Range-wide assessment of pallid sturgeon *Scaphirhynchus albus* (Forbes & Richardson, 1905) relative condition

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**Summary**
Pallid sturgeon *Scaphirhynchus albus* relative condition has been observed to be declining along the Nebraska reach (rkm 1212.6–801.3) of the Missouri River over the past several years; therefore, pallid sturgeon capture data was synthesized from the entire Missouri and Middle Mississippi rivers to document and compare how pallid sturgeon condition varies spatially and temporally throughout much of their current range. The study area was subdivided into four river reaches based on a priori statistical differences for pallid sturgeon catches from 2003 to 2015. Pallid sturgeon in the Middle Mississippi River (Alton Dam [rkm 321.9]) to the confluence of the Ohio River (rkm 0.0) were in the best condition while pallid sturgeon in the Middle Missouri River (Fort Randall Dam [rkm 1416.2]) to the Grand River confluence (rkm 402.3) were in the poorest condition. Furthermore, pallid sturgeon condition in the Upper Missouri River (Fort Peck Dam [rkm 2850.9] to the headwaters of Lake Sakakawea [rkm 2523.5] and lower Yellowstone River) and the Lower Missouri River (Grand River confluence to the Mississippi River confluence [rkm 0.0]) were significantly less than in the Middle Mississippi River but significantly higher than the Middle Missouri River. Temporally, pallid sturgeon condition was highly variable. Relative condition in the Middle Mississippi River was consistently above average (Kn = 1.1). Comparatively, Kn throughout the Missouri River rarely exceeded "normal" (Kn = 1.0), with Kn in the middle and lower reaches of the Missouri River having declined to the lowest observed. As pallid sturgeon recovery efforts continue, understanding the range-wide differences and effects on condition could be critical, as poor condition may cause maturation delays, reproductive senescence or even mortality, which affects the likelihood of natural reproduction and recruitment.

**1 | INTRODUCTION**

Historically, pallid sturgeon *Scaphirhynchus albus* had unrestricted access throughout the Mississippi and Missouri rivers and the lower reaches of their larger tributaries (Bailey & Cross, 1954; Kallemeyn, 1983). However, mainstem and tributary dams have segmented the historic range of the pallid sturgeon (Dryer & Sandvol, 1993; US Fish and Wildlife Service, 2013). These dams altered migration movements, limited access to suitable riverine habitats and likely extirpated populations isolated between dams (Dryer & Sandvol, 1993; Keenlyne & Evenson, 1989). Dams also negatively impacted the distribution and abundance of other native fish species considered prey for pallid sturgeon (Hesse, Mestl, & Robinson, 1993; Steffensen, Shuman, & Stukel, 2014). Depleted food resources and the change in the small-bodied fish community (i.e. pallid sturgeon prey) have likely contributed to the decline in pallid sturgeon condition (Hesse, 1994a; Steffensen et al., 2014; Huenemann, Steffensen, Mestl, Shuman, & Stukel, 2015; Steffensen and Mestl, 2016). Furthermore, abiotic riverine conditions were changed after dam construction by altering the natural hydrograph, temperature and turbidity profiles that historically cued...
migrational movements and spawning for most native fishes and then providing nursery habitats for the small fish. The natural hydrograph created habitat heterogeneity for which the different life stages of pallid sturgeon and their associated prey were adapted; however, many native fishes were unable to adapt to the rapidly altered systems and post-anthropogenic modifications to fulfill their habitat requirements. This resulted in the listing of the pallid sturgeon as an endangered species (55 FR 36641-36647; US Fish and Wildlife Service, 1990).

Pallid sturgeon were only recognized as a separate species in 1905 (Forbes & Richardson, 1905) after their populations were impacted by commercial fishing (Bettoli, Casto-Yerty, Scholten, & Heist, 2009). As a result, information is lacking to describe the species historic population abundance, distribution, size distribution and condition. Morphologic differences exist between pallid sturgeon from the Upper Missouri River, which attain much larger sizes compared to fish in the Middle Missouri River through the Mississippi River. More recently, genetic differences between these two populations have also been documented (Murphy, Hoover, George, & Kilgore, 2007; Schrey & Heist, 2007).

