

## Drift Dynamics of Larval Pallid Sturgeon and Shovelnose Sturgeon in a Natural Side Channel of the Upper Missouri River, Montana

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**Abstract.**—The drift dynamics of larval shovelnose sturgeon *Scaphirhynchus platyrhynchus* (1, 2, 6, and 10 d posthatch [dph]) and pallid sturgeon *S. albus* (1, 2, 5, 9, 11, and 17 dph) were examined in a natural side channel of the Missouri River to quantify the vertical drift location of larvae in the water column, determine the drift velocity of larvae relative to water velocity, and simulate the cumulative distance (km) drifted by larvae during ontogenetic development. Larvae were released at the side-channel inlet and sampled at points 100, 500, 900, and 1,300 m downstream. Larvae drifted primarily near the riverbed, as 58–79% of recaptured shovelnose sturgeon and 63–89% of recaptured pallid sturgeon were sampled in the lower 0.5 m of the water column. The transition from the drifting to the benthic life stage was initiated at 6 dph (mean length, 15.6 mm) for shovelnose sturgeon and at 11–17 dph (mean length, 18.1–20.3 mm) for pallid sturgeon. Across ages, the drift rates of larval shovelnose sturgeon averaged 0.09–0.16 m/s slower than the mean water column velocity. The drift rates of pallid sturgeon were similar to or slightly slower (0.03–0.07 m/s) than the mean water column velocity for 1–11-dph larvae. Conversely, 17-dph larval pallid sturgeon dispersed downstream at a much slower rate (mean, 0.20 m/s slower than the mean water column velocity) owing to their transition to benthic habitats. Drift simulations indicated that the average larval shovelnose sturgeon may drift from 94 to 250 km and the average larval pallid sturgeon may drift from 245 to 530 km, depending on water velocity. Differences in larval drift dynamics between species provide a possible explanation for differences in recruitment between shovelnose sturgeon and pallid sturgeon in the upper Missouri River.

Larvae of numerous fish species in streams and rivers are transported via water currents from upstream spawning and hatch locations to downstream habitats where they settle from the current (Muth and Schmulbach 1984; Robinson et al. 1998; D'Amours et al. 2001). Despite widespread recognition that larval fish drift and settle at some point downstream, limited information is available to discern how hydraulic forces (e.g., water velocity) and larval behavior (e.g., vertical drift location in the water column) interact to influence drift rate and cumulative distance transported during the free-drifting life stage. An understanding of these interactions is critical when viewed in the context of anthropogenic river modifications and the subsequent influence of these alterations on recruitment dynamics. For example, river fragmentation resulting

from alternating sequences of dams and reservoirs disrupts natural drift patterns of larvae by reducing the length of free-flowing riverine habitat. Populations of some river-spawning species may be little affected by the reduced length of free-flowing river downstream from spawning and hatch locations because their larvae do not require lotic habitat at the termination of the larval drift period (Mion et al. 1998). Conversely, river-spawning species whose larvae require an extended length of free-flowing river downstream from spawning areas are likely to exhibit limited to no recruitment in short river reaches terminating in reservoirs (Jager et al. 2002). Establishing mechanistic linkages between the length of free-flowing riverine habitat required by larvae and recruitment dynamics requires detailed information on larval fish behavior and drift rates relative to river hydraulic conditions.

Field and laboratory studies focusing on the early life history of sturgeons (family Acipenseridae) have contributed to an understanding of larval sturgeon

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behaviors and indicate that posthatch behaviors and larval drift characteristics vary broadly among sturgeon taxa. For example, lake sturgeon *Acipenser fulvescens* (Auer and Baker 2002; Smith and King 2005) and green sturgeon *A. medirostris* (Deng et al. 2002; Kynard et al. 2005) remain in close association with the substrate for at least the initial 5 d posthatch (dph) before initiating downstream drift at older ages. Conversely, larvae of white sturgeon *A. transmontanus* (Deng et al. 2002), Siberian sturgeon *A. baeri* (Gisbert and Ruban 2003; Gisbert and Williot 1997), kaluga *Huso dauricus* (Zhuang et al. 2003), Amur sturgeon *A. schrencki* (Zhuang et al. 2003), shovelnose sturgeon *Scaphirhynchus platyrhynchus* (Kynard et al. 2002), and pallid sturgeon *S. albus* (Kynard et al. 2002, 2007) initiate downstream drift immediately after hatching but exhibit a high level of variation in the duration of the drifting larval stage. For example, Siberian sturgeon transition from the drifting to benthic life stage at about 4 dph (Gisbert and Ruban 2003), whereas the pelagic drift period in pallid sturgeon persists for 11–12 dph (Kynard et al. 2007). Although differences in larval behavior among sturgeon taxa are well established, few studies have examined how river velocity and posthatch behavior interact to influence drift distance of larvae.

Pallid sturgeon and shovelnose sturgeon are sympatric in the Missouri River. Although shovelnose sturgeon are common, pallid sturgeon are rare throughout their range and were classified as endangered in 1990 under the Endangered Species Act (Dryer and Sandvol 1993). A population of pallid sturgeon occurs in the upper Missouri River and lower Yellowstone River of Montana and North Dakota. The population has access to about 340 km of riverine habitat in the Missouri River between Fort Peck Dam in Montana and the headwaters of the next downstream reservoir (Lake Sakakawea, impounded by Garrison Dam, North Dakota). Pallid sturgeon in the Yellowstone River primarily inhabit a 113-km reach below a diversion structure. There is no evidence of recruitment from this population during the last several decades, as the population of wild pallid sturgeon consists of large and presumably old individuals (Jordan 2006). Conversely, recruitment of shovelnose sturgeon from spawning events in the Missouri River and Yellowstone River occurs as age-0 fish are collected annually (Braaten and Fuller 2007; Braaten et al. 2007), and several year-classes are present in the adult population (Quist et al. 2002). However, age-0 shovelnose sturgeon have been sampled only in the lower reaches of these rivers upstream from the headwaters of Lake Sakakawea (Braaten and Fuller 2007; Braaten et al. 2007).

Initial information on the early life history of shovelnose sturgeon and pallid sturgeon presents the hypothesis that recruitment differences between these species are related to differences in the drift dynamics of the posthatch life stages relative to contemporary habitat conditions in the dam-fragmented Missouri River. In laboratory studies, Kynard et al. (2002) found that shovelnose sturgeon and pallid sturgeon initiated downstream drift immediately after hatch, but that duration of the drifting larval life stage was about two times greater for pallid sturgeon (9–11 d) than shovelnose sturgeon (4–5 d). Based on low water velocities used in the laboratory experiments ( $\leq 12$  cm/s), Kynard et al. (2002) estimated that the cumulative drift distance for shovelnose sturgeon and pallid sturgeon was about 13 km. In additional laboratory studies, Kynard et al. (2007) subjected larval pallid sturgeon to higher water velocities (17–30 cm/s) and indicated that pallid sturgeon may drift in excess of 300 km during the drift phase of the life cycle. The extended drift duration of larval pallid sturgeon coupled with the increase in drift distance as a function of water velocity is significant when viewed in the context of available riverine habitat because only 340 km of riverine habitat are available between Fort Peck Dam and the headwaters of the downstream reservoir. If larval sturgeon are obligate to riverine conditions, reservoir habitat conditions may be an impediment to survival because larval pallid sturgeon may drift into unsuitable reservoir habitat during the extended drift period and die (Kynard et al. 2007). A similar situation occurs in the Yellowstone River as less than 50 km of free-flowing habitat are available for drifting pallid sturgeon larvae between suspected spawning sites (Bramblett and White 2001) and the headwaters of Lake Sakakawea. Conversely, the shorter drift duration exhibited by larval shovelnose sturgeon would allow for at least some drifting larvae to settle in suitable riverine habitats and survive before encountering reservoir headwater environments.

Additional information on the drift behavior of larval shovelnose sturgeon and pallid sturgeon from field settings is needed to better understand the drift dynamics of these species in natural environments. In addition, water velocities in the Missouri River downstream from Fort Peck Dam and the Yellowstone River (Galat et al. 2001) greatly exceed velocities studied in earlier laboratory studies of larval shovelnose sturgeon and pallid sturgeon (Kynard et al. 2002, 2007). Therefore, results on the behavior and drift characteristics of larval sturgeon from laboratory studies may not be directly extrapolated to natural river conditions.

This study examined the drift dynamics of larval

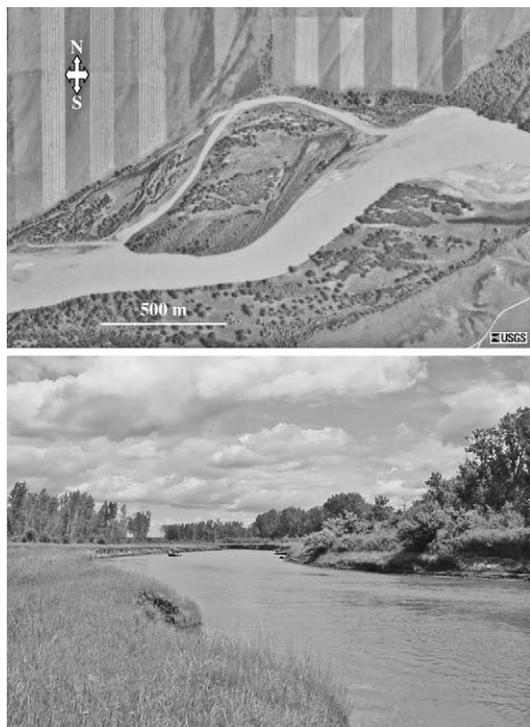


FIGURE 1.—Aerial view (top panel; flow is from left to right) and ground view (lower panel) of the 1.4-km-long side channel of the upper Missouri River used in larval drift studies during 2004. The ground view photo was taken at the inlet of the side channel; the boat located left of center is positioned at the 100-m sampling point. (Aerial photograph courtesy of the U.S. Geological Survey, TerraServer-USA.)

shovelnose sturgeon and larval pallid sturgeon in a side channel of the upper Missouri River, Montana. The objectives were to (1) quantify the vertical drift location of larval shovelnose sturgeon (age, 1–10 dph) and pallid sturgeon (age, 1–17 dph) in the water column, (2) determine the drift velocity of larvae relative to water velocity in the side channel, and (3) simulate the cumulative distance (km) drifted by larval sturgeon during ontogenetic development in a theoretical riverine reach.

