*, and 270 *Stictochironomus*. Shovelnose sturgeon consumed in total 691 *Dasyhelea*, 677 Chironomidae excluding *Stictochironomus*, and 106 *Stictochironomus*. Despite capturing nearly twice as many shovelnose sturgeon, the stomach contents of pallid sturgeon contained many more diet items in total, 2647 (mean = 10.8) versus 1798 (mean = 4.0), respectively.

Unique taxa (those consumed by one sturgeon species but not the other) found in the stomachs of each species varied between pooled sites and in the site analysis. At the pooled site scale, pallid sturgeon diets contained 5 unique taxa (*Chironomus*, *Paratendipes*, *Phaenopsectra*, *Orthocladus* [Diptera: Chironomidae]; Gomphidae [Odonata]), whereas shovelnose sturgeon diets contained 2 unique taxa (*Cricotopus* [Diptera: Chironomidae]; *Homoeoneuria* [Ephemeroptera: Oligoneuriidae]; Table 2). Examination of species consumption by UTC and DTC sites reduced the sample size considerably, but there were notable differences in the 10 unique prey items ingested. Upstream of the confluence of the Yellowstone River, pallid sturgeon consumed 8 unique genera (i.e. *Chironomus*, *Paracladopelma*, *Paratendipes*, *Phaenopsectra*, *Polypedilum*, *Orthocladus*, *Monodiaemesa* [Diptera: Chironomidae]; and *Caenis* [Ephemeroptera: Caenidae]) not consumed by larval shovelnose sturgeon at the same sampling sites. Shovelnose sturgeon larvae at UTC sites consumed 1 genus (i.e. *Cryptochironomus* [Diptera: Chironomidae]) that pallid sturgeon did not. Numbers of each of these unique prey taxa occurred in low abundance (maximum n = 19; *Monodiaemesa*). At

Table 1. Summary statistics for total length of larval pallid sturgeon *Scaphirhynchus albus* and shovelnose sturgeon *S. platyrhynchus* captured on the upper Missouri River, USA, at all sites (Pooled), and at sites upstream (UTC) and downstream (DTC) of the Yellowstone River confluence (Holley et al. 2022)

Site	Species of sturgeon	Total length (mm)				n
		Min	Max	Mean	SD	
Pooled	Pallid	25	110	49.7	18.7	75
Pooled	Shovelnose	15	95	35.2	11.2	148
DTC	Pallid	35	110	70.2	25.0	10
DTC	Shovelnose	15	95	34.7	9.8	143
UTC	Pallid	25	97	46.5	15.5	65
UTC	Shovelnose	26	92	50.4	30.0	5

Table 2. Taxa identified in the diet of larval pallid sturgeon *Scaphirhynchus albus* and shovelnose sturgeon *S. platyrhynchus* in the upper Missouri River (Holley et al. 2022) shown with count of invertebrates (n), first quartile, median, third quartile, and range values. N represents the number of pallid or shovelnose sturgeon that consumed a given prey type. Prey items were identified to the lowest taxonomic level possible