Due to the lack of natural reproduction and recruitment, a Pallid Sturgeon Conservation Augmentation Program was implemented throughout most of its current range to aid in population recovery and prevent local extirpation (US Fish and Wildlife Service, 2008). Since initiation of stocking in the Lower Missouri and Middle Mississippi rivers in 1992 (Huenemann, 2015), hundreds of thousands of hatchery-reared pallid sturgeon have been stocked, mainly in the Upper and Lower Missouri River. Stocking in the Middle Mississippi has not been as intensive compared to the Missouri River, and has been limited to the 1992 and 1997 year-class (Huenemann, 2015). These hatchery-reared pallid sturgeon are surviving (Rotella, 2015; Steffensen, Powell, & Koch, 2010; Steffensen, Powell, Stukel, Winders, & Doyle, 2015) and growing (Shuman et al., 2011) and in combination with the remaining wild fish make up the current pallid sturgeon population, which may be causing interspecific competition for available resources and might perhaps affect conditions if these resources are limited.

Length–weight relationships are key components of fisheries management and research (Anderson & Neumann, 1996). This relationship can be used to compare populations across time and space using mathematic equations or condition indices. Monitoring the condition of pallid sturgeon may be critical for species recovery, as declining condition is likely related to delayed maturation rates, decreased fecundity and interrupting reproductive cycles (Steffensen and Mestl, 2016). Fish in good condition are expected to allocate more energy into gamete production compared to fish in poor condition (Blackwell, Brown, & Willis, 2000), which presumably increases the likelihood of natural reproduction that is critical for endangered species recovery. Shuman et al. (2011) conducted a spatial comparison of hatchery-reared pallid sturgeon relative condition (Kn) by Recovery Priority Management Areas (RPMA) (see Dryer & Sandvol, 1993; for RPMA descriptions) on the Missouri River and determined that Kn was variable between RPMAs and declined after stocking. However, this analysis lacked a temporal component to describe annual variability.

During the spring of 2015, poor pallid sturgeon relative condition was observed; Steffensen and Mestl (2016) described the temporal variation and fluctuation of pallid sturgeon Kn in the Middle Missouri River along the eastern border to Nebraska (rkm 1212.6–801.3) but the analysis lacked a spatial comparison. Spatial comparisons, outside the Nebraska reach of the Middle Missouri River, will prove information as to whether this is an isolated occurrence or river(s) wide effect. Also, this might provide a baseline for the expected pallid sturgeon condition in our reach of the Middle Missouri River. Therefore, the objectives of this study are to (i) document the mean relative condition (Kn) of pallid sturgeon by river reaches, (ii) determine if relative condition (Kn) of pallid sturgeon changes by length or life stage, (iii) document annual variations in relative condition, and (iv) temporally and spatially compare pallid sturgeon relative condition (Kn) throughout the majority of its range.

2 | MATERIALS AND METHODS

The study area was divided into five reaches based on fragmenta-
tion of the Missouri River by dams and pallid sturgeon recovery management units as defined in the revised recovery plan (US Fish and Wildlife Service, 2013): (i) the Upper Missouri River, defined as the reach of the Missouri River from Fort Peck Dam (MO River rkm 2850.9) to the headwaters of Lake Sakakawea (MO River rkm 2523.5) and the lower reach of the Yellowstone River; (ii) the Inter-Reservoir reach of the Middle Missouri River, defined as the reach from Fort Randall Dam (MO River rkm 1416.2) to the headwaters of Lewis and Clark Lake (MO River rkm 1327.7); (iii) the Middle Missouri River, defined as the reach from Gavins Point Dam (MO River rkm 1305.2) to the Missouri and Grand River confluence (MO River rkm 402.3); (iv) the Lower Missouri River, defined as the reach from the Missouri and Grand River confluence through the Lower Missouri River to the confluence with the Mississippi River (MO River rkm 0.0); and (v) the Middle Mississippi River, defined as the reach from Alton Dam (MS River rkm 321.9) to the confluence of the Mississippi and Ohio rivers (MS River rkm 0.0; Fig. 1).