### Study Area

Drift experiments involving larval shovelnose sturgeon and pallid sturgeon were conducted in a 1.4-km-long natural connected side channel of the upper Missouri River near Culbertson, Montana (Figure 1). The side channel is located at river kilometer (rkm) 2,631 of the upper Missouri River (measuring upstream from its confluence at the Mississippi River), 219 km downstream from Fort Peck Dam. Discharge through the study area is regulated primarily by releases from

Fort Peck Dam, but additional inputs from upstream tributaries seasonally augment releases from the dam. The amount of water flow and the physical conditions in the side channel vary with discharge in the main-stem Missouri River. The side channel has a mean width of 24.0 m, mean depth of 0.9 m, maximum depth of 2.5 m, and mean water column velocity ranging between 0.43 and 0.56 m/s. Discharge in the side channel is about 5% of the main-stem discharge. The side channel exhibits a variety of habitat features common to the main-stem Missouri River, including a meandering pattern that contributes to the formation of well-defined outside-bend erosional zones, inside-bend depositional bars, and channel crossovers. Areas of low or zero velocity and eddies occur along the channel margins and in small pools behind sandbars. Snags and woody debris accumulations are present. Sand is the dominant substrate throughout the channel, although silt is also common in low-velocity channel-margin areas and in pools.

### Methods

*Sources of larval sturgeon.*—The larval shovelnose sturgeon and pallid sturgeon used in the study were progeny from wild-caught adults spawned under hatchery conditions. Adult shovelnose sturgeon were sampled during early June 2004 from the Yellowstone and Tongue rivers in Montana and transported to the Miles City State Fish Hatchery, Miles City, Montana. Twelve female shovelnose sturgeon were spawned to produce family lots of 10,000 1-dph larvae, 20,000 2-dph larvae, 20,000 6-dph larvae, and 22,500 10-dph larvae for use in the drift studies. Four adult pallid sturgeon sampled from the Missouri River and lower Yellowstone River during April 2004 were used to produce pallid sturgeon larvae. Two of the females (identified by unique passive integrated transponder [PIT] tags as codes 454B380D60 and 7F7F066452) were transported to the Miles City State Fish Hatchery and spawned in early July to produce family lots of 20,000 1-dph larvae. One female pallid sturgeon (PIT code 454910202B) transported to the U.S. Fish and Wildlife Service (USFWS) Garrison Dam National Fish Hatchery was spawned in mid-July to produce family lots of 25,000 2-dph larvae, 25,000 5-dph larvae, and 25,000 9-dph larvae. A second female pallid sturgeon (PIT code 114476216A) transported to the USFWS Garrison Dam National Fish Hatchery was spawned in mid-June to produce family lots of 30,000 11-dph and 17,000 17-dph pallid sturgeon larvae. Tissue samples from all female pallid sturgeon spawned in the hatcheries were sent to the USFWS Abernathy Fish Technology Center for genetic archiving. Genetic information from the female pallid

sturgeon was used in microsatellite-based parentage analysis (DeHaan et al., in press) to determine family lots of larval pallid sturgeon released during the study that survived and were subsequently recaptured as juveniles. Water temperature was monitored in the hatcheries and used to quantify thermal exposure experienced by larvae before drift studies. Thermal exposure was quantified as cumulative thermal units (CTU), calculated as the sum of mean daily water temperatures for each day of life before the experiments. Food was provided to the larval sturgeon beginning at 8 dph. Before the drift experiments were conducted, sturgeon larvae were packaged in plastic shipping bags filled with oxygen, stored in coolers, and transported to the side channel. Larvae appeared active and healthy in the shipping bags before release.

*Sampling points, sampling apparatus, and experimental protocol.*—Four sampling points were established in the side channel. The sampling points were located 100-, 500-, 900-, and 1,300-m downstream from the side-channel inlet and were positioned in the thalweg. At each sampling point, a cable was secured to the riverbanks and stretched to span the side channel. The cable served as a fixed attachment site for boats during sampling. A crew of four to five individuals was stationed in each boat.

The apparatus used to sample larval sturgeon at each site consisted of one pair of conical plankton nets (750- $\mu$ m mesh, 1.5 m long, 0.5 m in diameter at the leading end, and 0.09 m in diameter at the cod end) on the port and starboard sides of the boat. Each pair of nets consisted of one net positioned to sample the upper 0.5 m of the water column (hereafter, surface) and one net positioned to sample the lower 0.5 m of the water column (hereafter, bottom). The cod end of each net was fitted with a polyvinyl chloride (PVC) sleeve, and a 0.754-l PVC collecting cup partially screened with 750- $\mu$ m mesh was used to retain samples. The collecting cup was attached to the sleeve with an elastic cord to facilitate quick removal and replacement.

Drift experiments were conducted on several dates over a 1-month period during 2004 coinciding with the hatch dates and ages of sturgeon larvae. For shovelnose sturgeon, experiments were conducted on June 25 with 1- and 2-dph larvae (the experiment with 2-dph larvae was conducted after the experiment with 1-dph larvae was completed), June 29 with 6-dph larvae, and July 1 with 10-dph larvae. For pallid sturgeon, experiments were conducted on July 2 with 11-dph larvae, July 8 with 1- and 17-dph larvae (the experiment with 1-dph larvae was conducted after the experiment with 17-dph larvae was completed), July 20 with 2-dph larvae, July 23 with 5-dph larvae, and July 27 with 9-dph larvae.

Drift studies for shovelnose sturgeon and pallid sturgeon were conducted during the day from late morning through late afternoon corresponding to larval delivery times from the hatchery. Although wild-produced larval sturgeon may have been drifting in the side channel concurrent with the drift studies, the number of wild-produced larval sturgeon was minimal compared with the artificially high numbers of hatchery-produced larvae released en masse in the side channel (Braaten and Fuller 2007).

Larval sturgeon were released en masse from plastic shipping bags at the side-channel inlet. The larvae were released near the riverbed, and the release process was completed in about 15 s. A signal was sounded at release, and boats positioned at the four downstream sampling points started to log time. Travel time (min) to each sampling point (see below) was estimated before the study to provide an estimate of when sampling should commence at each sampling point. Sampling at the 100-m sampling point was initiated at 30 s postrelease. Sampling at the 500-m, 900-m, and 1,300-m sampling points was initiated at least 3 min before the predicted travel time to the points. At the predetermined sampling time, two crew members deployed one pair of nets from the boat. After a 30-s sampling interval, the pair of nets was retrieved as the second pair of nets was deployed simultaneously from the opposite side of the boat. The alternating process of deploying and retrieving nets every 30 s continued for 0.5–15 min, 7–43 min, 17–76 min, and 25–115 min postrelease at the 100-, 500-, 900-, and 1,300-m sampling points, respectively. Collecting cups were replaced after each sampling interval.

After sampling, larval sturgeon sampled in the surface and bottom collecting cups for each 30-s sampling interval were enumerated. Larvae sampled were preserved in a 10% solution of formalin or ethanol (for some samples of pallid sturgeon). A random sample of the formalin-preserved larval sturgeon from each age was measured in the laboratory with a stereo microscope fitted with an ocular micrometer.

*Hydraulic conditions in the side channel.*—Surface velocity in the side channel was estimated by releasing 10 floats (i.e., oranges) at the side-channel inlet and measuring the elapsed time between release and arrival at each sampling point (Gordon et al. 1992). Because surface velocity is greater than mean water column velocity and provides a close approximation to maximum velocity (Gordon et al. 1992), the travel time of floats provided estimations of time of first arrival to each sampling location under the possibility that larval sturgeon drift near the surface where current velocities are greatest. Time of first arrival to each

sampling point was used to estimate when sampling should be initiated at each sampling point (discussed above).

Detailed velocity conditions in the side channel were quantified on two dates (June 24 and July 1) with a Rio Grande 1,200-kHz acoustic Doppler current profiler (ADCP; RD Instruments, San Diego, California) mounted on an Oceanscience Riverboat. It was not logistically feasible to obtain ADCP measurements on all dates of the experiment. The ADCP and Oceanscience Riverboat were attached to a beam and support rope extending from the bow of a jet boat to prevent interference from ferrous materials, movement of the boat, and jet wash from the outboard motor. Velocity conditions were quantified with the ADCP on 14 transects. The transects were spaced at 100-m intervals starting from the 100-m sampling point but also included one transect located 50 m downstream from the side-channel inlet. Cross-sectional velocities at each transect were quantified as the ADCP was maneuvered perpendicular to flow between riverbanks. Mean water column velocity was estimated for each sampling point by a cumulative process. For the 100-m sampling point, cross-sectional velocities measured at 50-m and 100-m ADCP transects were averaged. For the 500-m sampling point, cross-sectional velocities measured at the 50-, 100-, 200-, 300-, 400-, and 500-m ADCP transects were averaged. Mean water column velocity for the 900-m sampling point was estimated by averaging cross-sectional velocities at the 50-, 100-, 200-, 300-, 400-, 500-, 600-, 700-, 800-, and 900-m ADCP transects. For the 1,300-m sampling point, velocities measured at all ADCP transects were used to estimate mean water column velocity. Diagnostic tests were performed on the ADCP on both dates, and all tests passed. A moving bed test conducted with the ADCP on June 24 showed no significant effects. The test was not repeated on July 1 because flow conditions were similar to those on June 24 (see Results).