Order	Family	Genus	Pallid					Shovelnose						
			n	25% Quartile	Median	75% Quartile	Range	N	n	25% Quartile	Median	75% Quartile	Range	N
Diptera			16	0	0	0	0–4	8	176	0	0	2	0–12	70
Diptera	Ceratopogonidae	<i>Dasyhelea</i>	1486	0	1	3.5	0–427	45	691	1	0	3	0–163	87
Diptera	Simuliidae		1	0	0	0	0–1	1	1	0	0	0	0–1	1
Diptera	Chironomidae		785	5	9	15	0–41	73	639	4	2	6	16	139
Diptera	Chironomidae	<i>Beckidia</i>	8	0	0	0	0–2	7	9	0	0	0	0–2	6
Diptera	Chironomidae	<i>Chironomus</i>	3	0	0	0	0–1	3	0	0	0	0	0	0
Diptera	Chironomidae	<i>Cryptochironomus</i>	1	0	0	0	0–1	1	3	0	0	0	0–1	3
Diptera	Chironomidae	<i>Paracladopelma</i>	2	0	0	0	0–1	2	18	0	0	0	0–3	10
Diptera	Chironomidae	<i>Paratendipes</i>	1	0	0	0	0–1	1	0	0	0	0	0	0
Diptera	Chironomidae	<i>Phaenopsectra</i>	2	0	0	0	0–1	1	0	0	0	0	0	0
Diptera	Chironomidae	<i>Polypedilum</i>	2	0	0	0	0–1	2	2	0	0	0	0–1	2
Diptera	Chironomidae	<i>Stictochironomus</i>	270	1	3	5	0–14	58	106	0	0	1	0–6	53
Diptera	Chironomidae	<i>Cricotopus</i>	0	0	0	0	0	0	1	0	0	0	0–1	1
Diptera	Chironomidae	<i>Orthocladus</i>	1	0	0	0	0–1	1	0	0	0	0	0	0
Diptera	Chironomidae	<i>Monodiamesa</i>	24	0	0	0	0–5	18	5	0	0	0	0–1	5
Ephemeroptera			22	0	0	0	0–6	12	80	0	0	1	0–5	48
Ephemeroptera	Caenidae	<i>Caenis</i>	5	0	0	0	0–2	3	61	0	0	0	0–15	24
Ephemeroptera	Acanthametropodidae	<i>Analetris</i>	17	0	0	0	0–9	6	5	0	0	0	0–3	2
Ephemeroptera	Oligoneuriidae	<i>Homoeoneuria</i>	0	0	0	0	0	0	1	0	0	0	0–1	1
Odonata	Gomphidae		1	0	0	0	0–1	1	0	0	0	0	0	0

DTC sites, pallid sturgeon diets contained 3 unique taxa (i.e. *Phaenopsectra*; *Analetris* [Ephemeroptera: Acanthametropodidae]; and Gomphidae), whereas shovelnose sturgeon diets contained 5 unique taxa (i.e. *Beckidia*, *Paracladopelma*, *Cricotopus* [Diptera: Chironomidae]; *Homoeoneuria*; and Diptera which could not be identified further). Similar to UTC sites, abundance of unique taxa consumed at DTC sites was low for both pallid and shovelnose sturgeon, with unidentified Diptera as an exception (n = 173).

ANCOVA across pooled sites for log-Diptera abundance indicated that the slopes were similar between pallid and shovelnose sturgeon ($F_{1,217} = 0.02$, $p = 0.89$), but the intercept was significantly different ($F_{1,218} = 9.26$, $p < 0.01$; Fig. 2A). In this pooled analy-

sis, Diptera abundance was significantly related to length for pallid sturgeon ($r^2 = 0.68$, $p < 0.01$, $n = 75$) and shovelnose sturgeon ($r^2 = 0.37$, $p < 0.01$, $n = 146$). Ephemeroptera abundance did not have a significant linear relation with fish length for pallid sturgeon ($r^2 = 0.03$, $p = 0.56$, $n = 15$) or shovelnose sturgeon ($r^2 < 0.01$, $p = 0.48$, $n = 59$). In the site analysis, sample sizes were low for pallid sturgeon DTC ($n = 10$) and shovelnose sturgeon UTC ($n = 5$), which limited statistical power. At the UTC site, the slope ($F_{1,66} = 2.05$, $p = 0.16$) and intercept ($F_{1,67} = 0.17$, $p = 0.68$) did not differ between the 2 species (Fig. 2B). Shovelnose sturgeon length had a strong relation with log-Diptera abundance ($r^2 = 0.85$, $p = 0.03$, $n = 5$), and pallid sturgeon length had a moderate relation with the response variable ($r^2 = 0.51$, $p < 0.01$, $n = 65$). At