Pallid sturgeon data for the Missouri River from 2003 to 2015 were obtained from the Pallid Sturgeon Population Assessment Program, Habitat Assessment and Monitoring Program, and the Off-Channel Monitoring and Assessment Program, which included sampling efforts from Fort Peck Dam to the confluence with the Mississippi River. Sampling protocols and gear specification are available in the program’s guideline documents (Welker & Drobish, 2012a,b). All captured pallid sturgeon were examined for hatchery marks (PIT tags, coded wire tags, elastomer marks, and/or scute removal) to determine their origin (hatchery-reared or naturally produced). A genetic sample was submitted for origin verification when no tags were present (DeHaan, Jordan, & Ardren, 2008; Schrey & Heist, 2007; Schrey, Sloss, Sheehan, & Heist, 2007). Fish were presumed to be of wild origin that genetically did not match any known parental crosses.

Pallid sturgeon length and weight data from 2003 to 2013 for the Middle Mississippi River were acquired from Southern Illinois University – Carbondale (Carbondale, IL, USA) and the national pallid sturgeon database archived by the US Fish and Wildlife Service.
FIGURE 1  Map of Missouri and Middle Mississippi rivers with pallid sturgeon *Scaphirhynchus albus* data. Ovals = study areas, based on mainstem Missouri River dams and the revised pallid sturgeon recovery management units. The Inter-Reservoir and Middle Missouri River reaches did not differ and were therefore combined post hoc.

North Dakota Ecological Services Field Office (Ryan Wilson, USFWS, Bismarck, ND, USA) with permission from the Missouri Department of Conservation (D. Herzog, Missouri Department of Conservation, Pers. Comm.). Data from autumn 2013 through spring 2015 were acquired from the Middle Mississippi River pallid sturgeon project (Brian Johnson, US Army Corps of Engineers, Pers. Comm.). Data included all pallid sturgeon capture records from the Middle Mississippi River from the confluence of the Ohio River (rkm 0.0) to Alton Dam (rkm

FIGURE 2 Relative condition (Kn) mean-to-mean comparison with associated confidence intervals for all sized pallid sturgeon by river reaches. Solid confidence interval bars represent a difference in Kn between river reaches; dashed confidence interval bars represent no difference. Test statistics are presented on the right y-axis.
Sampling methodology and gear were similar to those used in the Missouri River studies, therefore reducing any gear-related bias in the results. All pallid sturgeon in the Mississippi River were examined for hatchery marks; however, genetic analysis was not completed on unmarked fish. Therefore, pallid sturgeon identification and origin was based on field identification.

The predicted weight of pallid sturgeon was calculated using the length-weight relationship equation provided by Shuman et al. (2011):

$$\log_{10} W = -6.2561 + 3.2932 \times \log_{10} (FL)$$

then relative condition (Kn) calculated as:

$$\text{Kn} = \frac{W}{W'}$$

where $W$ is the observed weight of an individual and $W'$ is the predicted length-specific weight.

Prior to analysis, certain fish were eliminated so as to not bias the results. Shuman et al. (2011) did not report a minimum fork length for inclusion in the Kn equation, but they lacked small sized fish; therefore, fish $<200$ mm were omitted. Pallid sturgeon $>1200$ mm were also eliminated as they only occur in the Upper Missouri River; furthermore, their length-weight relationship would greatly skew the data for that reach. Finally, known hatchery-reared pallid sturgeon captured within 1 year post-stocking were omitted, as it is known that the condition of these fish decline after stocking and are likely not representative of the expected riverine condition. Since the Mississippi River pallid sturgeon populations were not included in the development of the Shuman et al. (2011) condition equation, the validity of the equation was tested to eliminate any potential erroneous comparisons and results. The length-weight relationship between the Mississippi and the Lower Missouri rivers pallid sturgeon data were transformed and statistically tested (ANCOVA, PROC GLM in SAS 9.4). The slopes relating to the transformed length-weight data were not statistically different ($t = 1.41, p = .1600$). Furthermore, pallid sturgeon have been documented to migrate between the Lower Missouri and Middle Missouri rivers (K. Steffensen, unpubl. data). Therefore, we concluded that utilizing the Shuman et al. (2011) equation is a valid assessment.

