3-17-2019

Emigration of hatchery-reared Pallid Sturgeon, Scaphirhynchus albus (Forbes and Richardson), through a Missouri River dam

Landon L. Pierce

Dane A. Shuman

Daniel A. James

Kirk D. Steffensen

Ryan Wilson

See next page for additional authors

Authors
Landon L. Pierce, Dane A. Shuman, Daniel A. James, Kirk D. Steffensen, Ryan Wilson, and Kyle Winders

Received: 24 April 2018 | Revised: 1 March 2019 | Accepted: 17 March 2019
DOI: 10.1111/fme.12349

ORIGINAL ARTICLE

Fisheries Management and Ecology WILEY

Emigration of hatchery-reared Pallid Sturgeon, *Scaphirhynchus albus* (Forbes and Richardson), through a Missouri River dam

Landon L. Pierce[1] | Dane A. Shuman[1] | Daniel A. James[1] | Kirk D. Steffensen[2] | Ryan Wilson[3] | Kyle Winders[4] | Adam McDaniel[4]

[1]Great Plains Fish and Wildlife Conservation Office, U.S. Fish and Wildlife Service, Pierre, South Dakota
[2]Nebraska Game and Parks Commission, Lincoln, Nebraska
[3]Missouri River Fish and Wildlife Conservation Office, U.S. Fish and Wildlife Service, Bismarck, North Dakota
[4]Missouri Department of Conservation, Chillicothe, Missouri

Correspondence
Landon L. Pierce, U.S. Fish and Wildlife Service, Great Plains Fish and Wildlife Conservation Office, Pierre, SD.
Email: landon_pierce@fws.gov

Funding information
U.S. Army Corps of Engineers

Abstract

The middle Missouri River (MMR; Fort Randall Dam, SD to Gavins Point Dam, NE-SD) is stocked with hatchery-reared pallid sturgeon, *Scaphirhynchus albus* (Forbes and Richardson), from upper Missouri River broodstock to aid recovery of this federally endangered species. Emigration of these fish through Gavins Point Dam restores genetic connectivity that likely existed pre-impoundment but could lead to outbreeding depression in the future. Recapture data of hatchery-reared pallid sturgeon stocked in the MMR were evaluated to improve understanding of pallid sturgeon emigration. From 2004 to 2015, 219 emigrants were caught: 4 stocked at age ≥2 years and 215 stocked at age ≤1 year. Emigration of the 2001-2007 year classes stocked at age 1 was a consistent phenomenon and appeared higher than emigration of year classes stocked at ages 2–3. Little evidence suggested emigration was associated with an unusually high-water event in 2011. The annual emigration probability of individuals stocked at age 1 estimated from multi-state mark–recapture models was 0.05 [95% confidence interval = 0.04–0.06] for fish ages ≥1 year. This study suggests that alterations to stocking practices (e.g. stocking age) may affect emigration rates and, therefore, connectivity among pallid sturgeon populations.

KEYWORDS
emigration, mark–recapture, Missouri river, pallid sturgeon, stocking, survival

1 | INTRODUCTION

Emigration of fishes between populations can affect population dynamic rates and genetic structure of populations. Emigration functions as a source of apparent mortality to the donor population by reducing population size but is a source of recruitment to the receiving population (Gotelli, 2001; Pracheil, Mestl & Pegg, 2014). Therefore, emigration results in overestimation of true mortality rates for the donor population. If conspecific individuals in donor and receiving populations differ genetically, then emigration could increase the potential for outbreeding depression (i.e. reduced fitness due to loss of locally adapted traits; Hallerman, 2003; Ludwig, 2006) in the receiving population. Conversely, genetic connectivity between populations can be beneficial by reducing the potential for inbreeding depression (i.e. reduction of fitness due to increased genetic homozygosity; Monson & Sadler, 2010; Saltzgiver, Heist & Hedrick, 2012), which is particularly important for imperilled species because inbreeding rate is inversely related to effective population size (Ludwig, 2006; Ryman & Laikre, 1991). Given these potential effects of emigration on fish populations, understanding the occurrence of such events is vital to the management of imperilled species.

Federally listed endangered pallid sturgeon, *Scaphirhynchus albus* (Forbes and Richardson), is reared in hatcheries and stocked in the Missouri River, USA, to prevent extirpation until populations are self-sustaining (USFWS, 2008, 2014). More than 1.1 million age-0 and 375,000 age-1 or older hatchery-reared pallid sturgeon (HRPS) were stocked throughout the Missouri River since 1994. Progeny from upper Missouri River [i.e. upstream of Lake Sakakawea, North Dakota; (UMR)] broodstock were stocked throughout the Missouri River from 1997 to 2007. Since 2008, however, the lower Missouri River [i.e. Gavins Point Dam, Nebraska-South Dakota to the confluence with Mississippi River; (LMR)] has been stocked with progeny from locally collected broodstock to minimise the potential for outbreeding depression (USFWS, 2008). Meanwhile, the middle Missouri River [i.e. between Fort Randall Dam, South Dakota and Gavins Point Dam; (MMR)] has been stocked with progeny of UMR broodstock since 2000 to re-establish this population and provide a reserve population of UMR pallid sturgeon genetics in case of catastrophic losses due to unforeseen stochastic events in the UMR (USFWS, 2008).

Emigration of HRPS through Gavins Point Dam may affect the genetic structure of the pallid sturgeon population in the LMR and Mississippi River, but the long-term implications of emigration are unclear. Emigration of UMR progeny from the MMR to the LMR restores the genetic connectivity that likely existed before impoundment of the Missouri River (USFWS, 2008) and reduces the potential for inbreeding depression. Conversely, emigration could lead to outbreeding depression because pallid sturgeon in the UMR are considered genetically distinct from pallid sturgeon in the LMR, Mississippi River and Atchafalaya River (Schrey & Heist, 2007). Currently, however, the causes and ecological relevance of genetic differences in pallid sturgeon populations, emigration rates and, therefore, genetic implications of emigration are unclear.

Given the potential effects of emigration on population demographics and genetic structure of pallid sturgeon populations, an improved understanding of pallid sturgeon emigration through mainstem dams is needed to manage this imperilled species. Although habitat use and movement of pallid sturgeon have been studied in the MMR using telemetry (Jordan, Klumb, Wanner & Stancill, 2006; Wanner, Klumb, Stancill & Jordan, 2007), emigration from this reach has not been evaluated. In particular, it is unclear if age, age at stocking, or the 500-year high-water event that occurred from May 2011 to July 2011 on the Missouri River (Reager, Thomas & Famiglietti, 2014; USACE, 2012) affected emigration of HRPS through mainstem Missouri River dams. Therefore, recaptures of HRPS stocked into the MMR were examined to evaluate the effects of age, age at stocking and the 2011 high-water event on emigration of HRPS through Gavins Point Dam.