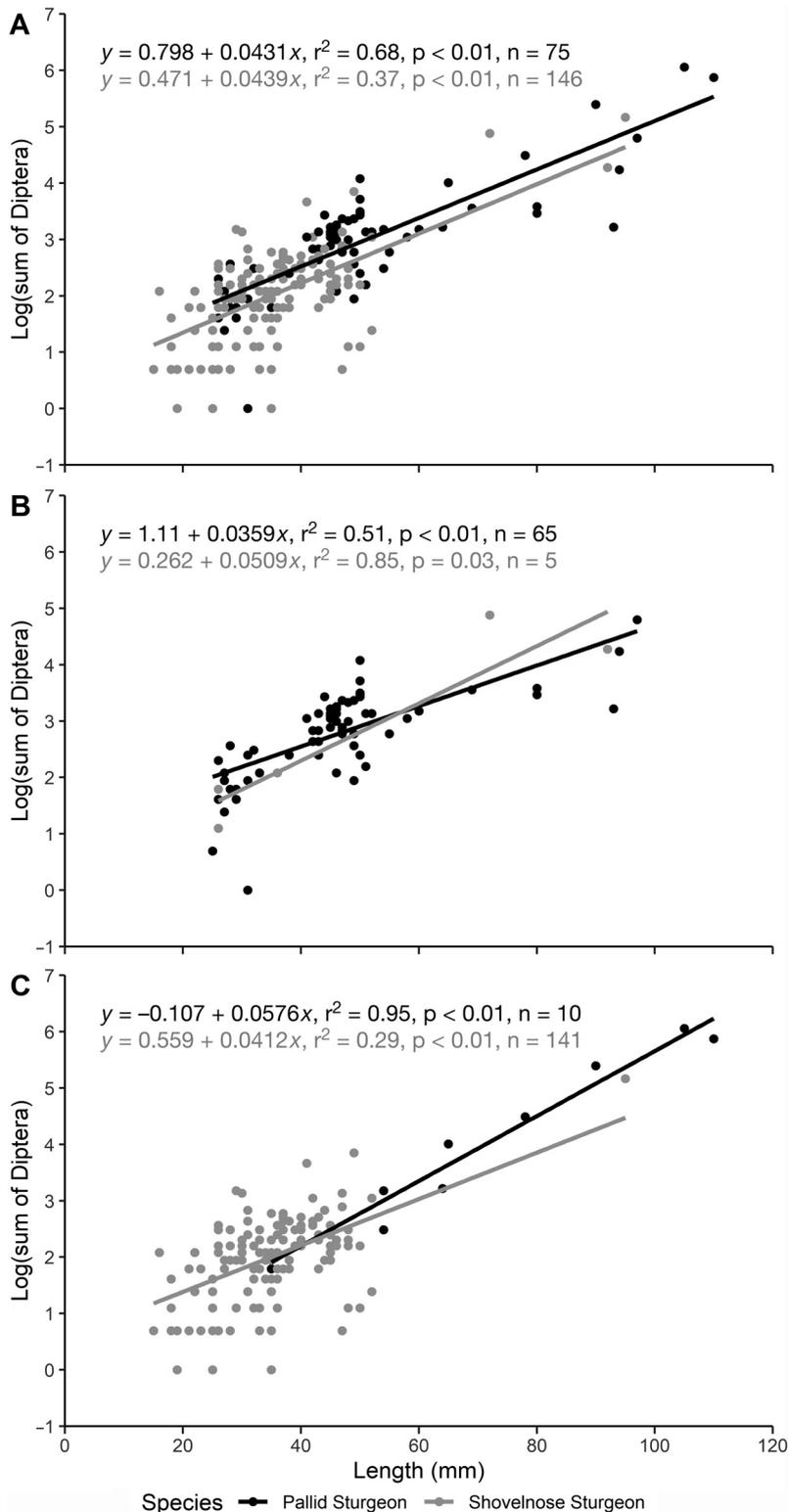


Fig. 2. Relationships between fish total length and number of Diptera in the diet (natural log-transformed) of larval pallid sturgeon *Scaphirhynchus albus* and shovelnose sturgeon *S. platyrhynchus* in the upper Missouri River across (A) all sites, (B) at the sites upstream of the confluence, and (C) downstream of the confluence of the Yellowstone River. Regression equations, R^2 values, p-values, and sample sizes are shown for each species

the DTC site, the slopes ($F_{1,147} = 2.71, p = 0.10$) and intercepts ($F_{1,148} = 1.46, p = 0.22$) between the 2 species were not significantly different (Fig. 2C). The pallid sturgeon captured DTC showed a strong relation between log-Diptera abundance and fish length ($r^2 = 0.95, p < 0.01, n = 10$), whereas the shovelnose sturgeon had a weak relation ($r^2 = 0.29, p < 0.01, n = 141$).

