Swimming Height and the Effect of Velocity on Dispersal of Free Embryo and Larval Pallid Sturgeon: An Experimental Study

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Report prepared for:

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Project completed under the following agreement with the Corps of Engineers: Project Number W59XQG12342308 to the S.O. Conte Anadromous Fish Research Center.

January 2004

Executive Summary

Understanding the dispersal dynamics of young pallid sturgeon Scaphirhynchus albus is important to evaluating the impact of damming and water regulation in the Missouri River on the species. The present project, conducted in 2003 on Missouri River pallid sturgeon, was a laboratory component of a comprehensive study on dispersal dynamics of pallid sturgeon. Our objectives in 2003 were to (1) verify the accuracy of the 12-13 day dispersal (about 243 cumulative temperature degree-units - CTU) period found for Missouri River pallid sturgeon in 1997, (2) evaluate the effect of slow, medium, and fast velocity environments on dispersal and drift rate, (2) determine fish use of eddy habitat in the three velocity treatments, (3) determine the daily preferred swimming height of fish during dispersal, (4) determine the daily cumulative temperature degree days (CTU) required for development to larva and the end of dispersal, and (5) suggest ways to apply the information to modeling fish dispersal.

We observed fish in three channel velocity regimes (mean velocity at 0.6 depth in parenthesis): slow (17.3 cm/s), medium (21.1 cm/s), and fast (30.1 cm/s). There were three tanks and 15 fish per velocity treatment (total, nine tanks with five fish each). We also observed 10 fish daily (five day: five night) for swimming height above the bottom in a 300 cm deep stream tube. We found the same pattern of dispersal during ontogenetic development observed in 1997, i.e., hatchling free embryos initiated downstream dispersal, feeding larvae continued dispersing, and dispersal ended after about 14 days (CTU =239.5). In all velocity treatments, water current determined movements of embryos, carrying them around the tank until they entered the eddy. However, their constant swim-up eventually returned them to the channel flow. Because fish were drifting into eddy habitat in all velocity treatments, their dispersal speed around the tank was always slower than channel velocity, usually about 1/3 channel velocity or less. Fish began holding position in the eddy in the slow and medium velocity tanks on day 8, but few ever held position in fast velocity tanks. Swimming height of days 0-5 embryos (CTU= 83.5) was < 50 cm. As embryos developed into larva on day 6 (CTU=100.7) and through day 9 (CTU=152.6), fish dispersed throughout the water column. Most (75-80%) day 10 and day-14 larvae in the swim tube were < 50 cm above the bottom. Comparison of swimming height of days 6-9 larvae in 150 cm and 300 cm tubes suggest swimming height is affected by water depth (pressure). Larvae swam higher and dispersed faster in the daytime. The present results show modeling of dispersal should be done separately for embryo and larval life stages and that the cumulative temperature degree-days (CTU) is the link between fish development stage (and dispersal behavior) and river water temperature. Modeling of embryo dispersal (0-83.5 CTU) should be based on near bottom velocities (< 50 cm above the bottom). Modeling of days 6-9 larval dispersal (CTU=100.7-152.6) should be based on fish distributed evenly throughout the water column to 300 cm. Modeling of days 10-14 larvae (CTU=169.8-239.5) should be based on 80% of the fish < 50 cm above the bottom. Effects of water velocity on swimming height are unknown, but if larvae show similar swimming heights at fast velocities as fish in 2 cm/s velocity in the present study, then during the 4 days larvae are distributed throughout the water column, individuals far above the bottom should move far downstream and larvae near the bottom move a much shorter distance.

Introduction

There is increasing evidence from laboratory research on many sturgeon species in North America, Asia, and Europe that the downstream dispersal of each new generation from a spawning site is done in 2-steps. For some species, well-developed larvae or juveniles initiate the first dispersal step. Examples of this dispersal style are shortnose sturgeon Acipenser brevirostrum and both sub-species of Atlantic sturgeon A. oxyrinchus (Kynard and Horgan 2002, Kynard and Parker In Press). However for seven sturgeon species yet studied, the first dispersal step is initiated by the free embryo life stage upon hatching and dispersal is continued by the second ontogenetic life stage, the larva (Kynard et al. 2002a, Kynard et al. 2002-b, Zhuang et al. 2002, Zhuang et al. 2003, Kynard et al. 2003). Pallid sturgeon Scaphirhynchus albus and shovelnose sturgeon S. platorynchus have this second style. Both species were similar in general dispersal style in laboratory tests, but differed for two behaviors, i.e., for free embryos, pallid sturgeon dispersed at a slower rate than shovelnose sturgeon, and for larvae, pallid sturgeon were diurnal while shovelnose sturgeon were nocturnal. [Interestingly, the paddlefish Polyodon spathula, which inhabits the same rivers as pallid and shovelnose sturgeons, also has the same dispersal style (Kynard and Parker unpublished data), suggesting a common adaptive strategy for the three sympatric species.]