TABLE 1 Total hatchery-reared pallid sturgeon stocked into the middle Missouri River (Fort Randall Dam, SD to Gavins Point Dam, NE-SD) from 2000 to 2015, and number stocked at age 1 with passive integrated transponder (PIT) tags used in multistate mark–recapture models

Year	Year class	Stocking age (year)	Total stocked	Stocked at age 1 with PIT tag
2000	1997	3	415	
2000	1998	2	98	
2002	1999	3	181	
2002	2001	1	558	558
2003	2002	1	601	601
2004	2003	1	515	515
2005	2004	1	868	868
2006	2005	1	1,005	1,005
2007	2006	1	600	
2008	2007	1	1,169	1,144
2008	2008	0	3,410	
2009	2008	1	637	297
2010	2004	6	26	
2010	2009	1	848	629
2011	2010	1	635	332
2013	1997	16	9	
2013	2003	10	25	
2013	2006	7	5	
2013	2010	3	39	
2013	2012	1	82	79
2014	2013	1	173	173
2015	2014	1	105	105[a]

Notes: [a]Excluded from mark–recapture modelling due to lack of recapture events prior to the end of this study.

2 | MATERIALS AND METHODS

The MMR extends from Fort Randall Dam (river kilometre [rkm] 1,416) to Gavins Point Dam (rkm 1,305). This reach includes a 58-rkm riverine section from Fort Randall Dam downstream to the Niobrara River confluence (rkm 1,358), a 29-rkm braided delta from the Niobrara River confluence downstream to the headwaters of Lewis and Clark Lake (rkm 1,329) and the 24-rkm long Lewis and Clark Lake. Lewis and Clark Lake is the most downstream Missouri River reservoir and was formed by the closure of Gavins Point Dam in 1955. Lewis and Clark Lake has a high flushing rate, as the storage volume of the reservoir can be discharged through the dam in as few as 5.5 days at maximum turbine discharge (Walburg, 1971). Current velocity in the reservoir is dependent on discharge and was measured at 0.06 m/s approximately 1.6 km upstream of the dam when the flushing rate was 5.3 days (Walburg, 1971). Under most conditions, water passes through the power plant at Gavins Point Dam via three Kaplan turbines (USACE, 2004). Water is passed through 14 tainter gates in the spillway when discharge exceeds the capabilities of the powerhouse (e.g. during turbine maintenance and high-water events; D. Becker, personal communication, 7 December 2016; USACE, 2004). Water intakes for the turbines span the bottom 16.9 m of the water column (D. Becker, personal communication, 5 December 2016). The LMR is unchannelised for approximately 127 rkm from Gavins Point Dam to Sioux City, Iowa. The remaining 1,178 rkm from Sioux City to the confluence with the Mississippi River at St. Louis, Missouri are channelised and leveed to maintain a navigation channel (Galat, Berry, Peters & White, 2005).

Hatchery-reared pallid sturgeon were stocked into the riverine (rkm 1,394 and 1,370) and delta (rkm 1353) portions of the MMR from 2000 to 2015 (Table 1). Initial stockings (i.e. 1997–1999 year classes) occurred at ages 2 and 3. More recent stockings primarily occurred at age 1 (i.e. 2001–2014 year classes); but 3,410 age-0 HRPS were stocked in 2008, and older individuals were stocked for research studies. Depending on fish size at stocking, HRPS were tagged [dangler tag or passive integrated transponder (PIT) tag] or marked [scute removal or visible implant elastomer (VIE)] prior to release so that year class and stocking location could be identified upon recapture (USFWS , 2008). Recaptures of these individuals in the MMR (i.e. stocking-reach recaptures) and LMR (i.e. emigrant recaptures) from June 2000 (when the 1997 year class was stocked) to October 2015 were compiled from available sources. Recaptures were primarily from the Pallid Sturgeon Population Assessment Program (PSPAP), which is a standardised monitoring programme for pallid sturgeon throughout the Missouri River (see Welker, Drobish & Williams, 2016 for more details). Recapture records were also acquired from the USFWS National Pallid Sturgeon Database that includes all captures of pallid sturgeon throughout the USA. Recaptures from the PSPAP are included in the USFWS National Pallid Sturgeon Database, but these databases were merged to ensure the most complete recapture data were used. The PSPAP began in the MMR in 2003 and was fully implemented in the LMR in 2005 (Welker et al., 2016). One recapture in the MMR occurred prior to PSPAP sampling, whereas all recaptures in the LMR occurred from 2004 to 2015. Notable changes in sampling for pallid sturgeon since the implementation of the PSPAP were the addition of trotline sampling for broodstock in the LMR in 2008, the addition of trotlines as a standard PSPAP sampling gear in 2010 for all reaches and contingency sampling that differed from other years during the 2011 high-water event (Welker et al., 2016). Although the sampling design differed in 2011 from other years, sampling effort of the most effective pallid sturgeon sampling gears in these reaches (i.e. trotline and gillnets) was similar to previous years because these gears are typically deployed from January to May and October to December and had minimal overlap with the high-water event.

Although minor deviations may have occurred throughout the extended recapture period and spatial extent of this study, captured pallid sturgeon were checked for PIT and dangler tags, removed scutes and VIE. These markings allow determination of stocking location and year class. PIT tags were implanted into pallid sturgeon that lacked a PIT tag. Beginning in 2006, genetic samples were taken from unmarked (i.e. lacking PIT or dangler tags, removed scutes or VIE) individuals to identify origin (hatchery or wild), year class and stocking location. Fish stocked into the MMR were identified first by PIT tag implanted at stocking, then by genetics and lastly by scute and VIE marks. This approach was used because PIT tags and genetics were considered more reliable than VIE due to difficulties distinguishing VIE colours as fish age. Emigrants from the 2010 year class (pink VIE) were not identified solely based on VIE because the data set included numerous individuals stocked into the LMR with red VIE that were misidentified as having pink VIE.

To describe differences in emigration between year classes, the percentages of HRPS recaptured (i.e. [number recaptured / number stocked]100) downstream of Gavins Point Dam (i.e. LMR) and in the stocking reach (i.e. MMR; as a standard for comparison) were calculated by year class. Catch curves (i.e. number of new individuals caught by calendar year) of emigrants and individuals caught in the stocking reach by year class were examined to assess whether emigration was associated with age or other event (e.g. the 2011 high-water event). Catch curves represented the first year an individual was captured in a river reach. Therefore, an individual recaptured multiple times in the MMR was only attributed to the year of first capture. Meanwhile, an individual that was captured in both reaches would be attributed to the year of first capture in the MMR and the year of first capture in the LMR.

Emigration-age windows were developed for emigrants that were captured in the stocking reach prior to recapture downstream of Gavins Point Dam to further refine understanding of what age individuals emigrated. Emigration-age windows represented the age range that emigration occurred. The emigration-age window was created for each individual by identifying the oldest age it was captured in the stocking reach and the youngest age it was captured downstream of Gavins Point Dam. For example, if an individual was last captured in the stocking reach (MMR) at age 5 and first captured downstream (LMR) at age 7, then its emigration-age window was ages 5-7.