A Pearson's correlation coefficient was calculated with sites pooled for the 2 most abundant genera. *Dasyhelea* had a moderate positive correlation with fish length for both pallid sturgeon ($r = 0.70, p < 0.01, n = 75$) and shovelnose sturgeon ($r = 0.66, p < 0.01, n = 148$). The second most abundant genus, *Stictochironomus*, was not significantly correlated with pallid sturgeon length ($r = -0.18, p = 0.11, n = 75$), whereas *Stictochironomus* abundance had a weak positive correlation with fish length for shovelnose sturgeon ($r = 0.24, p < 0.01, n = 148$).

Diet overlap between pallid and shovelnose sturgeon was high at the taxonomic scale of order and generally decreased when examined at the scale of family and genus (Table 3). For pooled sites, Morisita's index values at order, family, and genus levels were 0.94, 0.55, and 0.49, respectively. This pattern continued in the site analysis. At the UTC site, Morisita's index was 0.97 when prey taxa were grouped by order. This overlap decreased to 0.49 at the family level and 0.45 at the genus level. At the DTC sites, diet overlap was similarly high at 0.94 when grouped by order and decreased to 0.44 by families. Overlap slightly increased to 0.45 when prey items were grouped to genus.

Examination of diet composition graphically resulted in a similar pattern for both species. The larval pallid and shovelnose sturgeon examined in this study exhibited generalist feeding patterns (Fig. 3). The pallid sturgeon diets examined exhibited moderate prey-specific abundance and fre-

Table 3. Morisita’s overlap index calculated at 3 taxonomic levels for diet items of pallid sturgeon *Scaphirhynchus albus* and shovelnose sturgeon *S. platyrhynchus* from all sites on the upper Missouri River (Pooled), and sites upstream (UTC) and downstream (DTC) of the Yellowstone River confluence. Values range from 0.0 (no overlap) to 1.0 (complete overlap)

Site	Order	Family	Genus
Pooled	0.94	0.55	0.49
UTC	0.97	0.49	0.45
DTC	0.94	0.44	0.45

quency of occurrence of *Dasyhelea*, as it is grouped in the upper right portion of Fig. 3 (Amundsen et al. 1996), reflecting a narrow niche width where 3 taxa comprised the majority of the stomach contents (i.e. *Dasyhelea*, *Stictochironomus*, and Chironomidae). Larval shovelnose sturgeon had a broader niche width than pallid sturgeon, as fewer taxa are considered rare in the diet (e.g. clustered in the lower left portion of Fig. 3). Pallid and shovelnose sturgeon both consumed chironomids at the highest frequency of occurrence. However, *Dasyhelea* were the most

dominant taxa represented in the diets of the pallid sturgeon. At the finest taxonomic scale, pallid sturgeon consumed members of the genus *Stictochironomus* at a 77.3% frequency of occurrence and a prey-specific abundance of 19.6%, indicating that this taxon exhibited high within-individual niche width variation. All other groups of prey items were considered rare, with both low frequency of occurrence and prey-specific abundance. Shovelnose sturgeon diets also had *Dasyhelea* as a dominant taxon in the diet with a prey-specific abundance of 50.5%. Unidentifiable Diptera were consumed by shovelnose sturgeon at a 47.3% frequency of occurrence and 23.0% prey-specific abundance, indicating a generalized feeding approach.

4. DISCUSSION

The rarity of wild-produced larval pallid sturgeon has resulted in few captures throughout the Missouri River basin. The hatchery-reared pallid sturgeon larvae evaluated in this study represent the largest number captured in the wild (Braaten et al. 2012, Gosch et al. 2018, 2019). Furthermore, the