Velocity information obtained by means of the drifting floats and ADCP was used to quantify mean water column velocity in the side channel for all dates of the experiment. While the drifting floats provided an estimate of maximum water velocity in the side channel, it was necessary to obtain estimates of mean water column velocity for all experiment dates to better describe the average velocity conditions influencing downstream drift and transport of sturgeon larvae. For the two dates (June 24 and July 1) when surface (e.g., maximum) velocity was estimated with drifting floats and mean channel velocity was quantified concurrently with the ADCP, a correction factor was developed to estimate mean water column velocity from surface water velocity (Gordon et al. 1992). Thus, estimates of

mean water column velocity for each experimental date were obtained by multiplying surface velocity estimates by the correction factor.

*Statistical analysis and modeling.*—Chi-square analysis by larval age and species was used to test the hypothesis that the larval sturgeon were equally distributed between bottom and surface samples. Regression analysis was used to examine relations between the proportion of larvae sampled in bottom samples (dependent variable) and larval length and age (independent variables). For each age of larval shovelnose sturgeon and pallid sturgeon released, regression analysis was used to examine relations between the range of time (min; time of final capture minus time of initial capture) at which larvae were sampled at each sampling point (dependent variable) and sampling point distance (m) from release site (independent variable). For each age and species of larvae, the difference between larval drift velocity and mean water column velocity was calculated for each sampling point to estimate the drift velocity deviation from mean water column velocity. Drift velocity deviations were not calculated for the 100-m sampling point because water velocities were measured only at the 50- and 100-m transects. To examine differences in larval drift velocity among ages, a one-way analysis of variance (ANOVA) was used to compare drift velocity deviations among ages for both sturgeon species. The one-way ANOVA was structured with four age treatments for shovelnose sturgeon (1, 2, 6, and 10 dph) and six age treatments for pallid sturgeon (1, 2, 5, 9, 11, and 17 dph), and each age treatment had three replicates represented by drift velocity deviations from the 500-, 900-, and 1,300-m sampling points. Regression analysis was used to test for linear relations between drift velocity deviations (dependent variable) and larval age, larval length, and proportion of larvae sampled in bottom nets (independent variables).

Cumulative river distance drifted (km) by larval shovelnose sturgeon and pallid sturgeon during the drift phase of their life cycle was modeled on the basis of deviations in drift velocity from mean water column velocity. The drift rate deviations were averaged across sampling points to calculate average deviations from mean water column velocity for each age and species. Because drift dynamics were not examined in all ages of shovelnose sturgeon and pallid sturgeon, drift rate deviations were estimated for the missing ages by the following process. Drift rate deviations for missing ages adjacent to known ages were assigned the drift rate deviation for the known adjacent age. After this process was completed, drift velocity deviations for any remaining missing ages were estimated by averaging drift velocity deviations for adjacent ages. Based on age-

specific drift rate deviations, larval drift distance (km) was calculated for each age through a range of mean water column velocities. The calculation of daily drift distance for each age of larvae was based on a 24-h diel drift behavior, in that larvae drifted continuously during the day and night. Whereas other sturgeon species are known to drift almost exclusively at night (i.e., lake sturgeon; Smith and King 2005), available information suggests that larval shovelnose sturgeon and pallid sturgeon drift during the day and night. For shovelnose sturgeon, Kynard et al. (2002) suggested that drift of larval shovelnose sturgeon was primarily diurnal through 4 dph, then transitioned primarily to nocturnal at 5 dph and 6 dph. In the Missouri River and Yellowstone River, larval shovelnose sturgeon have been sampled during the day (Braaten and Fuller 2007) and night (P. J. Braaten and D. B. Fuller, unpublished data), suggesting a trend of continuous drift. For pallid sturgeon, Kynard et al. (2002) noted that day and night drift of larvae did not differ significantly through 8 dph. Results from Kynard et al. (2007) were variable, as some ages (1–10 dph) of larval pallid sturgeon exhibited a greater tendency for diurnal drift behavior in a fast-velocity treatment, whereas 3–5-dph larvae and 12–14-dph larvae exhibited similar drift patterns during the day and night in slow-velocity treatments. Daily larval drift distances for each age were summed to provide an estimate of cumulative distance drifted by the average larvae in the population. In addition to estimating cumulative distance drifted by the average larvae in the population, the cumulative distance drifted by the slowest 25, 10, and 1% of the drifting population was estimated to better define drift dynamics of the population. The estimation process followed the same process as described above for the average drifter in the population, except that drift velocity deviations for the slowest 25, 10, and 1% of the drifting larval population were used.

## Results

### *Hydraulic Conditions*

Discharge in the main-stem Missouri River varied from 173 to 228 m<sup>3</sup>/s among experimental dates, and these differences in discharge had an influence on the amount of water flowing into the side channel and on side-channel velocity conditions. Maximum velocity to each of the sampling points as estimated from drifting floats varied from 0.53 to 0.59 m/s at a main-stem discharge of 173 m<sup>3</sup>/s (July 1) to 0.64–0.69 m/s at a main-stem discharge of 228 m<sup>3</sup>/s (July 8; Table 1). Hydraulic measurements obtained with the ADCP on June 24 resulted in mean water column velocity estimates of 0.47 m/s ( $N = 772$ ,  $SD = 0.13$ ), 0.46 m/s ( $N = 1,301$ ,  $SD = 0.13$ ), and 0.44 m/s ( $N = 1,838$ ,  $SD = 0.12$ ) to the 500-, 900-, and 1,300-m sampling points,

respectively (Table 1). On July 1, ADCP estimates of mean water column velocity to the 500-, 900-, and 1,300-m sampling points were 0.48 m/s ( $N = 557$ ,  $SD = 0.16$ ), 0.46 m/s ( $N = 1,044$ ,  $SD = 0.14$ ), and 0.44 m/s ( $N = 1,637$ ,  $SD = 0.14$ ), respectively. Estimates of mean water column velocity from ADCP measurements averaged 81% (minimum = 76%, maximum = 85%) of surface velocities estimated from drifting floats (Table 1). Thus, a correction factor of 0.81 was applied to estimates of maximum velocity to estimate mean water column velocity for all sampling points and experimental dates. Gordon et al. (1992) similarly noted that mean water column velocity is about 80% of surface water velocity. Across experimental dates, only slight differences in mean water column velocities occurred in the side channel, as mean velocity varied from 0.43 m/s to 0.56 m/s (Table 1). Although depth in the side channel varied slightly among dates, the minimum thalweg depth (e.g., maximum depth) where sampling was conducted was 1.2, 1.8, 1.3, and 1.8 m for the 100-, 500-, 900-, and 1,300-m sampling points, respectively. Side-channel water temperature on experiment dates varied from 19.9°C to 21.4°C for shovelnose sturgeon and from 17.8°C to 24.5°C for pallid sturgeon.

### *Recaptures, Size, and Vertical Drift Characteristics of Larval Sturgeon*

Larval sturgeon were recaptured at all sampling points on all dates of the experiment (Table 2). Across all sampling points, recapture rates for shovelnose sturgeon varied from 3.0% for 6-dph larvae to 7.2% for 2-dph larvae. For pallid sturgeon, recapture rates were lowest for 17-dph larvae (2.6%) and highest for 2-dph larvae (5.2%). Mean length of formalin-preserved shovelnose sturgeon was 11.4 mm (1 dph), 11.9 mm (2 dph), 15.6 mm (6 dph), and 18.1 mm (10 dph) for larvae exposed to 17.7–182.5 CTU in the hatcheries (Table 2). Mean length of formalin-preserved pallid sturgeon larvae recaptured was 10.1 mm (1 dph), 10.3 mm (2 dph), 13.3 mm (5 dph), 17.2 mm (9 dph), 18.1 mm (11 dph), and 20.3 mm (17 dph; Table 2). Under hatchery rearing, thermal exposure for pallid sturgeon varied from 20.1 CTU (1-dph larvae) to 288.8 CTU (17-dph larvae). Owing to slightly higher thermal exposure, larval shovelnose sturgeon were slightly larger than similar-age ( $\pm 1$  dph) pallid sturgeon through 6 dph; however, lengths at 10–11 dph were similar between species.

Drifting larval sturgeon were not equally distributed between surface and bottom samples. For shovelnose sturgeon, significantly greater numbers of larvae ( $P < 0.0001$  for all ages) were sampled in bottom nets for 1-dph larvae (79%), 2-dph larvae (64%), 6-dph larvae (72%), and 10-dph larvae (58%). Larval pallid sturgeon exhibited a strong tendency to drift near the bottom, as

TABLE 1.—Estimates of maximum water velocity of drifting floats, mean water column velocity as determined from measurements obtained with an acoustic Doppler current profiler (ADCP) on June 24 and July 1 and mean water column velocity for all dates when larval shovelnose sturgeon (ages 1, 2, 6, and 10 d posthatch [dph]), and larval pallid sturgeon (ages 1, 2, 5, 9, 11, and 17 dph) were released into the side channel. The sampling point represents the distance downstream from the channel inlet at which species were released (NA = not applicable).