Multistate mark–recapture models were developed to estimate annual probability of emigration from the MMR and separate the potential effects of sampling efficiency [i.e. age of recruitment to sampling gears (Pierce, Shuman, James & Stacy, 2017) and effort (Welker et al., 2016)] from factors affecting emigration using Program MARK software (Cooch & White, 2011). Multistate mark–recapture models estimate annual recapture and survival probabilities for each state (i.e. river reach) and the annual probability of moving between states (i.e. emigration; Cooch & White, 2011). Multistate mark–recapture models were limited to individuals from the 2001–2013 year classes that were stocked at age 1 with PIT tags because recapture data of individuals stocked in the MMR at ages 2–3 recaptured in the LMR (n = 4 of 672 stocked) were deemed insufficient to evaluate the hypotheses of this study. Encounter histories were developed for each individual and indicated if the individual was captured in a given calendar year (i.e. from 2003 to 2015, resulting in 13 recapture occasions) in the MMR or the LMR. This approach assumed that individuals recaptured prior to the stocking date (i.e. month and day) in later years survived from the recapture date to the anniversary of their stocking date that year. This assumption, however, only applied to the year of recapture because annual survival was confirmed for the years at large between stocking and recapture by the subsequent recapture.

Fifty-six multistate models, consisting of combinations of four survival hypotheses, seven recapture hypotheses and two emigration hypotheses, were developed using the parameter index matrix in Program MARK (Table 2). These recapture and emigration hypotheses were informed, in part, by the catch curve analyses. For example, the effects of the 2011 flood on emigration were not evaluated with these models because that hypothesis was not supported by the catch curves. Models representing age-specific emigration, recapture and survival hypotheses were considered but not included in the final analysis because they often resulted in unrealistic parameter estimates (i.e. survival probability = 1.00), likely due to insufficient recapture data to support these highly parameterised models. Similarly, year-specific survival, recapture and emigration probabilities were not evaluated due to the inability of highly parameterised models to produce realistic parameter estimates. As a result, hypotheses representing the effects of age on survival, recapture and emigration probabilities were represented with simplified models that assumed similar probabilities among ages within age groups. Similarly, hypotheses representing the effects of sampling efficiency on recapture probability were represented with models that assumed similar recapture probabilities among years with similar sampling effort and gears. Finally, upstream passage is not possible at Gavins Point Dam, so the probability of emigrating upstream through Gavins Point Dam was fixed at zero and, therefore, the probability of remaining downstream of Gavins Point Dam was 1.00 in all models.

Survival hypotheses included:

1. Survival was constant across years and reaches (Hypothesis “Constant”; Table 2).
2. Survival was constant across years but differed among reaches (Hypothesis “Reach”).
3. Survival differed between age 1 fish and age ≥2 fish but was similar between reaches (Hypothesis “Age”).
4. Survival differed between age 1 fish and age ≥2 fish, and survival of age ≥2 fish differed between reaches (Hypothesis “Age*Reach”). Reach-specific age-1 survival rates were not evaluated because no individuals were stocked in the LMR at age 1 in this study. Therefore, age-1 survival was modelled as independent of reach and represents age-1 survival of fish stocked in the MMR.

Recapture hypotheses included:

1. Recapture probability was constant across years and reaches (Hypothesis “Constant”).
2. Recapture probability was constant across years but differed among reaches (Hypothesis “Reach”).
3. Recapture probability of age 2–3 fish differed from age ≥4 fish (Hypothesis “Age”).
4. Recapture probability of age 2–3 fish differed from age ≥4 fish and differed among reaches (Hypothesis “Reach*Age”).
5. Recapture probabilities were similar between reaches but differed between pre- and post-implementation of trotlines as a standard PSPAP gear in 2010 (Hypothesis “Pre-post trotline 2010).
6. Recapture probabilities differed between reaches and between pre- and post-implementation of trotlines as a standard PSPAP gear in 2010 (Hypothesis “Pre-post trotline 2010*Reach”).
7. Recapture probabilities differed between reaches and between pre- and post-implementation of trotlines as an experimental gear by PSPAP in the stocking reach in 2009, and pre- and post-implementation of trotlines for local broodstock in the LMR in 2008 (Hypothesis “Pre-post trotline 2009/2008*Reach”).

Emigration hypotheses included:

1. Emigration probability was constant across years and age groups (Hypothesis “Constant”).
2. Emigration probability for age 1–3 fish differed from age ≥4 fish (Hypothesis “Age”).

Models were ranked by Akaike's Information Criterion adjusted for small sample size and overdispersion ($QAIC_C$) scores, calculated as $-2\log_e(\text{likelihood})/c + 2k + 2k(k+1)/(n-k-1)$ where c is the measure of lack of model fit, k is the number of parameters, and n is sample size (Cooch & White, 2011). Model fit was assessed for the most parameterised model in the final candidate model set (i.e. Model 55) with the median $\hat{c}$ approach and default settings (i.e. lower bound=1; upper bound=4.5; 10 replicates at 10 intermediate values) in Program MARK (Cooch & White, 2011). A $\hat{c}$ value of 1.0 indicates the data fit the expectations of the model, whereas values greater than 1.0 indicate that the data do not meet the assumptions of the model (i.e. overdispersion; Cooch & White, 2011). Median $\hat{c}$ of Model 55 was 1.32, indicating that the data

TABLE 2 Multistate mark–recapture model results for hatchery-reared pallid sturgeon stocked at age 1 into the middle Missouri River (Fort Randall Dam, SD to Gavins Point Dam, NE-SD) from 2002 to 2015