Experimental studies have identified the three life stages of pallid sturgeon that disperse (embryo, larva, and yearling juvenile), and the general duration of dispersal. A study in 1997 using aquaria and an endless (oval) artificial stream 7 m long with water of 19-21°C found pallid sturgeon free embryos (hereafter, embryos) age days 0-4 and day 5+ larvae dispersed downstream for 12-13 days (Kynard et al. 2002a). The embryo life stage begins upon hatching and ends when fish develop into feeding larvae. After larval dispersal ceased in the artificial stream, older larvae and the next life stage (juveniles) did not initiate a second dispersal. These results suggest that wild fish likely forage and rear during the summer-fall-winter of their first year of life in the reach where the initial larval dispersal ceases. Later dispersal studies on yearling pallid sturgeon in a large endless artificial stream found this life stage initiated the second downstream dispersal. This dispersal, which may begin in the spring, occurred every week during July to December, with most daily movement at night (Kynard et al. In Review-a). Thus, it is likely the yearling life stage, not the earlier life stages that disperse each generation downstream throughout the entire range of the population. The dispersal drive is innate and can be studied in the laboratory because the behavior will be expressed in any stream environment, natural or artificial (Kynard et al. In Review-a)

Although the environmental factors that determine dispersal distance are not understood, two factors at the fish behavior–river environment interface that are important to understand dispersal are the response of migrants to water velocity and the swimming depth of migrant fish. Embryo and larval shovelnose sturgeon dispersal rate and distance traveled in an endless artificial stream was similar at fast or slow velocities suggesting fish may adjust dispersion rate to drift the same total distance regardless of velocity or river flow. If this mechanism is present in wild fish, it would enable fish to drift to the same rearing reach regardless of discharge (Kynard et al. 2002-a). However,

the test velocities were low (5–12 cm/s), much lower than in a river, so the test environment gave larvae control of their drift rate, a situation that may not exist during dispersal in rivers. Thus, the effect of water velocity on dispersal behavior and drift distance of pallid sturgeon is not understood. Also, swimming height above the bottom of migrants will greatly affect dispersal distance, i.e., if fish swim near the bottom, where velocity is slow (Gordon et al. 1992), fish should move at a slower rate than if they swim at mid-depth or at the surface where velocity is fast. Swimming height likely has great fitness value for survival of migrants and is an innate factor of migrant habitat preference (Kynard et al. 2002-a).

Factors that affect the survival of early-life stages of sturgeon are poorly understood, yet this is the period of life history when most mortality occurs and year class strength is established for each generation (Parsley et al. 2002, Gross et al. 2002, Kynard and Horgan 2002, Kynard et al. In Review-b). For each generation of sturgeon, spawning must produce fertilized eggs that attach and rear successfully at the spawning site, then hatch fish that disperse successfully to a rearing area. All aspects of dispersal behavior that affect survival of migrants are likely under strong natural selection.

Dispersal is an innate behavior that has evolved to adapt early-life stages to successfully move downstream to river reaches with appropriate rearing habitat. Many anthropogenic factors can affect the dispersal success of the three dispersing life intervals of pallid sturgeon (embryo, larva, and yearling). Any barrier or river regulation that changes the river environment (flow, temperature, or both) from the natural variation of conditions during sturgeon dispersal can potentially have a deleterious impact on dispersion success. Changes in the river from conditions in which the fish naturally evolved cause a mis-match of the naturally evolved migrant dispersal behavior and the altered environment.
The most drastic result of river alteration or regulation would result in migrants moving to an inappropriate rearing area where survival is poor. This could result from colder than natural waters, which would retard fish development and cessation of dispersion, or from higher than natural discharge, which carries migrants farther than natural flows. For any change in the river environment that affects survival of a dispersing life stage, there is certain to be strong directional selection for migrants to adapt to the altered river.

Dams and river regulation have the greatest potential impact on river fish species that move long distances during their life history. Fragmentation of the Missouri River by a series of dams and reservoirs has created many up- and downstream passage problems for fish species, like pallid sturgeon, that move great distances up- and downstream. However, the impact of river fragmentation on any dispersing life interval of pallid sturgeon is unknown.