Date of drift study (2004)	Species released	Age at release (dph)	Sampling point (m)	Maximum velocity of floats (m/s)	ADCP mean velocity (m/s)	Side-channel mean velocity (m/s)
Jun 24	NA	NA	500	0.62	0.47	0.50
			900	0.58	0.46	0.47
			1,300	0.55	0.44	0.45
Jun 25	Shovelnose sturgeon	1, 2	500	0.61		0.49
			900	0.57		0.46
			1,300	0.55		0.45
Jun 29	Shovelnose sturgeon	6	500	0.61		0.49
			900	0.58		0.47
			1,300	0.55		0.45
Jul 1	Shovelnose sturgeon	10	500	0.59	0.48	0.48
			900	0.54	0.46	0.44
			1,300	0.53	0.44	0.43
Jul 2	Pallid sturgeon	11	500	0.60		0.49
			900	0.56		0.45
			1,300	0.54		0.44
Jul 8	Pallid sturgeon	1, 17	500	0.69		0.56
			900	0.64		0.52
			1,300	0.64		0.52
Jul 20	Pallid sturgeon	2	500	0.64		0.52
			900	0.60		0.49
			1,300	0.58		0.47
Jul 23	Pallid sturgeon	5	500	0.60		0.49
			900	0.61		0.49
			1,300	0.58		0.47
Jul 27	Pallid sturgeon	9	500	0.63		0.51
			900	0.56		0.45
			1,300	0.54		0.44

significantly more larvae ( $P < 0.0001$  for all ages) were sampled in bottom nets for 1-dph larvae (66%), 2-dph larvae (63%), 5-dph larvae (83%), 9-dph larvae (64%), 11-dph larvae (75%), and 17-dph larvae (89%). The proportion of larval shovelnose sturgeon sampled in bottom nets was not significantly related to larval length ( $r^2 = 0.07$ ,  $P = 0.322$ ,  $N = 16$ ) or dph ( $r^2 = 0.08$ ,  $P = 0.28$ ,  $N = 16$ ). For pallid sturgeon, the proportion of larvae sampled in bottom nets was not significantly

related to larval length ( $r^2 = 0.13$ ,  $P = 0.083$ ,  $N = 24$ ). There was a significant positive relation between the proportion of larval pallid sturgeon sampled in bottom nets and dph, but the model had low explanatory power ( $r^2 = 0.17$ ,  $P = 0.045$ ,  $N = 24$ ).

#### Larval Sturgeon Drift Patterns

The downstream drift and recapture patterns of larval shovelnose sturgeon varied among ages and sampling

TABLE 2.—Age (days posthatch [dph]), mean length (standard deviation and sample size in parentheses) of formalin-preserved larvae, prerelease water temperature exposure (cumulative thermal units [CTU]), and release and recapture data pooled among sampling points for the larval shovelnose sturgeon and pallid sturgeon used in drift experiments during 2004.

Species	Age (dph)	Mean length (mm)	Prerelease thermal exposure (CTU)	Estimated number released	Recaptures	
					Number	Percentage
Shovelnose sturgeon	1	11.4 (0.54; 87)	17.7	10,000	409	4.1
	2	11.9 (0.42; 100)	35.6	20,000	1,431	7.2
	6	15.6 (0.84; 100)	108.8	20,000	596	3.0
	10	18.1 (0.73; 100)	182.5	22,500	869	3.9
Pallid sturgeon	1	10.1 (0.32; 50)	20.1	20,000	677	3.4
	2	10.3 (0.38; 50)	35.6	25,000	1,308	5.2
	5	13.3 (0.25; 100)	90.3	25,000	1,005	4.0
	9	17.2 (0.58; 50)	152.6	25,000	1,114	4.5
	11	18.1 (0.49; 150)	185.5	30,000	1,252	4.2
	17	20.3 (0.45; 50)	288.8	17,000	447	2.6

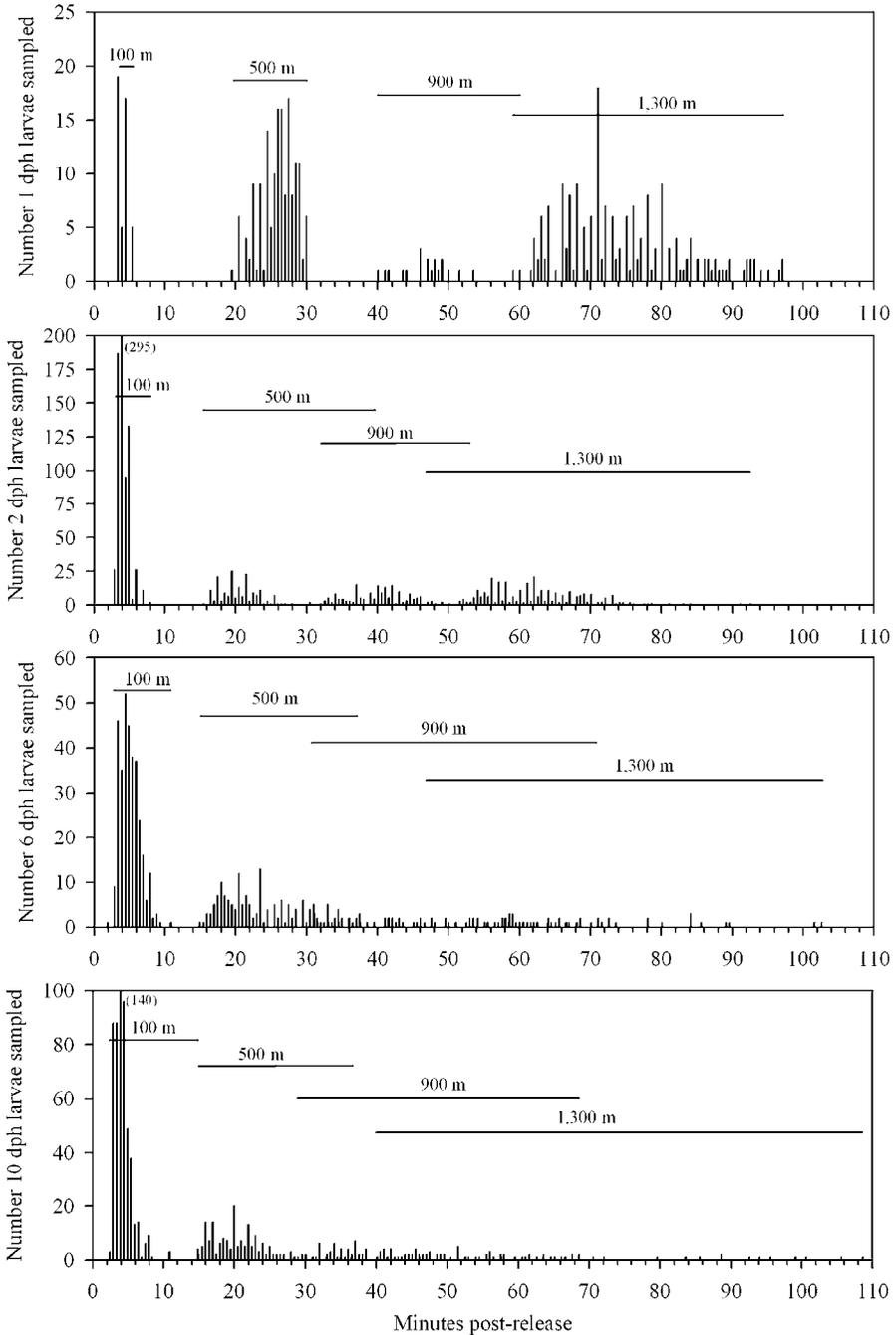


FIGURE 2.—Numbers of 1-, 2-, 6-, and 10-d posthatch (dph) larval shovelnose sturgeon sampled at the 100-, 500-, 900-, and 1,300-m sampling points, by time after release. The horizontal lines indicate the time ranges during which larval shovelnose sturgeon were sampled at the different sampling points. Note the values in parentheses where the y-axes have been truncated.

points (Figure 2). Frequency distributions of recaptures through time for 1- and 2-dph larvae indicated that larvae drifted downstream as a cohesive group among sampling points and exhibited discrete patterns of

arrival, central tendency of abundance, and passage through the sampling points. In addition, the range of time (time of last capture minus time of first capture) over which 1- and 2-dph larvae were sampled at each

TABLE 3.—Estimated relationships between the range of time during which larval shovelnose and pallid sturgeon were sampled in the drift and downstream sampling point distance, by age (days posthatch [dph]). The regressions are linear regressions of time (min) on sampling point distance (m); the sample size for each regression is 4.

Species	Age (dph)	$r^2$	$P$	Regression model	
				Slope	Intercept
Shovelnose sturgeon	1	0.96	0.018	0.029	-2.938
	2	0.84	0.081	0.029	3.275
	6	0.99	0.001	0.040	4.138
	10	0.94	0.029	0.046	2.913
Pallid sturgeon	1	0.39	0.376	0.010	10.75
	2	0.98	0.012	0.011	8.05
	5	0.78	0.115	0.011	8.30
	9	0.98	0.012	0.020	10.0
	11	0.92	0.041	0.032	6.488
	17	0.98	0.008	0.040	9.788

point minimally overlapped with adjacent sampling points. At 6 dph and 10 dph, cohesive groups of drifting larvae were evident only at the 100- and 500-m sampling points. Beyond the 500-m sampling point, cohesiveness of the drifting population decreased, fewer larvae were sampled, and the range of time at which larvae were sampled at each point increased and overlapped with adjacent sampling points. The absence of a clearly defined drift pattern for 6- and 10-dph larval shovelnose sturgeon at the 900- and 1,300-m sampling points, in conjunction with the low numbers of larvae recaptured at these sampling points, suggested that larval shovelnose sturgeon initiated the transition from the drifting life stage to the benthic life stage at or just slightly after 6 dph. For each age, the range of time at which larval shovelnose sturgeon were sampled at each point tended to increase as the distance from the release point increased (Table 3; Figure 2).