	Hypothesis							
Model	Survival	Recapture	Emigration	QAICc	Delta QAICc	QAICc weight	K	−2Ln(L)
30	Age	Age	Constant	6403.90	0.00	0.38	6	8437.29
29	Age	Age	Age	6404.79	0.89	0.24	7	8435.83
44	Age[a] Reach	Age	Constant	6405.71	1.81	0.15	7	8437.04
43	Age[a] Reach	Age	Age	6406.80	2.90	0.09	8	8435.82
42	Age	Reach[a] Age	Constant	6407.84	3.94	0.05	8	8437.20
41	Age	Reach[a] Age	Age	6408.20	4.29	0.04	9	8435.02
56	Age[a] Reach	Reach[a] Age	Constant	6409.58	5.68	0.02	9	8436.85
55	Age[a] Reach	Reach[a] Age	Age	6410.17	6.27	0.02	10	8434.99
15	Reach	Age	Age	6460.61	56.71	0.00	7	8509.50
14	Constant	Reach[a] Age	Constant	6460.75	56.85	0.00	7	8509.69
16	Reach	Age	Constant	6460.86	56.96	0.00	6	8512.48
28	Reach	Reach[a] Age	Constant	6461.57	57.67	0.00	8	8508.12
2	Constant	Age	Constant	6462.37	58.47	0.00	5	8517.12
13	Constant	Reach[a] Age	Age	6462.68	58.77	0.00	8	8509.58
1	Constant	Age	Age	6463.26	59.36	0.00	6	8515.65
27	Reach	Reach[a] Age	Age	6463.40	59.50	0.00	9	8507.89
24	Reach	Pre-post trotline 2010[a] Reach	Constant	6504.46	100.56	0.00	8	8564.74
10	Constant	Pre-post trotline 2010[a] Reach	Constant	6505.00	101.09	0.00	7	8568.09
23	Reach	Pre-post trotline 2010[a] Reach	Age	6505.88	101.98	0.00	9	8563.97
9	Constant	Pre-post trotline 2010[a] Reach	Age	6506.99	103.09	0.00	8	8568.08
20	Reach	Pre-post trotline 2009/2008[a] Reach	Constant	6512.75	108.85	0.00	8	8575.69
6	Constant	Pre-post trotline 2009/2008[a] Reach	Constant	6512.76	108.86	0.00	7	8578.34
12	Constant	Reach	Constant	6514.17	110.27	0.00	5	8585.50
19	Reach	Pre-post trotline 2009/2008[a] Reach	Age	6514.49	110.59	0.00	9	8575.33
5	Constant	Pre-post trotline 2009/2008[a] Reach	Age	6514.66	110.76	0.00	8	8578.20
11	Constant	Reach	Age	6515.85	111.95	0.00	6	8585.07
26	Reach	Reach	Constant	6516.03	112.13	0.00	6	8585.31
25	Reach	Reach	Age	6516.94	113.04	0.00	7	8583.87
8	Constant	Pre-post trotline 2010	Constant	6523.66	119.76	0.00	5	8598.02
7	Constant	Pre-post trotline 2010	Age	6524.55	120.65	0.00	6	8596.56
4	Constant	Constant	Constant	6528.42	124.51	0.00	4	8606.94
3	Constant	Constant	Age	6529.31	125.41	0.00	5	8605.47
18	Reach	Constant	Constant	6529.88	125.98	0.00	5	8606.23
17[a]	Reach	Constant	Age					
21[a]	Reach	Pre-post trotline 2010	Age					
22[a]	Reach	Pre-post trotline 2010	Constant					
31[a]	Age	Constant	Age					
32[a]	Age	Constant	Constant					
33[a]	Age	Pre-post trotline 2009/2008[a] Reach	Age					
34[a]	Age	Pre-post trotline 2009/2008[a] Reach	Constant					
35[a]	Age	Pre-post trotline 2010	Age					
36[a]	Age	Pre-post trotline 2010	Constant					
37[a]	Age	Pre-post trotline 2010[a] Reach	Age					

(Continues)

TABLE 2 (Continued)

	Hypothesis							
Model	Survival	Recapture	Emigration	QAICc	Delta QAICc	QAICc weight	K	−2Ln(L)
38[a]	Age	Pre-post trotline 2010[a] Reach	Constant					
39[a]	Age	Reach	Age					
40[a]	Age	Reach	Constant					
45[a]	Age[a] Reach	Constant	Age					
46[a]	Age[a] Reach	Constant	Constant					
47[a]	Age[a] Reach	Pre-post trotline 2009/2008[a] Reach	Age					
48[a]	Age[a] Reach	Pre-post trotline 2009/2008[a] Reach	Constant					
49[a]	Age[a] Reach	Pre-post trotline 2010	Age					
50[a]	Age[a] Reach	Pre-post trotline 2010	Constant					
51[a]	Age[a] Reach	Pre-post trotline 2010[a] Reach	Age					
52[a]	Age[a] Reach	Pre-post trotline 2010[a] Reach	Constant					
53[a]	Age[a] Reach	Reach	Age					
54[a]	Age[a] Reach	Reach	Constant					

Notes: QAICc was calculated using $\hat{c}$ = 1.32 for all models.
K,number of parameters; Ln(L), maximised log-likelihood.
[a]Excluded due to unrealistic parameter estimates.

met the assumptions of the model reasonably well, and this value was used for *c* to calculate $QAIC_C$ for all models. The number of parameters used to calculate $QAIC_C$ reflects the number of parameters in the model and an additional parameter to calculate $\hat{c}$ (Anderson, 2008). Models with delta $QAIC_C$ (i.e. $QAIC_C$ of the model - $QAIC_C$ of the most supported model) <7 were considered to have meaningful support (Anderson, 2008) and were examined to determine if they were more parameterised versions of the most supported model because unsupported models may have delta $QAIC_C$ <7 if they are more parameterised versions of the most supported model (Anderson & Burnham, 2002; Anderson, Burnham & Thompson, 2000; Burnham & Anderson, 2002). This phenomenon occurs because the more parameterised models explain a similar amount of information [i.e. similar $\log_e$(likelihood)] as the most supported model but are penalised approximately two $QAIC_C$ units per additional parameter depending on the number of parameters and sample size (see $QAIC_C$ calculation above). For example, a model that explained identical information as the most supported model but required three more parameters than the most supported model would have a delta $QAIC_C$ of approximately 6. Models that produced unrealistic parameter estimates (i.e. survival probability = 1.00) of estimable parameters were removed from consideration in the final candidate model set.

3 | RESULTS

Of the 12,004 HRPS stocked into the MMR from 2000 to 2015, 893 (7.4%; including 48 of unknown year classes) were caught in the stocking reach and 219 (1.8%) were caught downstream of Gavins Point Dam. The first emigrant was detected in 2004, and the number of new emigrants detected annually generally increased from 2004 to 2015 (Figure 1). Emigrants were primarily (*n* = 210; 96%) from the 2001–2008 year classes (Figure 2). Few individuals of the 1997–1999 (*n* = 4) or 2009-2013 (*n* = 5) year classes were recaptured in the LMR (Figure 2). Individuals from the 2014 year class were not caught in the MMR or LMR and, subsequently, were omitted from analyses. Patterns in percent of HRPS recaptured by year class differed between the MMR and LMR (Figure 2). Percent recaptures in the MMR decreased from 17.2% for the 1997 year class to 9.4% for the 1999 year class and from 21.1% for the 2001 year class to 1.1% for the 2008 year class. A higher percentage of individuals were recaptured in the MMR from the 2009 year class (5.4%) than the 2007 and 2008 year classes, but recapture percentages from the 2010, 2012 and 2013 year classes were low relative to older year classes. Unlike the MMR, the percentages of HRPS from the 1997–1999 year classes recaptured in the LMR (<1% per year class) were low compared with the 2001–2007 year classes (2.3%–6.8%). Similar to the MMR, recapture percentages in the LMR of the youngest year classes (e.g. 2008–2013 year classes) were generally low (<1%) compared with the 2001–2007 year classes.

Emigration of HRPS through Gavins Point Dam began at young ages and continued at older ages. One individual from the 2010 year class was recaptured in the LMR at age 1 during November 2011, approximately 7 months after stocking, and most year classes stocked at age 1 (*n* = 8 of 12) were first caught in the LMR by age 3 (Figure 3). Most year classes (except for the 1997–1999 and 2002 year classes) were caught in the LMR within 2 years of first capture in the MMR. Across year classes, 35% of individuals caught in the MMR were caught by age 4, and 27% of emigrants were first caught by age 4. Few individuals (*n* = 16; 7% of emigrants) were caught in the stocking reach prior to emigration.

These individuals were last observed in the stocking reach at ages 1-12 with the majority (*n* = 13) last captured in the MMR at age 4 or older, indicating that emigration of older (e.g. age 12) individuals occurred (Figure 4).