For managers of pallid sturgeon and dam regulators, the laboratory study in 1997 by Kynard et al. (2002-a) on early life intervals of pallid sturgeon provided information on dispersal style and duration, habitat preference, and swimming depths during development, but the data had many limitations. Fish dispersion was observed in an artificial stream with slow velocity (5-12 cm/s) and fish swimming height tests were done

in a stream tube 150 cm deep. Dispersing fish in the Missouri River encounter much faster velocity and deeper water. Additionally, the 1997 study lacked data on swimming depth for days 0–1 embryos and days 9 and older larvae, so the data on daily swimming depth was incomplete. The data did show that days 2-5 embryos swam near the bottom (<60 cm above the bottom) and when fish developed into larvae on day 6, they swam far above the bottom (all days 7-8 fish swam to the surface of the 150 cm tube). The high swimming height of days 7-8 larvae suggested these fish had the behavioral drive to swim even higher than 150 cm. Thus, additional study is needed in laboratory environments that more closely resemble Missouri River conditions.

After the 1997 study found dispersal lasted for many days and that larval migrants swam 150 cm (or higher) above the bottom, the importance of understanding drift dynamics of young pallid sturgeon was clear. For young pallid sturgeon spawned downstream of Fort Peck Dam in the Missouri River, this means understanding their dispersal dynamics in the river flowing downstream to Lake Sakakawea, a maximum dispersal distance of 330 km, assuming adults spawn just downstream of Fort Peck Dam, which is unknown.

The present project is a laboratory component of a comprehensive study on the dispersal dynamics of pallid sturgeon embryos and larvae. Our objectives for 2003 were to (1) collect information missing on dispersal and swimming height in the 1997 study and verify the accuracy of the 12-13 day dispersal period, (2) evaluate the effect of slow, medium, and fast velocity environments on fish behavior, dispersal duration, and drift rate, (2) determine fish use of eddy habitat and holding behavior in the three velocity treatments, (3) determine the daily preferred swimming height of fish, (4) determine the daily cumulative temperature degree days (CTU) required for each day of development to the end of dispersal, and (5) suggest use of the information for modeling fish dispersal.

Methods

Test pallid sturgeon

We received 1,000 fertilized eggs on 27 June 2003 from Garrison Dam National Fish Hatchery, which hatched on 1 July 2003. Fish were the progeny of one female and one male (Missouri River stock). We reared eggs in a McDonald hatching jar and transferred 700 hatchling embryos (day-0 fish) to an oval endless stream channel for rearing (see Figure 1, Kynard and Horgan 2002). The stream channel was 32 cm wide, 7.3 m in circumference, with water 20 cm deep, and a small pump created a mean current velocity of 3.5 cm/s (range, 1-9 cm/s). Early larvae were fed a sturgeon starter diet (see Acknowledgements) 6-8 times daily using a timed feeder (rearing tank) or by hand (migration experiment tanks) and 6 times daily with live *Artemia* nauplii and frozen Cyclop-eeze (bioengineered micro-crustaceans, Argent Laboratories, Redmond, WA).

We transferred hatchling fish into the stream channel to enable fish to move downstream at all times. This situation also existed in each velocity test tank. Thus, when a fish died in a test tank, we replaced it with a fish that had been reared in an

environment that provided a similar dispersal opportunity. Previous experience with pallid sturgeon larval dispersal showed a strong tank effect on dispersal behavior, where the dispersal behavior of fish reared in a circular tank, where they could not move downstream, was retarded compared to fish allowed to consummate this behavioral drive (Kynard et al. 2002-a).

We used the number of days post-hatching to characterize age of fish, not the number of days after fertilization, because we did not know how early rearing conditions (particularly water temperature) varied during shipping before we received the eggs. We used dechlorinated city water (Montague, MA) for rearing and experiments. Temperature in both situations was ±1°C. We maintained the natural photoperiod for the Turners Falls, MA latitude location (42.6°N), which is similar to the latitude of Fort Peck Dam (48.05°N) on the Missouri River.

Velocity tests

Tests were conducted in nine 1.5 m diameter circular tanks constructed identically (Figure 1). There were three tanks in each of the three velocity treatments: low, medium, and high velocity. Low, medium, and high velocity characterized the velocity environment present around the outside wall of the tank. Each tank had a circular insert placed offset from the center of the tank. Width of the narrow part of the test arena was 28 cm and the widest part was 75 cm wide. This configuration created channel flow around the tank periphery and an eddy with reverse flow in the wide part of the tank. Four 10 cm diameter rocks in the eddy provided shelter for fish.