To determine the validity of our reach designations, pallid sturgeon Kn was compared (ANOVA, SAS 9.4) between the aforementioned river reaches. A pairwise comparison analysis was conducted when the overall model was significant, to determine which reaches were statistically similar and if the reaches could be combined. Fish were then divided into 100 mm length groups to determine significant changes in condition as fish grew and matured. Length groups were then compared (ANOVA) to determine if there were significant differences between length groups. When differences existed, a post hoc analysis would test whether length groups could be combined.

Annual mean Kn by years and river reaches were then regressed to determine if Kn had changed over the past several years. Heat maps were generated (SAS 9.4) to display the annual mean Kn within the pallid sturgeon management units as well as from 2003 to 2015. Annual Kn values were presented only when $\geq 3$ fish were collected with the year for each life stage and river reach. The scale was adjusted to minimum Kn (dark red) to maximum Kn (dark green), with white representing a Kn between 0.95 and 1.05. All statistical tests were performed using SAS 9.4 (SAS Institute, Cary, NC) and significance was determined at $\alpha = 0.05$. 

**FIGURE 3** Mean relative condition by 100-mm fork length intervals for all river reaches. Letters denote significant difference amongst 100-mm length groups.

**FIGURE 4** Overall juvenile (400–699 mm, top) and adult (700–1,199 mm, bottom) pallid sturgeon relative condition (Kn) within each river reach. Letters denote significant differences amongst reaches.
3 | RESULTS

The global relative condition model by river reach was significantly different ($F = 333.47$, df = 4, $p < .001$). Post hoc pairwise comparisons were different for all reaches, except for between the Inter-Reservoir and Middle Missouri River reaches ($t = 1.54$, $p = .5322$, Fig. 2). Therefore, the Inter-Reservoir and the Middle Missouri River reaches were combined into a single management unit and hereinafter, referenced as the Middle Missouri River. The overall relative condition model by 100 mm length groups was significantly different ($F = 81.68$, $p < .001$). Post hoc pairwise comparisons for pallid sturgeon $\bar{x} \pm SE$ from 200 to 299 sized fish were significantly higher than all length categories ≥300 mm and pallid sturgeon $\bar{x} \pm SE$ for 300–399 mm sized fish were also significantly higher than all length categories ≥400 mm. However due to the limited number of recaptures from certain reaches, no temporal comparisons are presented. Pallid sturgeon were then merged into two length categories and classified as juveniles (400–699 mm) and adults (700–1,199 mm; Fig. 3). Lastly, post hoc analysis confirmed a statistical difference between these juvenile and adult length classifications ($t = 2.92$, $p = .0035$).

Overall Kn for juvenile sized pallid sturgeon were significantly different among all river reaches (Fig. 4). The highest Kn (1.08 ± SE 0.02) occurred in the Middle Mississippi River followed by the Upper Missouri River (Kn = 0.95 ± 0.01). A similar trend was observed for adult sized pallid sturgeon, except Kn was similar for the Upper and Lower Missouri River (Fig. 4). Relative condition decreased from the juvenile to adult length classes in the Upper and Middle Missouri River reaches, but increased in the Lower Missouri and Middle Mississippi rivers. Similar increases in Kn occurred in juvenile to adult sized fishes in the lower two reaches. The Lower Missouri River increased from a juvenile Kn of 0.92 to an adult Kn of 0.96; in the Middle Mississippi River, Kn increased from 1.07 to 1.11.

The mean annual Kn of juvenile sized pallid sturgeon in the Upper Missouri River has steadily increased since 2005; the past 2 years were above the long-term mean ($x = 0.95$), recovering from 2013.