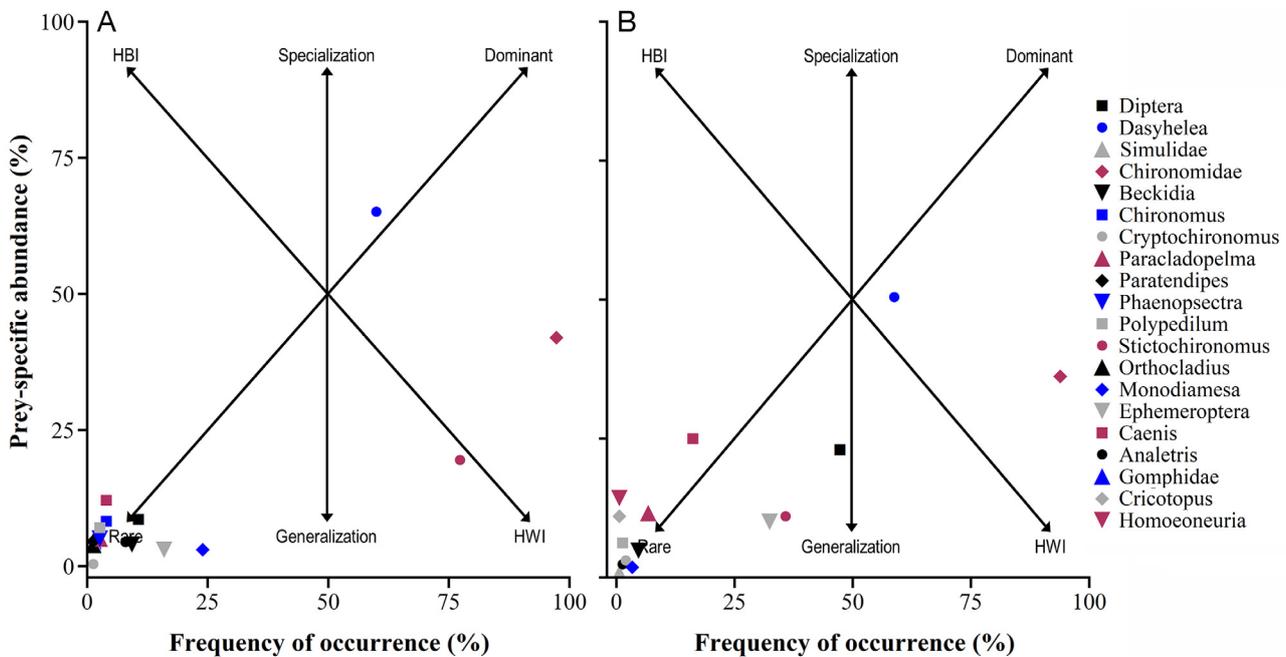


Fig. 3. Graphical model of the diet composition of larval (A) pallid sturgeon *Scaphirhynchus albus* and (B) shovelnose sturgeon *S. platyrhynchus* captured from the upper Missouri River in Montana and North Dakota, USA. Prey-specific abundance is the percentage a given prey taxon comprises of all prey taxa in only the predators that consumed that prey. Frequency of occurrence of a given prey taxon is the number of fish that consumed that prey divided by the total number of fish with any prey items in their stomachs. This method assesses the feeding strategy, relative prey importance, and niche width (high between-individual [HBI] and high within-individual [HWI] variation) of a fish population. Prey items were identified to the lowest taxonomic level possible. Adapted from Amundsen et al. (1996)

diet compositions assessed from the 75 pallid sturgeon larvae are the largest sample size of diets currently available for fish outside of a laboratory study and for larvae that have recently transitioned to exogenous feeding in a natural environment (Braaten et al. 2012, Rapp 2014, Gosch et al. 2018, 2019). Previous reports indicate that the proportion of empty stomachs in juvenile *Scaphirhynchus* spp. is usually low (Braaten et al. 2007, Harrison et al. 2014, Civiello et al. 2018). None of the fish examined in this study had empty stomachs; however, the abundance of organisms in the gut varied substantially among fish. Fish length accounted for a portion of the variation in Diptera prey abundance for both species, and it is likely that additional variation in prey abundance is related to differences in feeding cycles, gut-evacuation schedules, and foraging capabilities among larvae. Most larval pallid sturgeon collected in this study were located at UTC sites, and most shovelnose sturgeon were collected at DTC sites. Shovelnose sturgeon are found throughout the upper Missouri and lower Yellowstone Rivers (Bramblett & White 2001) and are known to spawn in both river systems (Braaten & Fuller 2007). The disparity in species numbers between sites may be because of the drifting nature of *Scaphirhynchus* spp. free embryos, and the dispersal time prior to settlement leads to many of the shovelnose sturgeon free embryos surviving and dispersing to DTC sites. However, the 5 dph pallid sturgeon released at rkm 2739.0 were developmentally advanced enough to initiate benthic settling and consequently settled at UTC sites.