Pallid sturgeon at 1, 2, and 5 dph drifted among sampling points as cohesive groups characterized by well-defined periods of arrival, maximum abundance, and passage past the sampling points (Figure 3). Minimal overlap in the range of time at which larvae were sampled among adjacent sampling points occurred for 1-, 2-, and 5-dph pallid sturgeon larvae with the exception of 1-dph larvae at the 500-m sampling point. In this case, a single larva was sampled at 37.5 min postrelease. Before collection of this one larva, no larvae had been sampled at the 500-m sampling point since 23.5 min postrelease. This observation strongly suggests that the single larva sampled at 37.5 min postrelease was an outlier relative to the population of drifting larvae at the 500-m sampling point. At 9 and 11 dph, frequency distributions of recaptures through

time were discrete at the 100-m sampling point, but recapture distributions over time overlapped among the 500-, 900-, and 1,300-m sampling points (Figure 4). Despite the overlapping frequency distributions, well-defined drift periodicities were evident at these sampling points. At 17 dph, frequency distributions of pallid sturgeon recaptures through time overlapped among all sampling points, and cohesiveness of the drifting population was evident only at the 100-m sampling point (Figure 4). Similar to observations for 6-dph larval shovelnose sturgeon, these results indicated that pallid sturgeon larvae transitioned from the drifting life stage to the benthic life stage at 11 dph or between 11 dph and 17 dph. Additional sampling evidence confirms this conclusion. Drift studies with 17-dph larval pallid sturgeon were conducted on the same date (July 8) as drift studies with 1-dph larvae, but the experiment with 17-dph larvae was conducted 3–4 h before that conducted with 1-dph larvae. While sampling for 1-dph larvae, 17-dph larvae were collected at all sampling locations. Thus, although some 17-dph pallid sturgeon larvae drifted downstream to all sampling points during the drift experiment, individuals also settled to the riverbed immediately after release. Similar to that observed for shovelnose sturgeon, the range of time over which larval pallid sturgeon were sampled in the drift at each sampling point tended to increase as the distance from the release site increased (Table 3; Figures 3, 4).

#### *Larval Sturgeon Drift Rates Relative to Side-Channel Water Velocity*

The drift rate of larval shovelnose sturgeon relative to mean water column velocity differed significantly among ages ( $F = 11.26$ ;  $df = 3, 8$ ;  $P = 0.003$ ). Although all ages of larvae drifted slower than mean water velocity, the drift rate deviation was greater for 1-dph larvae (mean,  $-0.16$  m/s) and 6-dph larvae (mean,  $-0.13$  m/s) than for 10-dph larvae (mean,  $-0.09$  m/s) and 2-dph larvae (mean,  $-0.09$  m/s). Larval drift rates did not follow a pattern, as indicated by the lack of significant relationships between mean drift rate deviation and age of larval shovelnose sturgeon ( $r^2 = 0.18$ ,  $P = 0.16$ ,  $N = 12$ ), length of larval shovelnose sturgeon ( $r^2 = 0.14$ ,  $P = 0.23$ ,  $N = 12$ ), and proportion of larvae sampled in bottom nets ( $r^2 = 0.24$ ,  $P = 0.11$ ,  $N = 12$ ).

For pallid sturgeon, the drift rate deviation from mean water column velocity differed significantly among ages ( $F = 13.08$ ;  $df = 5, 12$ ;  $P = 0.0002$ ), as 17-dph larvae drifted more slowly than other age-groups and exhibited the greatest drift rate deviation (mean,  $-0.20$  m/s) from mean water velocity. Drift rate deviations from mean water velocity were less for 5-

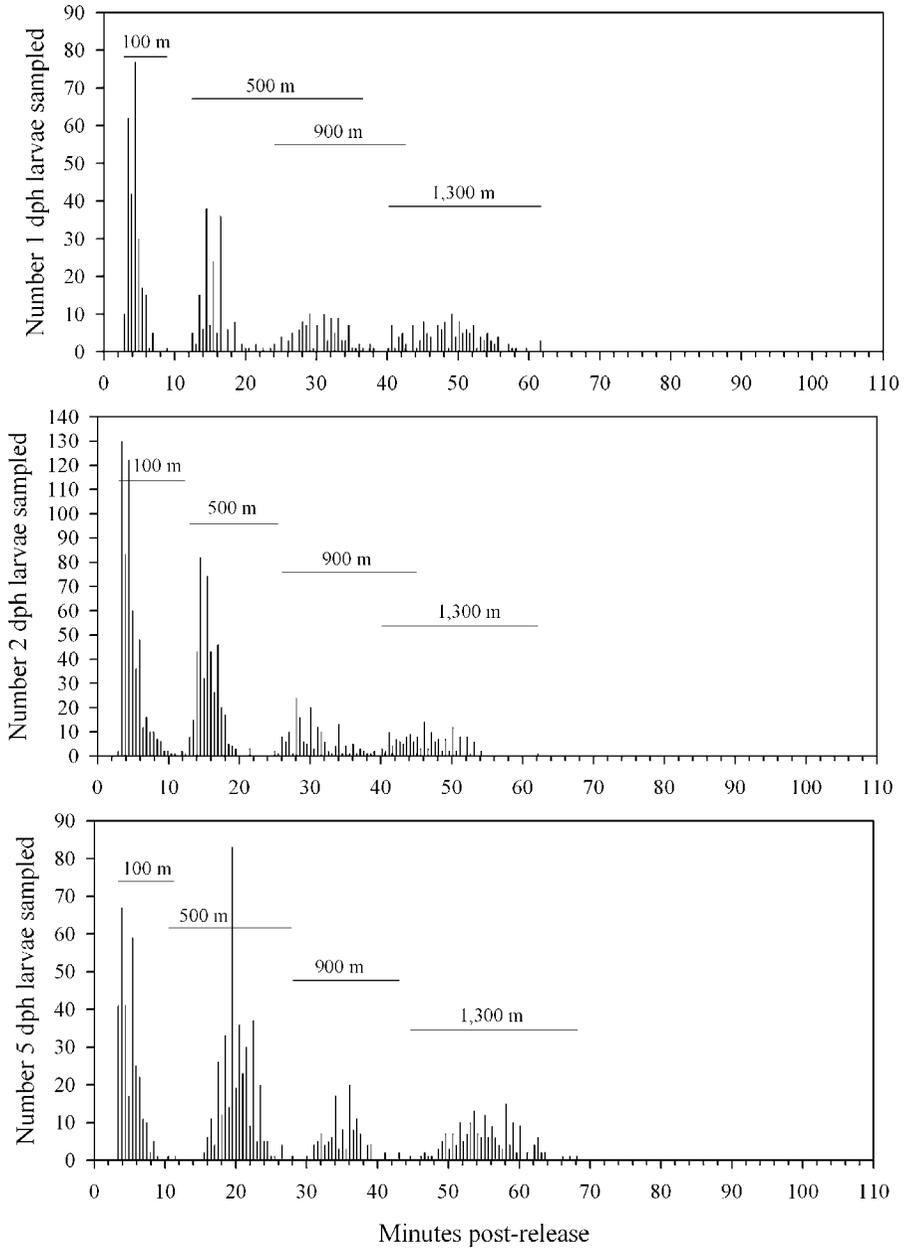


FIGURE 3.—Numbers of 1-, 2-, and 5-d posthatch (dph) larval pallid sturgeon sampled at the 100-, 500-, 900-, and 1,300-m sampling points, by time after release. The horizontal lines indicate the time ranges during which larval pallid sturgeon were sampled at the different sampling points.

dph larvae (mean,  $-0.07$  m/s), 11-dph larvae (mean,  $-0.06$  m/s), 1-dph larvae (mean,  $-0.04$  m/s), 9-dph larvae (mean,  $-0.03$  m/s), and 2-dph larvae (mean,  $-0.01$  m/s). For the six ages of larval pallid sturgeon studied, mean drift rate deviation was significantly and inversely related to age ( $r^2 = 0.57$ ,  $P = 0.0003$ ,  $N = 18$ ), length of larval pallid sturgeon ( $r^2 = 0.43$ ,  $P = 0.0029$ ,

$N = 18$ ), and the proportion of larvae sampled in bottom nets ( $r^2 = 0.26$ ,  $P = 0.031$ ,  $N = 18$ ).

*Cumulative Larval Sturgeon Drift Distance*

Modeling of larval shovelnose sturgeon total drift distance as a function of water velocity included only 1–6-dph larvae because the transition from the drifting