Little evidence suggested emigration was associated with the record discharges observed for the Missouri River in 2011. Individuals from the 2001–2008 year classes were observed in the LMR prior to the 2011 high-water event, and the number of new emigrants detected downstream did not consistently increase across year classes after the high-water event (Figure 3). Although an increase in the number of new emigrants from the 2007 year class was detected in 2011, most (*n* = 6 of 10) were caught in April and May of 2011, prior to the high-water event. Additionally, the increased catches of the 2007 year class in 2011 and the 2008 year class in 2012 were consistent with increased catches at age 4 of multiple year classes in the MMR and the LMR.

Of the 6,201 HRPS stocked at age 1 with PIT tags used in mark–recapture analysis, 466 were recaptured in the MMR and 162 were recaptured in the LMR. Of these, 87 individuals were recaptured multiple times in the MMR and 21 were recaptured multiple times in the LMR, resulting in a total of 569 recaptures in the MMR and 186 recaptures in the LMR. Model 30 was considered the most supported mark–recapture model because it had the lowest $QAIC_c$ value and the other models that received meaningful support (i.e. delta $QAIC_c$ <7; Table 2) were more parameterised versions of Model 30. Model 30 represented age-group specific survival and recapture probabilities and constant probability of emigration among age groups (Table 2). The additional parameters used to incorporate the effects of reach on survival and recapture probabilities and the effect of age on emigration probabilities in Models 29, 41–44, 55 and 56 did not improve model fit enough to overcome the penalty incurred in $QAIC_c$ calculations for the additional parameters. The annual probability of emigration of HRPS stocked at age 1 estimated from Model 30 was 0.05 [95% confidence interval (CI) = 0.04 to 0.06] for fish age ≥ 1. The annual apparent survival probability estimate for HRPS in the MMR and LMR was 0.38 (95% CI = 0.31 to 0.45) for age 1 fish and 0.96 (95% CI = 0.92 to 0.98) for age ≥2 fish. Annual recapture probability of HRPS in the MMR and LMR was 0.02 (95% CI = 0.02 to 0.03) for age 2–3 fish and 0.05 (95% CI = 0.04 to 0.06) for age ≥4 fish.

4 | DISCUSSION

Emigration of HRPS from the MMR to the LMR was documented for most year classes and may vary among stocking ages but likely was not associated with the 2011 high-water event. Recapture percentages of the 1997–1999 year classes, stocked at ages 2–3, indicate that these year classes recruited to the MMR population. Meanwhile, the low recapture percentages of these year classes in the LMR compared with year classes stocked at age 1 (2001–2007 year classes) suggest emigration was lower for HRPS stocked at ages 2–3 than for HRPS stocked at age 1, but this evidence is not definitive because it is limited to the first 3 year classes stocked. The

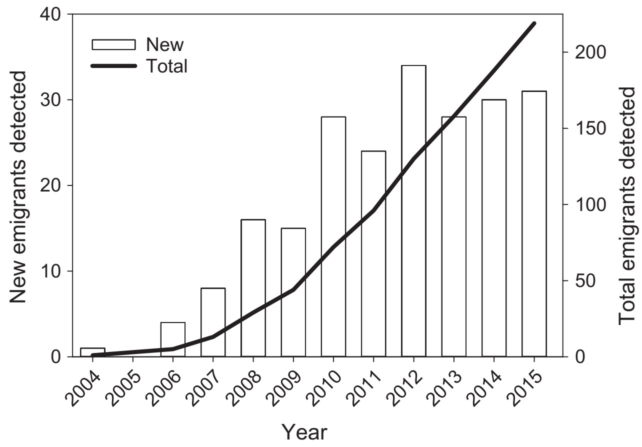

FIGURE 1 Number of new individual (white bars) and cumulative total of individual (i.e. sum of new emigrants from current and previous years, black line) hatchery-reared pallid sturgeon stocked into the middle Missouri River that were recaptured downstream of Gavins Point Dam from 2004 to 2015 by year

lower recapture percentages of the 2008–2013 year classes stocked at age 1 compared with those of the 2001–2007 year classes were consistent between the MMR and LMR and may indicate limited recruitment to sampling gears of the 2008–2013 year classes, rather than a lack of emigration, because HRPS typically do not recruit well to sampling gears until ages 4–6 (Pierce et al., 2017). Finally, trends in the number of new emigrants detected through time (i.e. catch curves by year class) were consistent with increased sampling effort and recruitment to sampling gears rather than the 2011 high-water event or age, but the effects of the high-water event on younger year classes (e.g. 2008–2010) remain unclear because these individuals were not fully recruited to sampling gears during this study.

Emigration of HRPS stocked at ages 2–3 may be lower than emigration of HRPS stocked at age 1 due to differences in dispersal behaviour between stocking ages. Downstream movement >400 rkm from stocking locations of age 1 HRPS was observed in the UMR (Oldenburg, Guy, Cureton, Webb & Gardner, 2011) and LMR (Steffensen, Hamel & Spurgeon, 2019). Meanwhile, initial dispersal of age-1 HRPS in the MMR under normal conditions is relatively unclear. Net upstream movement of age-1 HRPS was observed in the MMR during the 2011 high-water event (Pierce, James, Shuman & Klumb, 2016), but it is possible that downstream dispersal was underestimated because few telemetry surveys were done downstream of the riverine portions of the MMR (i.e. Lewis and Clark Lake or the LMR). Furthermore, initial dispersal of age-1 HRPS has not been examined in the MMR under normal flow conditions. Unlike HRPS stocked at age 1 in the UMR and LMR, HRPS stocked at age 3 in the MMR were primarily relocated near or upstream of the stocking location during the year following stocking (Jordan et al., 2006). Additionally, differences in initial (30-day) post-stocking movements of HRPS between stocking ages were documented in the LMR by Eder, Steffensen, Haas and Adams (2015), but these authors found that age-1 HRPS were generally located upstream of the stocking

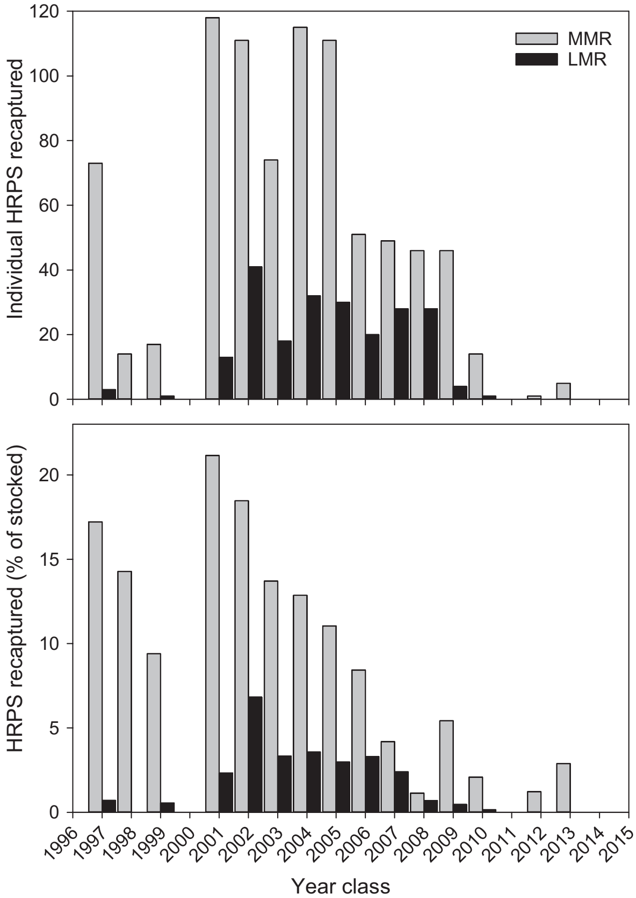

FIGURE 2 Number (top) and percent (bottom) of hatchery-reared pallid sturgeon (HRPS) stocked into the middle Missouri River (MMR) that were recaptured in the MMR (grey bars) and downstream of Gavins Point Dam [i.e. lower Missouri River (LMR); black bars) from 2000 to 2015 by year class

location, while age-4 HRPS were generally located downstream of the stocking location. Currently, however, it is unclear if initial dispersal of HRPS in the MMR differs among stocking ages because post-stocking movements of HRPS stocked at age 1 and age 2–3 have not been evaluated under comparable flow conditions.