Larval pallid and shovelnose sturgeon exhibited similar diet compositions at a coarse taxonomic scale but exhibited notable shifts in diet overlap at fine taxonomic scales. In total, pallid sturgeon consumed 11 unique taxa of aquatic macroinvertebrates, whereas shovelnose sturgeon consumed 6 unique taxa in the site analysis. Identifying prey items to genus expands upon previous research conducted in this study area where stomach contents of larval pallid sturgeon were identified to order and fish sample sizes were lower (Braaten et al. 2012). While in general these groups were present in stomachs in low abundances, cataloging stomach contents to the finest taxonomic scale possible may provide insight into the differences between these species and increase confidence in future management decisions relating to assumptions of diet surrogacy (Gosch et al. 2019).

We did not assess macroinvertebrate availability and abundance among habitats; thus, we cannot

directly link larval diet composition to specific foraging habitats, nor can we assess selectivity. Nonetheless, the macroinvertebrates consumed by larval pallid sturgeon and shovelnose sturgeon are taxa that have varied habitat affinities in large rivers. For example, *Dasyhelea* larvae that comprised a substantial proportion of the Dipteran diet for pallid and shovelnose sturgeon are associated with algae and other decaying plant matter (Mullen & Hribar 1988) in depositional habitats of rivers (Merritt et al. 2008). *Stictochironomus* larvae are primarily found in the sandy substrate of rivers (Na & Bae 2010), including the upper Missouri River (Burress et al. 1982), and are adapted to the higher temperatures and lower oxygen levels that can be found in large lowland rivers (Pinder 1995). The chironomid genera *Chironomus*, *Paratendipes*, *Paracladopelma*, and *Cryptochironomus* are known from lotic-depositional habitats, and *Monodiamesa* that has been documented in the Yellowstone River (Newell 1977) is associated with lotic-erosional habitats (Merritt et al. 2008). The mayfly genus *Anaetris* associates with sand in large prairie rivers, and 1 species (*A. eximia*) is a potential species of concern in Montana (Stagliano 2016). The mayfly genera *Caenis* and *Homoneuria* use lotic-depositional habitats (Merritt et al. 2008). Several Diptera genera consumed by larval pallid sturgeon in this study (i.e. *Dasyhelea*, *Beckidia*, *Chironomus*, *Phaenopsectra*, *Stictochironomus*, *Monodiamesa*) were not observed in the diet of 4 larval pallid sturgeon collected from the lower Missouri River (Gosch et al. 2019). Information about the habitat affinities of the dominant prey items identified at fine taxonomic scales may be useful as future studies continue to elucidate the feeding patterns of pallid and shovelnose sturgeon larvae in the wild.

Diet overlap between larval pallid and shovelnose sturgeon assessed by Morisita's index was high at coarse taxonomic scales (0.94–0.97) but decreased at finer taxonomic scales (0.45–0.49). To our knowledge, diet overlap has not been evaluated at varying taxonomic scales for *Scaphirhynchus* spp., with few examples available for other taxa (Shuai et al. 2019). In the lower Missouri River, Gosch et al. (2019) indicated high diet similarity between larval pallid sturgeon ($n = 4$) and larval shovelnose sturgeon ($n = 18$) based on diet organisms identified to genus and, in some cases, species. Graphical interpretation of larval pallid sturgeon and shovelnose sturgeon diet composition elucidated which taxonomic groups comprised a dominant portion of their diets or which they consumed in a more general feeding pattern.