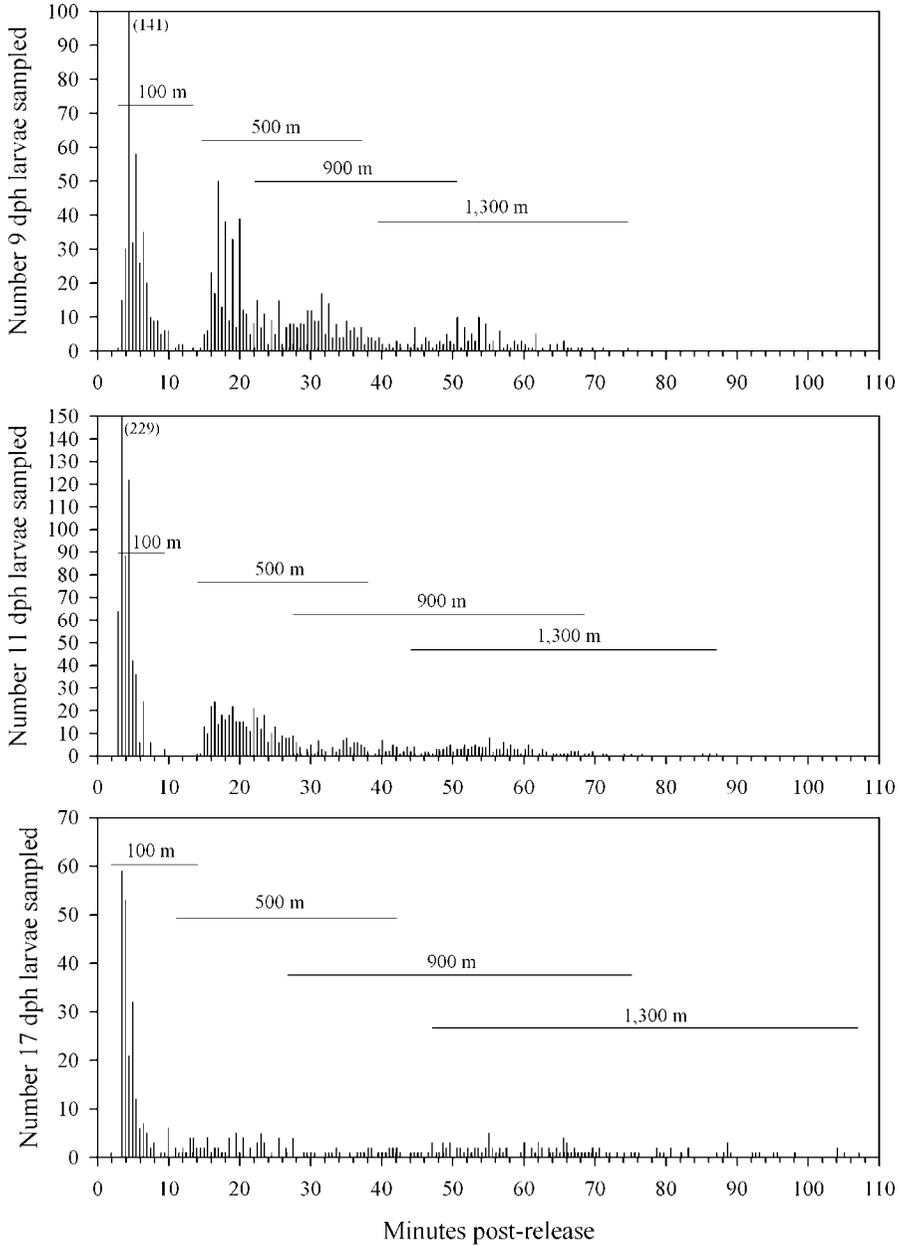


FIGURE 4.—Numbers of 9-, 11-, and 17-d posthatch (dph) larval pallid sturgeon sampled at the 100-, 500-, 900-, and 1,300-m sampling points, by time after release. The horizontal lines indicate the time ranges during which larval pallid sturgeon were sampled at the different sampling points. Note the values in parentheses where the y-axes have been truncated.

life stage to the benthic (postdrift) life stage was initiated at 6 dph. Estimations of total drift distance for shovelnose sturgeon were based on empirical data for 1-, 2-, and 6-dph larvae and on estimated data for 3-, 4-, and 5-dph larvae. Based on drift rate deviations, the estimated cumulative 6-d drift distance for a larval shovelnose sturgeon representing an average individual

in the population increased from 94 km at a mean water column velocity of 0.30 m/s to 250 km at a mean water column velocity of 0.60 m/s (Figure 5). Restricting the drift distributions to include slower-drifting larvae in the population, the cumulative drift distance of larval shovelnose sturgeon was reduced to 74–229 km for the slowest 25% of the population, 59–215 km for the

slowest 10% of the population, and 39–195 km for the slowest 1% of the drifting population through the range of modeled velocities (Figure 5).

Total drift distance as a function of water velocity for pallid sturgeon encompassed ages 1–11 dph because pallid sturgeon larvae initiated the transition from the drifting life stage to the benthic life stage at or just slightly after 11 dph. Total drift distance was estimated based on empirical drift rate deviations for 1-, 2-, 5-, 9-, and 11-dph larvae and estimated drift rate deviations for 3-, 4-, 6-, 7-, 8-, and 10-dph larvae. The estimated cumulative 11-d drift distance for an average drifting individual in the population varied from 245 km at mean water column velocity of 0.30 m/s to 530 km at mean water column velocity of 0.60 m/s (Figure 5). Models for slower-drifting pallid sturgeon predicted a cumulative drift distance of 216–501 km for the slowest 25% of the population, 183–468 km for the slowest 10% of the population, and 134–418 km for the slowest 1% of the drifting population between 0.30 m/s and 0.60 m/s (Figure 5).

### Discussion

The larval shovelnose sturgeon and pallid sturgeon used in this study were produced from wild stocks and reared under hatchery conditions for only a limited duration ( $\leq 17$  d). Because drift and dispersal behaviors are innate (Kynard et al. 2007), it is unlikely that artificial rearing had an influence on the drift behaviors observed in these species. In addition, the side channel provided many of the natural habitat elements encountered by larval sturgeon during the drift phase of their life cycle. The side channel lacked gravel and cobble substrates that would typically be available to newly hatched larvae and drifting larvae in main-stem river environments. However, it is probable that this limitation had minimal influence on the observed behaviors and larval drift dynamics of shovelnose sturgeon and pallid sturgeon. For example, laboratory studies indicate that both species initiate pelagic drift immediately after hatch and do not seek cover in rocky substrate (Kynard et al. 2002). These findings are also supported by field studies, as recently hatched drifting larvae have been sampled in the water column despite the presence of gravel and cobble substrates at the collection locations and at upstream hatch locations (Braaten and Fuller 2007). Based on these considerations, drift behaviors exhibited by larval shovelnose sturgeon and pallid sturgeon during the side-channel experiments are probably indicative of those expressed by naturally spawned larvae.

#### Vertical Drift Location

All ages of larval shovelnose sturgeon and pallid sturgeon exhibited a strong tendency to drift in the

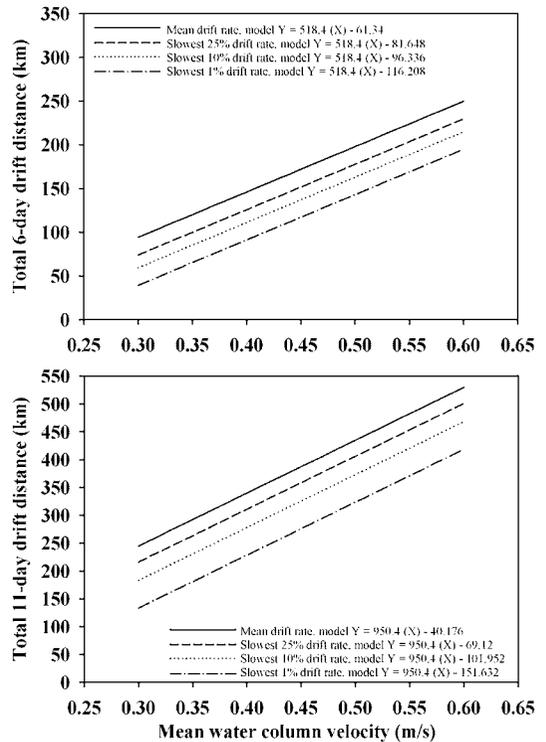


FIGURE 5.—Total estimated drift distances of larval shovelnose sturgeon (top panel) and pallid sturgeon (bottom panel) at various drift rates over a range of mean water column velocities.

lower 0.5 m of the water column. The propensity to drift primarily near the bottom was relatively consistent among the suite of ages examined in this study, as supported by the lack of significant relations between the proportion of larvae collected in bottom samples and larval age and length. The exception to this pattern occurred in pallid sturgeon, where there was weak evidence to suggest that the proportion of larvae sampled near the bottom increased with age. The tendency to drift near the bottom is a behavioral characteristic expressed in lake sturgeon (D'Amours et al. 2001), green sturgeon (Kynard et al. 2005), and other sturgeon species and may become more pronounced as the distance from hatch location increases (D'Amours et al. 2001). For shovelnose sturgeon and pallid sturgeon, observations under laboratory conditions suggest that larvae exhibit differences in vertical drift locations among ages. For example, in low-velocity (2-cm/s) vertical swim tubes (150 cm deep), Kynard et al. (2002) found that larval shovelnose sturgeon at 1–4 dph were distributed primarily in the lower one-third of the water column, 5–6-dph larvae were distributed primarily in the middle one-third of

the water column, and older larvae (7–10 dph) were distributed primarily in the upper one-third of the water column near the water surface. Under similar laboratory conditions, Kynard et al. (2002) observed that 2–5-dph pallid sturgeon were primarily distributed in the lower one-third of the water column, whereas older fish (6–8 dph) were distributed in the upper one-third of the water column near the surface. Expanding on earlier studies, Kynard et al. (2007) subjected pallid sturgeon to increased depth availability (swim tube depth, 300 cm) and low velocities (2 cm/s) and observed that 0–5-dph larvae were distributed in the lower one-third of the water column near the bottom, 6–9-dph larvae were distributed in the middle portions of the water column, and 10–14-dph larvae were distributed in the lower one-third of the water column. Differences in the vertical distribution of larval sturgeon between this field study and laboratory studies may be related to differences in hydraulic conditions and the subsequent influence of hydraulic conditions on drift behavior. Under low-velocity conditions such as those in the laboratory swim tubes, larval sturgeon can move vertically to a preferred depth without the constraint of velocity effects on behavior. However, in the side channel used in this study and in natural rivers, velocities are greater and may exert an overriding influence on vertical distribution of the majority of larval sturgeon. The strong tendency to drift near the bottom as observed in this side channel is similar to natural patterns of larval sturgeon drift observed in the upper Missouri River basin. For example, sampling for larval sturgeon with paired bottom and midwater column nets in the main-stem Missouri River and lower Yellowstone River has shown that the majority (64–86%) of larval sturgeon (*Scaphirhynchus* spp.) were collected in nets fished on the bottom (Braaten and Fuller 2002, 2003, 2004, 2005). These similarities indicate that the vertical drift behaviors observed in the side channel are representative of natural drift behaviors expressed by larval sturgeon in large rivers such as the upper Missouri River and Yellowstone River.