The low percent recaptures in the LMR of HRPS stocked at ages 2–3 compared with those stocked at age 1 may reflect higher entrainment mortality for HRPS stocked at ages 2–3 than those stocked at age-1, rather than a lack of entrainment. Successful emigration in this study required entrainment and survival until recapture. Two common injuries that occur during dam passage are turbine blade strike and barotrauma (Brown et al., 2014). The probability of blade strike and the severity of injury increase with body size (Hammar et al., 2015). Therefore, entrainment mortality from blade strike may be higher for the older, larger HRPS stocked at ages 2–3 than for smaller HRPS stocked at age 1 (see Pierce et al., 2017). Although smaller fish (e.g. HRPS stocked at age 1) are more susceptible to barotrauma than larger individuals (Brown et al., 2014), barotrauma-related mortality may be relatively low for pallid sturgeon because they are physostomes and can release gas from their swim bladder during decompression (Brown et al., 2012, 2014). Differences in entrainment mortality among year classes may explain the observed pattern in percent recaptures in the LMR, but the factors affecting mortality of pallid sturgeon entrained through Gavins Point Dam are unknown.

The lack of observed effects of the 2011 high-water event on emigration of HRPS through Gavins Point Dam is consistent with movement and habitat use of pallid sturgeon. Pallid sturgeon use low-velocity areas downstream of instream structures (e.g. wing dams, rock structures and woody debris) during high-discharge events (Jordan et al., 2006), so increased discharge may not affect the near-bottom velocities experienced by benthic fishes like pallid sturgeon (Gerrity, Guy & Gardner, 2008; Quist, Tillma, Burlingame & Guy, 1999). Furthermore, HRPS had a net upstream movement in the MMR during the 2011 high-discharge event based on telemetry relocations (Pierce et al., 2016), although downstream movement may have been underestimated because limited tracking was done downstream of the riverine portion of the MMR (i.e. in Lewis and Clark Lake and LMR).

Survival and recapture probabilities of HRPS estimated in this study were generally consistent with other studies in the MMR and LMR. The annual survival probability estimate of HRPS stocked at age 1 in the MMR (0.38) for the first year at large in this study was intermediate to the estimate by Rotella (2017) for the MMR (0.68) and the estimate by Steffensen et al. (2019) for the LMR (0.28). However, the difference in estimates between this study and Rotella (2017) likely is partially due to the differences in time intervals used for these estimates [i.e. 1 year in this study vs. 9.4 months in Rotella (2017)]. Survival probability estimates of age ≥2 HRPS in this study (0.96) were similar to estimates by Rotella (2017; ≥0.91 for fish ≥4.8 years old) for HRPS in the MMR and estimates by Steffensen et al (2019; 0.95) for HRPS stocked in the LMR. However, the estimates from Rotella (2017) may have underestimated true survival because the model assumed emigration to the LMR was mortality. Recapture probability estimates for HRPS in this study (0.02 for age 2–3 HRPS and 0.05 for age ≥4 HRPS) were consistent with those of Steffensen et al. (2019; <0.01 to 0.04). Finally, the observed increase in recapture probability with age is consistent with Pierce et al. (2017), who indicated that pallid sturgeon recruitment to sampling gears increased at ages 4–6 in the MMR.

Emigration of HRPS from the MMR through Gavins Point Dam can affect the size and genetic structure of the LMR pallid sturgeon population and may justify re-evaluation of stocking practices for the MMR. Emigration of HRPS from UMR broodstock stocked in the MMR may have a positive effect on the LMR population by restoring genetic connectivity and reducing the potential for inbreeding depression or a negative effect by increasing the potential of outbreeding depression. Currently, however, the causes and fitness implications of genetic differences among populations are unclear. Despite this uncertainty, simple alterations to stocking practices could be implemented to reduce outbreeding depression concerns in the LMR. This study suggests that