Both species consumed chironomids at the highest frequency of occurrence in this study, and similar results have been found in other areas of the Missouri River (Sechler et al. 2012, Gosch et al. 2018). However, the genus *Dasyhelea* had a higher prey-specific abundance for each species although it was not consumed by as large a proportion of the individuals examined. Both species consumed most prey items that could be identified to genera at low abundances. *Stictochironomus* is an exception, as larval pallid sturgeon consumed this group more than any other genus. Increased understanding of the diets of larval pallid and shovelnose sturgeon in the upper Missouri River basin through this type of analysis may aid future pallid sturgeon early life history management efforts.

Diet surrogacy of larval shovelnose sturgeon for pallid sturgeon is currently subject to debate among stakeholders in the management of pallid sturgeon in the Missouri River basin. The adoption of the widespread shovelnose sturgeon as a proxy for the rare pallid sturgeon has been adopted in some areas (González et al. 2021); however, our results from the upper Missouri River basin suggest that there are differences in diet between the 2 species when assessed at fine taxonomic levels. As capturing wild larval pallid sturgeon is exceptionally rare, using the congener shovelnose sturgeon as a surrogate for scientific inference and large-scale management decisions is of interest (Gosch et al. 2018, 2019). Recommendations for (Gosch et al. 2019) and against (Wanner et al. 2007) diet surrogacy have been made. Wanner et al. (2007) concluded that diet overlap of juvenile pallid sturgeon and adult shovelnose sturgeon was not sufficient to promote surrogacy. Notably, pallid sturgeon in the study by Wanner et al. (2007) had transitioned to piscivory, whereas adult shovelnose sturgeon typically remain insectivorous, thus minimizing diet overlap. More recent assessments of larval pallid and shovelnose sturgeon diets have suggested that shovelnose sturgeon can be a useful surrogate for pallid sturgeon (Gosch et al. 2018, 2019). The wild-produced pallid sturgeon captured in these studies ranged from 20 to 48 mm TL ($n = 3$; Gosch et al. 2018) and 20 to 25 mm TL ($n = 4$; Gosch et al. 2019) and had recently begun exogenous feeding based on their size at time of capture (Snyder 2002, Kynard et al. 2007, Braaten et al. 2008). The 75 larval pallid sturgeon used in our study ranged from 25 to 110 mm TL, and therefore fill a knowledge gap about the diets of larval sturgeon in the weeks after transitioning from endogenous to exogenous feeding and benthic settlement.

The use of surrogates in ecology is a contentious subject where definitions are still being established (Caro 2010, Hunter et al. 2016) and applications are highly individualized (Caro & O'Doherty 1999, Favreau et al. 2006). Therefore, care should be taken during the selection, application, and assessment of these approaches (Caro & O'Doherty 1999, Wiens et al. 2008). There are several important things to consider prior to the implementation of such approaches. For example, the spatial and temporal extents to which the proxy will be applied should be considered (Favreau et al. 2006). One limitation of surrogacy is that the relation between species may not be transferable between locations or over time (Lindenmayer & Likens 2011). Stakeholders should also evaluate an acceptable level of uncertainty in conducting management or conservation activities with a surrogate approach (Wiens et al. 2008). In the case of larval pallid sturgeon, diet surrogacy of shovelnose sturgeon is often used to determine habitat quality. Proxy-based measures of habitat quality may be useful at some spatial scales (Stephens et al. 2015), but using data from organisms to infer habitat quality requires a number of considerations (Johnson 2007).

In addition to diet surrogacy as a method of developing habitat criteria, several studies have conducted modeling on data largely (or exclusively) from shovelnose sturgeon and discussed implications at the genus level (Phelps et al. 2010, Sechler et al. 2012, Gemeinhardt et al. 2019). Given the varying level of diet overlap found in our study, future research should consider genetically confirmed pallid sturgeon where possible. This study demonstrates the efficacy of direct measurement (Lindenmayer & Likens 2011) utilizing experimental hatchery releases of pallid sturgeon to test hypotheses such as habitat suitability and diet surrogacy, and provides insight regarding potential food and habitat limitations for age-0 pallid sturgeon. Our results suggest that caution be exercised when considering larval shovelnose sturgeon as a dietary surrogate for age-0 pallid sturgeon in the upper Missouri River basin because of the moderate degree of diet overlap and the number of unique taxa each species consumed while collected from the same locations.

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