#### *Drift Periodicity, Duration, and Rate*

The range of time (min) during which larval sturgeon were sampled in the drift tended to increase from the upstream to the downstream sampling points for both sturgeon species and all ages of larvae, and it is probable that a combination of primarily passive and to a lesser extent active mechanisms contributed to this pattern. For example, larval sturgeon immediately after release were transported as a relatively cohesive group to the 100-m sampling point as evidenced by the short range of time during which larvae were sampled at this point. As larvae were transported to successive

downstream sampling points, cohesiveness of the drifting larval population decreased owing to increased exposure to different hydraulic conditions. Entrainment of a portion of the drifting larval population to channel or nearshore eddies and areas of reduced velocity would reduce the drift rate of entrained individuals, while the majority of the larval population continued to drift in the main current. In laboratory studies, Kynard et al. (2007) found that larval pallid sturgeon entrained into low-velocity eddies ( $\leq 0.10$  m/s) were redistributed to the main-channel flow field and could not consistently maintain position in eddies until about 11 dph. Thus, entrainment of larvae into eddies and reentry into the main-channel flow field probably contributed to the protracted range of time during which larvae were sampled at each successive sampling point. Auer and Baker (2002) also reported that the catch distributions of larval lake sturgeon broadened through time as larvae drifted from upstream to downstream sampling stations. As inferred from the side-channel results, the frequency distributions of drifting sturgeon would be expected to expand markedly as larvae continued to drift downstream owing to increased encounters with eddies and varying hydraulic conditions.

The duration of the drifting life stage was about two times longer in pallid sturgeon than in shovelnose sturgeon, as the transition from drifting to benthic behavior was initiated earlier in shovelnose sturgeon (6 dph: mean length, 15.6 mm; 109 CTU) than in pallid sturgeon (11–17 dph: mean length, 18.1–20.3 mm; >186 CTU). The transition from the drifting to benthic life stage is probably related to the initiation of exogenous feeding. For example, exogenous feeding by shovelnose sturgeon in the Missouri River is initiated by 16-mm-length fish (Braaten et al. 2007). The length of the smallest pallid sturgeon sampled from benthic habitats has been 21–23 mm (Braaten and Fuller 2003; Schrey and Heist 2004; Braaten and Fuller 2005), similar to lengths of 17-dph larval pallid sturgeon that exhibited settling behavior after release. Results from laboratory studies closely corroborate our results as the transition from drifting to benthic behavior, and initiation of exogenous feeding occurred at 4–5 dph (72–108 CTU) for shovelnose sturgeon (Kynard et al. 2002) and 11–12 dph (198–205 CTU) for pallid sturgeon (Kynard et al. 2007).

Larval shovelnose sturgeon and pallid sturgeon exhibited drift rate patterns that were markedly different, as all ages of shovelnose sturgeon drifted much more slowly than mean water velocity and all ages of pallid sturgeon exclusive of 17-dph larvae drifted at rates similar to or only slightly less than mean water column velocity. The slow drift rate of 17-dph

larval pallid sturgeon relative to water velocity was attributed to their larger size, greater age, and affinity for the bottom as suggested by significant inverse relations between drift rate deviations and these variables. Although shovelnose sturgeon were slightly larger than pallid sturgeon at most ages, it is unlikely that size differences alone can account for differences in drift dynamics between the species. For example, smaller and younger (e.g., 1–2 dph) shovelnose sturgeon tended to drift slower relative to mean water velocity than did larger and older pallid sturgeon (e.g., 5–11 dph). Under low-velocity ( $\leq 0.12$  m/s) laboratory conditions, Kynard et al. (2002) observed that larval pallid sturgeon and most ages of larval shovelnose sturgeon drifted slower than mean water column velocity. At higher-velocity laboratory conditions (0.17–0.30 m/s), Kynard et al. (2007) found that 1–13-dph larval pallid sturgeon drifted much slower than mean water column velocity, as drift rates were only 20–33% of mean velocity. These slow drift rates contrast with population mean drift rates observed in the present study where larval pallid sturgeon drifted at rates that were only slightly slower than or very similar to mean water column velocities. Drift rate discrepancies between the two studies may be related to differences in hydraulic conditions experienced by larvae in both studies. Entrainment of larvae into eddies would be expected to reduce the drift rate of larvae relative to mean water column velocities in both the side-channel and experimental laboratory settings. Consequently, drift rates would decrease as the areal extent of eddies and encounter rates with eddies increased. Although the areal extent of eddies was not quantified in the side channel, small eddies were common along the riverbanks throughout the 1,300-m length of the side channel. Based on a continuous series of eddies within 0.5 m of both streambanks, an estimated 4% of the total surface area (based on a 24-m mean width) of the side channel would be representative of near-bank eddy habitat. Conversely, based on schematics of the areal extent of eddy habitat presented in Kynard et al. (2007), eddies in the laboratory streams composed a larger proportion of the experimental stream area. Thus, larvae in the laboratory study were subjected to a greater likelihood of eddy entrainment than in this field study, and this difference provides a possible explanation as to why larvae in the laboratory studies drifted at much slower rates relative to mean water column velocity. Similar to this study, other field studies suggest that drift velocities of beluga *H. huso*, Russian sturgeon *A. gueldenstaedti*, and stellate sturgeon *A. stellatus* are about 80–90% of the river water velocity (Khodorevskaya 2002, cited by Gisbert and Ruban 2003).

#### *Cumulative Drift Distance*

The simulations of total drift distance based on the results from the side channel included behavioral and hydraulic assumptions that need to be considered in the context of natural drift patterns in the main-stem Missouri River. First, drift rates relative to mean water column velocity were not examined for all ages of larvae; thus, the estimation process for missing ages may have introduced a source of error into the simulations. Second, although the side channel exhibited heterogeneous hydraulic conditions (e.g., depth, velocity, eddies, and erosional and depositional zones), the side channel was reduced in scale relative to the main-stem Missouri River. The reduced scale of the side channel would probably have minimal effects on velocity-driven larval transport mechanisms (e.g., 0.50-m/s velocity in the side channel would transport larvae similarly to 0.50-m/s velocity in the main stem); however, the main-stem Missouri River has larger eddies that may entrain passively drifting larvae for a greater duration and reduce total downstream drift distance. Third, larval sturgeon drift rates at each site were based on larval samples collected in the thalweg, where velocity is greater than in other cross-sectional areas of the channel. Thus, larval drift rates at each site may reflect exposure to highest velocity conditions. Additional sampling along the channel margins or in lower-velocity areas at each sampling site was not conducted to ascertain the possibility that larvae entrained into these areas exhibited slower drift rates or settled to the bottom. However, it is unlikely that the availability of lower velocities at each sampling site would significantly influence drift behavior or observed drift patterns because Kynard et al. (2007) demonstrated that larval sturgeon entrained into low-velocity eddies did not consistently maintain position in eddies until 11 dph; individuals that drifted into eddies were quickly redistributed to the main-channel flow field, where sampling in the present study was conducted. Last, the relatively short length of the side channel in comparison to the total length of river drifted by larval sturgeon during ontogenetic development could introduce a source of error into estimating cumulative drift distance. This error would be most directed toward the slowest drifting proportion of the population. For example, although the range of time during which larvae were sampled in the drift increased as the population drifted downstream in the side channel, the range of time would be expected to increase substantially given an additional 100–400 km of river because the tail of the population distribution representing the slowest drifters would broaden. Although cumulative drift distance for the average

drifter in the population probably would not change appreciably with increased length of river, it is likely that the cumulative drift distance for slower drifters would be less than estimated based on results from the side channel.

In light of these considerations, simulations of total drift distance as a function of water velocity suggest that larval sturgeon are dispersed long distances downstream from their spawning and hatch locations. As predicted by the cumulative drift models, the average larval shovelnose sturgeon would drift 95–250 km and pallid sturgeon would drift 245–530 km at mean water column velocities between 0.30 and 0.60 m/s. Initial laboratory studies conducted at low velocities ( $\leq 0.12$  m/s) reported that shovelnose sturgeon and pallid sturgeon dispersed about 13 km during the larval drift phase. This short drift distance was probably an artifact of the low velocities used in the study. At higher-velocity (0.17–0.30 m/s) laboratory treatments, Kynard et al. (2007) demonstrated that drift speed increased with velocity and predicted that larval pallid sturgeon may drift in excess of 300 km during ontogenetic development. This estimate is greater than predicted by our model at 0.30 m/s (245 km) but less than predicted for higher-velocity conditions in the side channel. As in the present study, evidence for long-distance downstream transport of larvae is available for other sturgeon species. For example, embryos of Siberian sturgeon that initiate drift immediately after hatching are suspected to drift 300–440 km downstream (Gisbert and Ruban 2003). Larval white sturgeon disperse in excess of 150 km during the drift period (McCabe and Tracy 1994). Conversely, short drift distances ( $< 60$  km) are characteristic of lake sturgeon (Auer and Baker 2002; Smith and King 2005; Benson et al. 2006) that do not initiate drift until at least 5 dph (Auer and Baker 2002).

The predictions of the drift distance models suggest that the cumulative distance drifted by shovelnose sturgeon and pallid sturgeon for a specific velocity is not fixed but varies according to the different drift rates exhibited by individuals in the population. As a result, the transition from drifting to settling in benthic habitats will occur over a broad reach of river as depicted by McCabe and Tracy (1994) for white sturgeon in the lower Columbia River. Settlement of larvae along an extended length of river may reduce competition for food and space by distributing resource use across a broad spatial scale (McCabe and Tracy 1994; Gisbert and Ruban 2003). Settling in a habitat patch with abundant food resources is probably a major factor of survival during the transition from endogenous to exogenous feeding because lack of food during this life stage affects growth and survival of young

sturgeons (Gisbert and Williot 1997; Gisbert and Doroshov 2003).