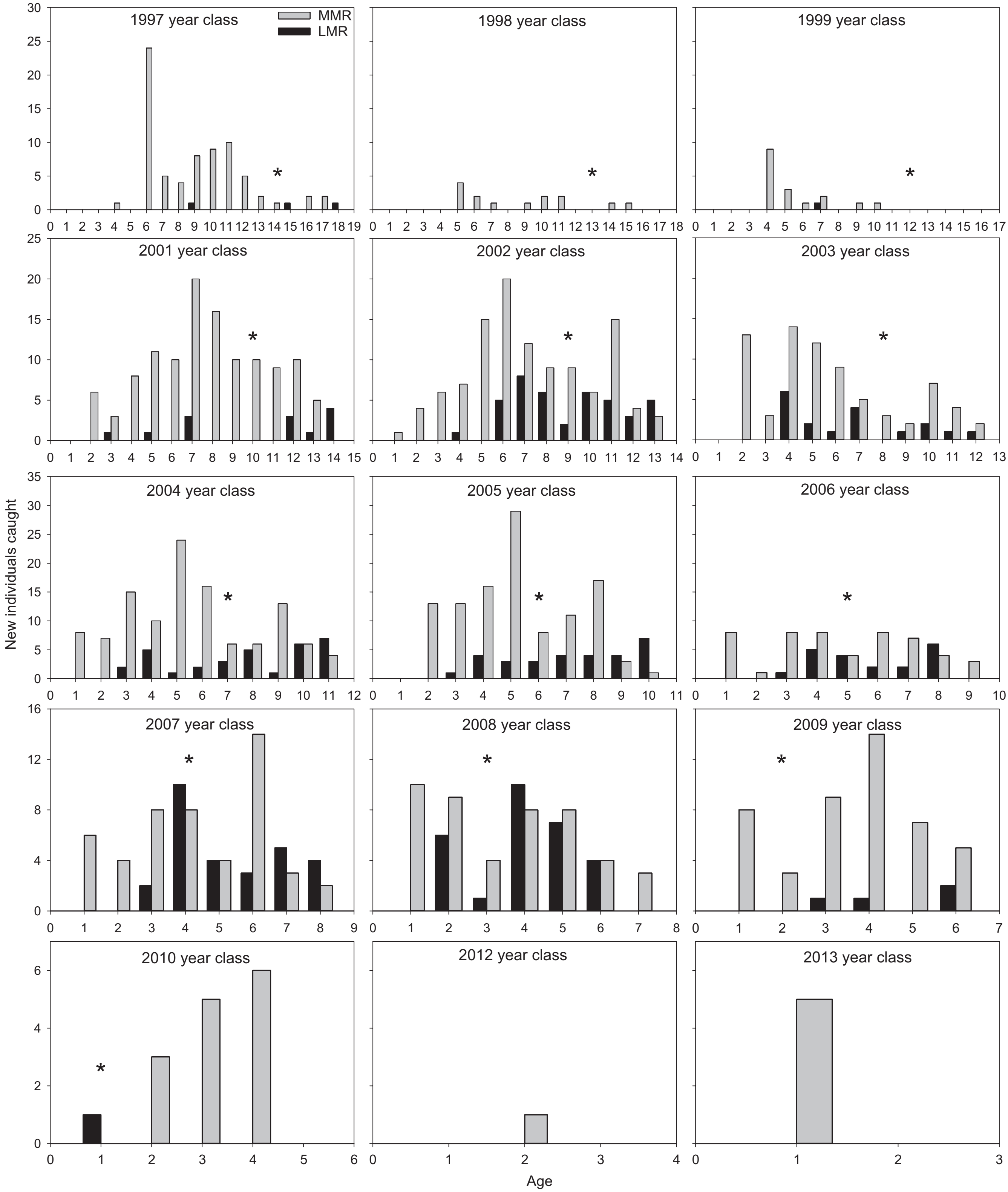

FIGURE 3 Number of new individual hatchery-reared pallid sturgeon caught in the middle Missouri River (MMR) and lower Missouri River (i.e. downstream of Gavins Point Dam; LMR) from 2000 to 2015 by year class and age. Asterisk (*) denotes the year 2011

emigration and, therefore, outbreeding depression concerns may be reduced by stocking older (e.g. age ≥2) pallid sturgeon in the MMR. Alternatively, progeny of LMR pallid sturgeon broodstock could be stocked in the MMR. This alternative would allow managers to continue to conserve the genetic diversity of the LMR pallid sturgeon population by maximising the number of families stocked

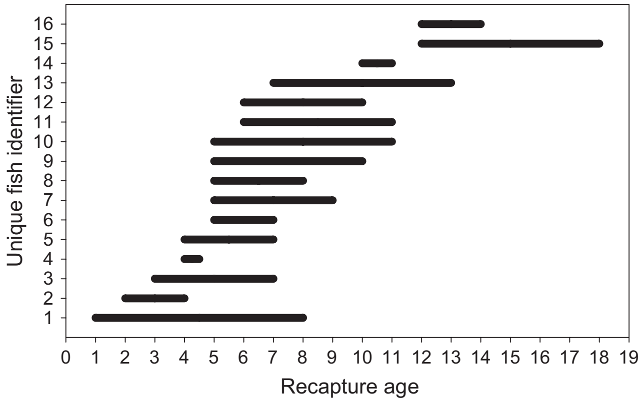

FIGURE 4 Emigration-age window of 16 hatchery-reared pallid sturgeon emigrants from the middle Missouri River that were recaptured in the stocking reach prior to emigration through Gavins Point Dam and recaptured downstream. The left side of each bar is the age the individual was last captured in the stocking reach, and the right side is the youngest age it was recaptured downstream

without increasing competition for resources downstream of Gavins Point Dam where food competition was identified as a potential cause of recent declines in pallid sturgeon body condition (Randall et al., 2017; Steffensen & Mestl, 2016; Steffensen, Mestl & Phelps, 2016). Furthermore, this option would create a refugium population to store LMR pallid sturgeon genetics, similar to the one that currently exists in the MMR for the UMR population (USFWS, 2008), in case of a catastrophic loss of pallid sturgeon downstream of Gavins Point Dam. Although this option may increase potential interactions between progeny of UMR broodstock and progeny of LMR broodstock, it likely would not increase the risk of outbreeding depression because reservoir and inter-reservoir reaches, such as the MMR, are not expected to support natural recruitment of pallid sturgeon (Jacobson et al., 2016). Finally, this study highlights the connectedness of the MMR and LMR populations and the need to consider the potential effects of management actions (e.g. population augmentation) in the MMR on pallid sturgeon populations downstream of Gavins Point Dam.

ACKNOWLEDGMENTS

We thank the staff at U.S. Fish and Wildlife Service Gavins Point Dam and Garrison Dam National Fish Hatcheries, USFWS Missouri River Fish and Wildlife Conservation Office, and Montana Fish, Wildlife, and Parks for their broodstock collection and propagation efforts. We thank the staff at Nebraska Game and Parks Commission; South Dakota Department of Game, Fish, and Parks; Missouri Department of Conservation; U.S. Fish and Wildlife Service Columbia and Great Plains Fish and Wildlife Conservation Offices; and U.S. Geological Survey Columbia Environmental Research Center for their assistance in the field. Finally, we thank the U.S. Army Corp of Engineers for funding. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

REFERENCES

Anderson, D. R. (2008). *Model based inference in the life sciences: A primer on evidence*. New York, NY: Springer. https://doi.org/10.1007/978-0-387-74075-1

Anderson, D., & Burnham, K. (2002). Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management*, *66*, 912–918.

Anderson, D. R., Burnham, K. P., & Thompson, W. L. (2000). Null hypothesis testing: Problems, prevalence, and an alternative. *Journal of Wildlife Management*, *64*, 912–923.

Brown, R. S., Colotelo, A. H., Pflugrath, B. D., Boys, C. A., Baumgartner, L. J., Deng, Z. D., … Singhanouvong, D. (2014). Understanding barotrauma in fish passing hydro structures: A global strategy for sustainable development of water resources. *Fisheries*, *39*, 108–122.

Brown, R. S., Pflugrath, B. D., Colotelo, A. H., Brauner, C. J., Carlson, T. J., & Deng, Z. D. (2012). Pathways of barotrauma in juvenile salmonids exposed to simulated hydroturbines passage: Boyles law vs. Henry's law. *Fisheries Research*, *121–122*, 3–50.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd ed. New York, NY: Springer.

Cooch, E., & White, G. (Eds.). (2011). Program MARK: A gentle introduction (9th ed.)Available: http://www.phidot.org/software/mark/docs/book/

Eder, B. L., Steffensen, K. D., Haas, J. D., & Adams, J. D. (2015). Short-term survival and dispersal of hatchery-reared juvenile pallid sturgeon stocked in the channelized Missouri River. *Journal of Applied Ichthyology*, *31*, 991–996.

Galat, D. L., Berry, C. R. Jr, Peters, E. J., & White, R. G. (2005). Missouri River Basin. In A. C. Benke, & C. E. Cushing (Eds.), *Rivers of North America* (pp. 427–480). Oxford, UK: Elsevier.

Gerrity, P. C., Guy, C. S., & Gardner, W. M. (2008). Habitat use of juvenile pallid sturgeon and shovelnose sturgeon with implications for water-level management in a downstream reservoir. *North American Journal of Fisheries Management*, *28*, 832–884.