FIGURE 5 Annual mean ±2 SE relative condition factor (Kn) per reach for juvenile sized (400–699 mm) pallid sturgeon captured 2003 to 2015. Note: y-axis scale is different between the panels
which was below average (Fig. 5). Relative condition for adult sized pallid sturgeon in the Upper Missouri shows a significant negative regression; however, this is influenced by fish captured in 2009, where only four fish with extremely high variability were included (Fig. 6). In the past 5 years, the mean annual Kn ranged from 0.91 to 0.95, with no discernible trend (Fig. 7). In the Middle Missouri River, juveniles and adults had similar trends with the mean annual Kn steadily increasing and peaking in 2010 for juveniles and in 2012 for adults. However, rapid declines were observed over the past several years. In the Lower Missouri River, a declining trend has occurred for juveniles but increased in adults, although individual conditions were highly variable. Currently, juvenile Kn in the Middle and Lower Missouri River reaches are at the lowest levels observed over the past 12 years. Mean annual Kn for juvenile pallid sturgeon captured in the Middle Mississippi River has shown no discernable trend and are typically in much better average condition (x = 1.07) compared to those in the Missouri River reaches. The trend for adult pallid sturgeon in the Middle Mississippi River has slowly declined, although remaining higher than in the Missouri River reach.

4 | DISCUSSION

Pallid sturgeon relative condition was highly variable, both spatially and temporally. Spatially, the most robust pallid sturgeon occur in the Middle Mississippi River, while fish in the Middle Missouri River are in the poorest condition. Based on the mean adult Kn, a 1,000 mm pallid sturgeon would weigh approximately 20% more in the Middle Mississippi River compared to the Middle Missouri River. Furthermore, pallid sturgeon Kn in the Middle Mississippi River were also substantially different compared to those in other reaches of the Missouri River (14%–17%). The Middle Mississippi River is free-flowing and exhibits lower average water velocities relative to the Missouri River. This likely requires less energy expenditure by pallid sturgeon and better utilization of its caloric intake for growth, condition, and maturation. Furthermore, benthic chubs (e.g. sturgeon and sicklefin chubs), which are likely the preferred food source for adult pallid sturgeon (Gerrity, Guy, & Gardner, 2006; Hoover, George, & Killgore, 2007), are more abundant in the Middle Mississippi River (D. Herzog, Missouri Department of Conservation, Pers. Comm.).
The Upper Missouri River had the second highest relative condition likely due to the more natural channel morphology and habitat dynamics in this reach compared to the Middle and Lower Missouri River reaches. Potential pallid sturgeon prey items (e.g., benthic chubs) are higher in relative abundance compared to the lower reaches of the Missouri River (Steffensen et al., 2014), perhaps because of the more natural channel morphology and habitat dynamics of these reaches. Anthropogenic modification, specifically the navigation channel and main stem dams, throughout the middle and lower reaches of the Missouri River are likely the main contributor to poor relative condition for pallid sturgeon. These modifications have significantly reduced the quantity and quality the available habitat, causing a significant decline in the native fish populations (Galat et al., 2005; Hesse, 1994a,b; Huenemann et al., 2015; Steffensen, Shuman, Klumb, & Stukel, 2014; Steffensen et al., 2014), increased average depths and velocities in the channelized reaches (Dryer & Sandvol, 1993), altered the natural hydrograph (Pegg, Pierce, & Roy, 2003), and negatively affected the temperature and turbidity profile (Hesse & Mestl, 1993).