Field collections of larvae and age-0 individuals in the Missouri River support the predictions of the drift distance models and establish linkages among ontogenetic development, drift distance, and sturgeon survival and recruitment. Newly hatched (0–1 dph) shovelnose sturgeon larvae (length, 7–9 mm) are collected annually in the Missouri River near rkm 2,750 (Braaten and Fuller 2007). The exact upstream spawning and hatch locations are not known. The 6-d drift model for shovelnose sturgeon predicts that larvae will drift about 250 km at a mean water column velocity of 0.60 m/s. An average velocity of 0.60 m/s is a reasonable estimate for the Missouri River below Fort Peck Dam based on low flows (Galat et al. 2001) that have occurred in recent years. Thus, assuming the larvae sampled at rkm 2,750 are 1 dph, the drift model predicts that the average larvae would drift an additional 5 d (210 km) and transition from drifting to benthic habitat near rkm 2,540. This prediction closely corresponds to the reach of the Missouri River where small (16–60 mm) age-0 shovelnose sturgeon are sampled with a bottom trawl between mid-July and early September (Braaten and Fuller 2007; Braaten et al. 2007). Age-0 shovelnose sturgeon are also sampled in the reach between rkm 2,499 and rkm 2,563, and these individuals probably represent the faster and slower portions of the drifting population.

As with shovelnose sturgeon, recaptures of several pallid sturgeon larvae, age-0 individuals, and yearlings originating from the pallid sturgeon drift experiments provide several lines of evidence supporting the drift model predictions and permit inferences on the interactions among ontogenetic development, drift behavior, and survival. First, as part of ongoing studies in 2004, benthic trawling in the Missouri River was conducted at weekly intervals between mid-July and early September 2004. The trawling area spanned from rkm 2,499 (near the headwaters of Lake Sakakawea) to rkm 2,563. On July 29, four 19-mm larval pallid sturgeon were sampled at rkm 2,499. These individuals were genetically confirmed to be progeny of one male (PIT code 1F47606357) and one female (PIT code 454910202B) spawned in the hatchery for the larval drift studies (DeHaan and Ardren 2007). Larvae from this mating were released at 2 dph (July 20), 5 dph (July 23), and 9 dph (July 27). No additional larvae or age-0 pallid sturgeon representing the experimental release of these age-classes were recaptured during subsequent weekly sampling intervals through early September. This information strongly suggests that the 19-mm larval pallid sturgeon sampled with the benthic trawl were drifting when recaptured and had not

transitioned from the drifting to benthic life stage. It was not possible to discriminate which age-class of released larvae represented recaptures because the 2-, 5-, and 9-dph larvae shared a common gene pool. However, we suspect that the 19-mm pallid sturgeon probably represented larvae released at 9 dph 2 d before the capture date based on the following rationale. Excluding about 19 km of oxbow lakes and cutoff reaches of the river that were not connected to the main-stem Missouri River during 2004, the larvae had drifted about 113 km after release. The portion of the drift model specific to drift distance between 9 and 11 dph suggests that larval pallid sturgeon would drift about 95 km at a mean channel velocity of 0.6 m/s. This estimate closely approximates the actual drift distance and capture location, providing support that the 19-mm individuals originated from releases of 9-dph larvae. Owing to the lack of recaptures to date of any juveniles representative of the 1-, 2-, 5-, and 9-dph larvae released, we suspect that the larvae drifted into the headwaters of Lake Sakakawea and exhibited little to no survival.

Second, in contrast to the lack of any indication of survival of fish stocked as 2-, 5-, and 9-dph larvae, recaptures of several age-0 and yearling pallid sturgeon representative of older larvae released during the drift experiments provide conclusive evidence that the survival of larval pallid sturgeon is related to ontogenetic development and drift distance, as predicted by the drift model. In September 2004, a 127-mm pallid sturgeon was sampled in the Missouri River downstream from the side-channel drift site. This individual was genetically confirmed as progeny from the female (PIT code 114476216A) spawned in the hatchery to produce 11- and 17-dph larvae (Jordan 2006). Yearling pallid sturgeon sampled in the Missouri River during July 2005 (210 mm, rkm 2,534; 190 mm, rkm 2,537), August 2005 (212 mm, rkm 2,507), and September 2005 (213 mm, rkm 2,623; 230 mm, rkm 2,603) were genetically determined to be survivors from the female used to produce 11- and 17-dph larvae (Jordan 2006; DeHaan and Ardren 2007). These two age-classes of larvae shared the same genetic pool; therefore, we cannot determine specifically which age-class contributed to the survivors. However, it is probable that some of the survivors originated from releases of 17-dph larvae, as the results clearly indicated that these individuals settled in the side channel following release. Some survival also may have occurred from larvae released at 11 dph, as the transition from drifting to settling may have been initiated as the larvae drifted downstream for an additional 1–2 d.

The similarities between the drift model predictions

and the observed drift patterns and survival–recruitment dynamics for larval shovelnose sturgeon and pallid sturgeon suggest that drift model inferences are applicable to the main-stem Missouri River. However, additional field studies in the main-stem river focusing on larval drift rates, channel velocities, and the influence of eddy entrainment on cumulative drift distance are necessary to more thoroughly test this hypothesis. Nonetheless, results from this study and corroborating field observations strongly suggest that although the larval life stage of both sturgeon species includes an extended drift period and drift distance, the drift distance exhibited by pallid sturgeon is much greater than that exhibited by shovelnose sturgeon. Differences in drift distance, when coupled with alterations that have occurred in the Missouri River through dam and reservoir construction (Galat et al. 2005), provide a possible explanation for differences in larval survival and recruitment that occur between shovelnose sturgeon and pallid sturgeon in the upper Missouri River basin. For example, about 340 km of riverine habitat exists between Fort Peck Dam and the headwaters of the next downstream main-stem reservoir (Lake Sakakawea). This reach of the Missouri River provides suitable spawning habitat for shovelnose sturgeon and a sufficient length of river for larval drift, settlement to benthic habitat, and survival. Recruitment in shovelnose sturgeon occurs annually, as evidenced by collections of age-0 individuals (Braaten and Fuller 2007; Braaten et al. 2007) and several year-classes of adults (Quist et al. 2002). Conversely, recruitment of pallid sturgeon in the upper Missouri River basin has not occurred for several decades because the wild population exclusively consists of large and presumably old fish (Jordan 2006). Although pallid sturgeon are suspected to spawn near rkm 14 of the lower Yellowstone River (Bramblett and White 2001), less than 50 km of free-flowing river is available for drifting larvae below the spawning areas before the larvae enter the headwaters of Lake Sakakawea. If larval pallid sturgeon cannot survive in reservoir headwater environments (Kynard et al. 2007), an insufficient length of free-flowing river downstream from spawning and hatch locations serves as a possible mechanism for the lack of larval survival and recruitment exhibited by this species in the contemporary upper Missouri River system.

#### *Management Applications*

Information on drift behavior and cumulative distance drifted by sturgeons during the larval life stage has applications to sturgeon management and recovery efforts. First, programs designed to sample for larval shovelnose sturgeon and pallid sturgeon should

include protocols in which sampling effort is focused in the lower 0.5 m of the water column because the majority of larvae drift near the riverbed. This practice will not only increase the number of sturgeon sampled from which important biological information can be derived (e.g., size of drifting individuals) but also increase statistical precision that is dependent on the number of larvae sampled (Cyr et al. 1992). Sample precision is an important management consideration for detecting population responses to management activities and natural environmental variation.

Second, although the results are specific to the side-channel hydraulic conditions, the inferences from this study provide a framework for understanding sturgeon biology and ecology in other regions. Spawning areas used by shovelnose sturgeon and pallid sturgeon in many reaches of the Missouri River are not specifically known. However, if larval sturgeon are sampled in the drift during research or monitoring surveys, spawn and hatch locations can at least be estimated and researchers can be directed to possible spawning locations for more refined studies. For example, lengths of field-caught larvae preserved in formalin can be compared to lengths, ages, and CTU exposure of larval sturgeon reported in this study to estimate age (Braaten and Fuller 2007). With this information, drift distance from the upstream hatch location to the point of capture can be estimated if the investigator has some information on mean water column velocities for the upstream reach.

Finally, applications extend directly to restoration and recovery efforts for pallid sturgeon in the upper Missouri River basin. Currently, much of the 340-km reach of the Missouri River downstream from Fort Peck Dam is considered unsuitable for pallid sturgeon spawning owing to altered discharge regimes and suppressed water temperatures resulting from hypolimnetic operations of Fort Peck Dam (USFWS 2000). Habitat enhancements for this reach are proposed whereby operations of Fort Peck Dam will be modified as a mechanism to increase flows and enhance water temperature suitability for spawning pallid sturgeon (USFWS 2000). If enhanced discharge and water temperature conditions facilitate spawning by pallid sturgeon similar to that observed after habitat enhancements for other sturgeons (Auer 1996; Paragamian and Kruse 2001), larval pallid sturgeon would be provided an extended length (>340 km) of free-flowing Missouri River to complete ontogenetic development, provided that suitable spawning habitat was available. As with the Missouri River, habitat enhancements are proposed for the Yellowstone River that may increase survival of larvae and facilitate recruitment in this critically imperiled species. Specifically, a diversion

dam located at rkm 113 of the Yellowstone River near Intake, Montana, is considered a barrier to upstream passage (USFWS 2000) that may preclude pallid sturgeon from gaining spawning access to upstream reaches. Replacement of the diversion dam with a structure more conducive to upstream passage (USACE 2006) is planned to provide spawning access to a greater upstream portion of the Yellowstone River. Thus, the length of river available to drifting larval pallid sturgeon below spawning and hatch locations would be greatly increased and would provide suitable drift and settling habitat for larvae before they drift into the headwaters of Lake Sakakawea.

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