Gotelli, N. J. (2001). *A primer of ecology*. Sunderland, MA: Sinauer Associates Inc.

Hallerman, E. (2003). Co-adaption and outbreeding depression. In E. M. Hallerman (Ed.), *Population genetics: Principles and applications for fisheries scientists* (pp. 239–259). Bethesda, MD: American Fisheries Society.

Hammar, L., Eggertsen, L., Andersson, S., Ehnberg, J., Arvidsson, R., Gullström, M., & Molander, S. (2015). A probabilistic model for hydrokinetic turbine collision risks: Exploring impacts on fish. *PLoS ONE*, *10*, 1–25.

Jacobson, R. B., Annis, M. L., Colvin, M. E., James, D. A., Welker, T. L., & Parsley, M. J. (2016). *Missouri River Scaphirhynchus albus (Pallid Sturgeon) Effects Analysis—Integrative Report 2016 (U.S. Geological Survey Scientific Investigations Report 2016–5064)*. Reston, VA: U.S. Geological Survey. https://doi.org/10.3133/sir20165064

Jordan, G. R., Klumb, R. A., Wanner, G. A., & Stancill, W. J. (2006). Poststocking movements and habitat use of hatchery-reared juvenile pallid sturgeon in the Missouri River below Fort Randall Dam, South Dakota and Nebraska. *Transactions of the American Fisheries Society*, *135*, 1499–1511.

Ludwig, A. (2006). A sturgeon view of conservation genetics. *European Journal of Wildlife Research*, *52*, 3–8.

Monson, C. A., & Sadler, K. C. (2010). Inbreeding depression and outbreeding depression are evident in wild-type zebrafish lines. *Zebrafish*, *7*, 189–197.

Oldenburg, E. W., Guy, C. S., Cureton, E. S., Webb, M. A. H., & Gardner, W. M. (2011). Effects of acclimation on poststocking dispersal and physiological condition of age-1 pallid sturgeon. *Journal of Applied Ichthyology*, *27*, 436–443.

Pierce, L. L., James, D. A., Shuman, D. A., & Klumb, R. A. (2016). Pallid sturgeon detectability, catchability and post-handling survival with four standardized sampling gears, and movement of pallid sturgeon during the 2011 flood. Pierre, SD: U.S. Fish and Wildlife Service, Great Plains Fish and Wildlife Conservation Office.

Pierce, L. L., Shuman, D. A., James, D. A., & Stacy, W. L. (2017). 2016 Annual Report. Pallid sturgeon population assessment and associated fish community monitoring for the Missouri River: Segments 5 and 6. Pierre, SD: U.S. Fish and Wildlife Service, Great Plains Fish and Wildlife Conservation Office.

Pracheil, B. M., Mestl, G. E., & Pegg, M. A. (2014). Movement through dams facilitates population connectivity in a large river. *River Research and Applications*, *31*, 517–525.

Quist, M. C., Tillma, J. S., Burlingame, M. N., & Guy, C. S. (1999). Overwinter habitat use of shovelnose sturgeon in the Kansas River. *Transactions of the American Fisheries Society*, *128*, 522–527.

Randall, M. T., Colvin, M. E., Steffensen, K. D., Welker, T. L., Pierce, L. L., & Jacobson, R. B. (2017) *Assessment of adult pallid sturgeon fish condition, Lower Missouri River—Application of new information to the Missouri River Recovery Program (U.S. Geological Survey Open-File Report 2017–1121)*. Reston, VA: U.S. Geological Survey. https://doi.org/10.3133/ofr20171121

Reager, J. T., Thomas, B. F., & Famiglietti, J. S. (2014). River basin flood potential inferred using GRACE gravity observations at several months lead time. *Nature Geoscience*, *7*, 588–592.

Rotella, J. (2017). *Upper basin pallid sturgeon survival estimation project: 2017 update*. Bozeman, MT: Montana State University.

Ryman, N., & Laikre, L. (1991). Effects of supportive breeding on the genetically effective population size. *Conservation Biology*, *5*, 325–329.

Saltzgiver, M. J., Heist, E. J., & Hedrick, P. W. (2012). Genetic evaluation of the initiation of a captive population: The general approach and a case study in the endangered pallid sturgeon (*Scaphirhynchus albus*). *Conservation Genetics*, *13*, 1381–1391.

Schrey, A. W., & Heist, E. J. (2007). Stock structure of pallid sturgeon analyzed with microsatellite loci. *Journal of Applied Ichthyology*, *23*, 297–303.

Steffensen, K. D., Hamel, M. J., & Spurgeon, J. J. (2019). Post-stocking pallid sturgeon *Scaphirhynchus albus* growth, dispersal, and survival in the lower Missouri River. *Journal of Applied Ichthyology*, *35*, 117–127. Advance online publication. https://doi.org/10.1111/jai.13646

Steffensen, K. D., & Mestl, G. E. (2016). Assessment of pallid sturgeon relative condition in the upper channelized Missouri River. *Journal of Freshwater Ecology*, *31*, 583–595.

Steffensen, K. D., Mestl, G. E., & Phelps, Q. E. (2016). Range-wide assessment of pallid sturgeon *Scaphirhynchus albus* (Forbes & Richardson, 1905) relative condition. *Journal of Applied Ichthyology*, *33*, 13–21.

USACE (U.S. Army Corps of Engineers). (2004). *Gavins Point Dam/Lewis and Clark Lake Master Plan Missouri River, Nebraska and South Dakota*. Omaha, NE: U.S. Army Corps of Engineers.

USACE (U.S. Army Corps of Engineers). (2012). *Post 2011 Flood Event Analysis of Missouri River*. Omaha, NE: U.S. Army Corps of Engineers.

USFWS (U.S. Fish and Wildlife Service) (2008). *Pallid sturgeon (Scaphirhynchus albus) range-wide stocking and augmentation plan*. Billings, MT: U.S. Fish and Wildlife Service.

USFWS (U.S. Fish and Wildlife Service) (2014). *Revised recovery plan for the pallid sturgeon (Scaphirhynchus albus)*. Denver, CO: U.S. Fish and Wildlife Service.

Walburg, C. H. (1971). Loss of young fish in reservoir discharge and year-class survival, Lewis and Clark Lake, Missouri River. *Reservoir fisheries and limnology*. *American Fisheries Society*, *Special Publication*, *8*, 441–448.

Wanner, G. A., Klumb, R. A., Stancill, W. J., & Jordan, G. R. (2007). Habitat use and movements of adult pallid sturgeon in the Missouri River downstream of Fort Randall Dam, South Dakota and Nebraska. *Proceedings of the South Dakota Academy of Science*, *86*, 21–33.

Welker, T. L., Drobish, M. R., & Williams, G. A. (Eds.). (2016). *Pallid sturgeon population assessment project*, *guiding document*, *volume 1.8*. Yankton, SD: U.S. Army Corps of Engineers.

How to cite this article: Pierce LL, Shuman DA, James DA, et al. Emigration of hatchery-reared Pallid Sturgeon, *Scaphirhynchus albus* (Forbes and Richardson), through a Missouri River dam. *Fish Manag Ecol*. 2019;26:295–305. https://doi.org/10.1111/fme.12349