The water system was a constant circulating system that linked a head tank, which regulated water flow through the system, to the nine tanks and a chiller-heat pump, and finally to a drain tank. The chiller-heat pump within the water system maintained water temperature at 16-18°C. Water was constantly draining from the head tank to each tank and overflowing into a common drain, then was pumped back to the head tank.

Individual pumps at each of the tanks provided a slow, medium, or fast water velocity regime. In the three slow velocity tanks, a submersible pump inside the circular insert withdrew water from inside the insert and pumped it outside the insert to the test arena through an outlet in the ramp in the video viewing area (Figure 1). Large pumps for the medium and fast velocity tanks were located outside and underneath each tank and circulated water from the test tank to the pump and back into the tank to the test arena through an outlet pipe under the ramp.

Water depth in test tanks was 30 cm, except in the video viewing area where the ramp reduced depth to 13.5 cm and brought fish closer to the camera. We placed four rocks approximately 10 cm in diameter in the widest part of the channel to slow the current and provide bottom shelter for fish seeking to remain in the slower eddy habitat. Each tank was covered with a fine-mesh netting to exclude insects and aerial debris from falling into the water. The entire test system was built outside on a platform and protected from weather by a tent.

We characterized the velocity regime in 1 of the 3 tanks with each velocity treatment: slow, medium, and fast velocity. Velocity was measured with an electronic velocity meter with scans of 10 sec at two water depths (5 cm above the bottom and 0.6 depth) along 14 radial transects of the circular tank. The number of sample stations on radials ranged from 3 (narrow channel) to 5 (wide channel). We characterized the high velocity environment of each treatment and the eddy environment by determining the mean of the bottom and 0.6 depth measurements for each environment. The probe was always pointed into the direction of the main channel flow, so velocity readings in the eddy, which had reverse flow direction, were mostly negative readings.

We planned to observe small and large size fish and determine the drift rates of individuals. However, preliminary observations during optimal viewing conditions in a prototype test arena on preserved pallid sturgeon embryos showed an observer viewing the video tape of small and large embryos could not distinguish between the two fish—fish were too small and moving too fast, even in a slow velocity condition. Thus, determining individual fish drift rates was impossible unless only one fish per treatment tank was used. We rejected this protocol because of the small sample size (N=3 fish/treatment) that would result. We decided the best option was to observe groups of fish in each tank and determine the number of loops all fish made around the tanks in each treatment and compare the mean number of loops between velocity treatments. We introduced five fish into each tank on the day of hatching (day 0) and replaced fish that died with new fish from the oval rearing tank as needed.

We mounted color video cameras above the slow and medium velocity tanks to observe fish. A lamp with a 60-watt red bulb was mounted on either side of each camera to illuminate the video field of view at night and the ramp was painted white to enhance observing the small fish at night. The video system recorded the fish for 5 min per hour each 24 h. We reviewed the videotapes and counted the number of up- and downstream fish passes per 5 min. Preliminary tests revealed that, in the fast velocity tanks, fish were moving too rapidly to be counted accurately on video, so we used live observations instead. The same observer (EP) counted the number of downstream fish passes for 5 min every 3 h each 24 h. As in the tanks with video cameras, two red lights provided illumination for nighttime observations in each fast velocity tank.

We used the number of fish passes to compare fish among slow, medium, and fast velocity treatments. We also used the mean number of fish passes/day and the distance around the tank to compare fish in slow, medium, and fast velocity treatments for mean number of loops around the tank, mean cm/s traveled, and mean distance traveled (575 cm/loop in channel flow). While using the number of passes per 5 min (=loops around the tank) to determine swim speed does not use movements of individual fish, it correctly represents the speed of young pallid sturgeon dispersing in a migration tank similar to the present tanks (Kynard et al. 2002-a). We used one-way ANOVA to compare the mean number of fish passes, mean distance traveled, etc., among velocity treatments (3 replicate tanks combined).

Use of the eddy by fish was determined twice daily by visually counting the number of fish (of 5 total) in the eddy habitat (Figure 1) of one tank of low, medium, and fast velocity. We observed fish between 0000 hours and 0230 hours and again between 1630 hours and 1930 hours and counted fish present in the eddy at the moment the observer looked in the tank (i.e. a point sample). The same observer (EP) made all counts. We used this information to calculate the daily percent of fish in the eddy (number fish in eddy divided by 5 times 100). We also recorded the number of these fish that held position in the eddy.