Although the Gavins Point Dam bisects the Middle Missouri River as defined in this paper, pallid sturgeon Kn were not statically different between the Inter-Reservoir reach and the open reach below the dam. The Inter-Reservoir Missouri River reach has a relatively natural river morphology, but a highly altered water management and flow regime (Hesse & Mestl, 1993). Comparatively, the Middle Missouri River below Gavins Point transitions from a reach with a fairly natural river morphology with a highly altered flow regime from Gavins Point Dam to a more natural flow regime but highly altered channelized system. Furthermore, pallid sturgeon condition throughout the Middle Missouri River reach, especially for adult fish, may be affected by food availability. Grohs, Klumb, Chipps, and Wanner (2009) determined that pallid sturgeon in the Inter-Reservoir reach between Fort Randall and Gavins Point mainly consumed *Etheostoma nigrum*, plus a small amount of channel catfish *Ictalurus punctatus*. Whereas in the lower portion of the Middle Missouri River reach, Winders and Steffensen (2014) reported pallid sturgeon were relying on Ictaluridae and Cyprinidae species. Benthic chubs along with other benthic minnows are probably the preferred food source for pallid sturgeon (Gerrity et al., 2006; Hoover et al., 2007), but neither reach supports abundant populations of these species (Steffensen et al., 2014).

The length classifications (juvenile [400–699 mm] and adult [700–1,199 mm]) developed within this analysis appear to have a biological meaning. Pallid sturgeon shift their diet from macroinvertebrates
to fish between lengths of 500 and 700 mm, and are completely piscivorous by 700 mm (Gerrity et al., 2006; Grohs et al., 2009; Winders & Steffensen, 2014). Juvenile pallid sturgeon readily feed on diptera, ephemeroptera, decapoda, and trichoptera (Grohs et al., 2009; Winders & Steffensen, 2014), which have a mean caloric density of 3065.8 J/g compared to a caloric content of 4473.5 J/g (Wildhaber et al., 2015). To consume the caloric equivalent of a single, small-bodied fish, a juvenile pallid sturgeon feeding on macroinvertebrates likely needs a longer forage period. Furthermore, while the pallid sturgeon relative condition equation is a linear relationship, pallid sturgeon growth is not. As pallid sturgeon grow and reach maturity, adult Kn is expected to increase; however, this is only occurring in the Lower Missouri and Middle Mississippi rivers. Relative condition for adult pallid sturgeon decreased in the Upper and Middle reaches of the Missouri River, perhaps indicating lack of transitional food sources for adults or inter- or intraspecific competition.

The Pallid Sturgeon Conservation Augmentation Program has stocked the highest density of hatchery-reared fish in the Upper and the Middle Missouri River (Huenemann, 2015; Rotella, 2015; Steffensen, Pegg, & Mestl, 2013; Steffensen et al., 2010). The goal of this program is to increase the number of reproductive adults in a system otherwise likely inadequate to maintain the population. Comparatively, only limited stocking efforts have occurred in the Lower Missouri and Middle Mississippi river, principally because of concerns of a genetic drift of fish stocked in the Lower Missouri River into the Mississippi River, where some level of natural recruitment might still be occurring (Columbo, Garvey, & Willis, 2007; Killgore et al., 2007, 2007). Stocking efforts have been curtailed in the Upper Missouri River, while stocking efforts in the Middle Missouri River have always been much lower than the stocking targets originally developed for this reach (US Fish and Wildlife Service, 2008). A population estimate for the an 80.5-rkm reach of the Middle Missouri River estimated 5.4–8.9 wild and 28.6–32.3 hatchery fish per rkm. Compared to the densities of other piscivorous predators such as the flathead catfish Pylodictis olivaris that also occupy this reach, these numbers would seem to indicate that the population is nowhere near carrying capacity.

As recovery efforts continue, the poor condition of pallid sturgeon, especially in the Middle Missouri River, is of great concern. The Middle Missouri River currently contains the highest density of wild and hatchery-reared adult pallid sturgeon in the open river system downstream of Gavins Point Dam (Steffensen, Powell, & Pegg, 2012). Steffensen and Mestl (2016) reported that this low and declining relative condition might be affecting size or age-at-maturity and reducing pallid sturgeon maturation cycles. Pallid sturgeon condition can fluctuate significantly within a short period of time and in the Middle Mississippi River have proven an ability to achieve and maintain a much higher Kn than those observed in the Missouri River. The preferred condition needed to attain to maintain adequate growth and maturation is unknown. In the Middle Mississippi River, they have attained and maintained a Kn of >1.0, while Missouri River pallid sturgeon rarely exceed 1.0 and have dropped well below that level over the past several years.

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