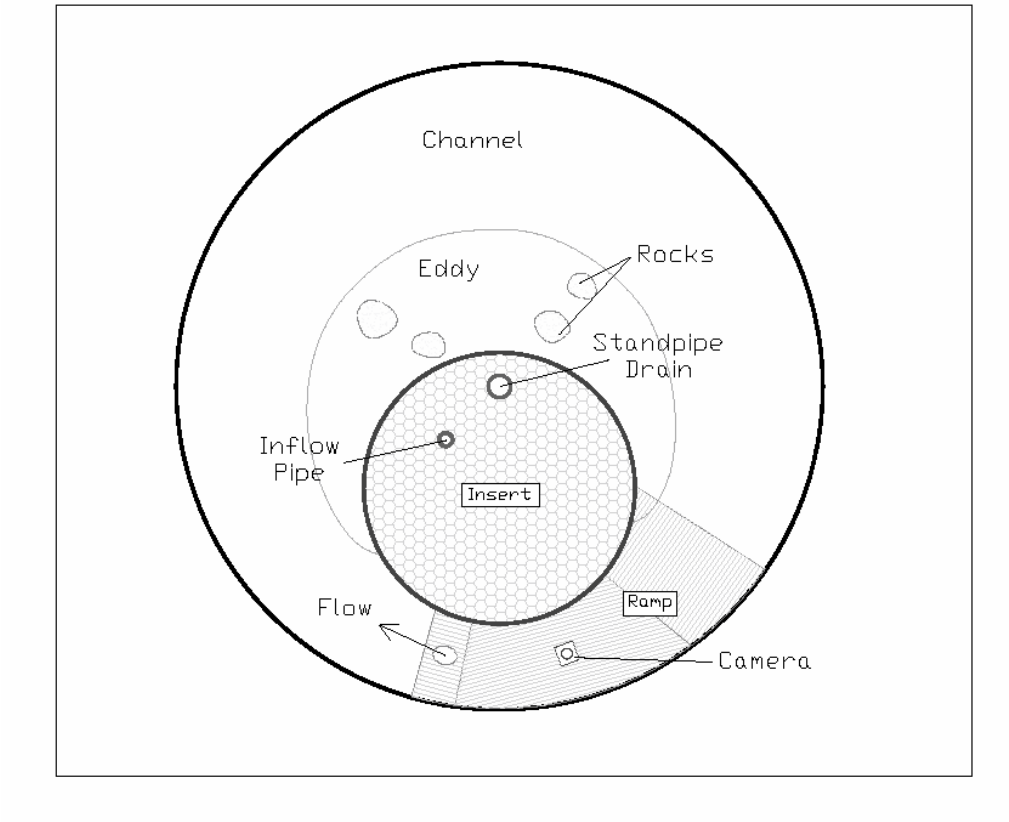

Figure 1. Plan view of one of nine circular tanks (1.5-m diameter) used to create channel and eddy flows and observe downstream dispersal and use of eddy habitat of free embryo and larval life stages of pallid sturgeon in relation water velocity. The insert was a thin 3 mm thick perforated plastic wall, which allowed water exchange between the insert area and remainder of the tank, but the small holes in the insert wall prevented fish in the test arena (channel and eddy) from entering the insert area. The general configuration of the eddy is shown by a faint line; four 10-cm diameter rocks in the eddy provided shelter for fish. Pumps at each of the nine tanks created slow, medium, and fast channel velocities (three tanks per velocity treatment) and circulated water within each tank. The drain and water inflow connected the water in each tank to a temperature controlled water circulating system among all tanks, a head tank, and water heater-chiller. Water depth was 30 cm except at the fish viewing ramp where depth was 13.5 cm to improve seeing fish. Fish were observed with a color video camera and red illumination (for seeing fish at night).

Swimming height tests

Each day, we individually tested five sturgeon in the day and five sturgeon at night for swimming height above the bottom in an artificial stream tube that simulated a vertical section of stream with horizontal water flow (Figure 2). The stream tube was a clear plastic cylinder 302 cm long x 15 cm inside diameter with water 300 cm deep. A clockwise rotating paddlewheel that extended down the center of the tube created a horizontal water flow circling the tube at a velocity of 2 cm/s. A tan cloth was placed on the opposite side of the stream tube from the viewer to provide a uniform background and contrast to see the small fish. During tests, illumination level measured inside the water-filled tube (top to bottom) was 300-50 lx to 30-5 lx depending on time of day. The tube was partially drained after each test to remove fish, replace water, and maintain water temperature within 1°C of rearing tanks. Day tests began at 1325-1635 hours and night tests began at 2150-2255 hours, except for the day tests on day 0, which began at 1830 hours. Each test of five fish usually required 2 h.

We captured sturgeon for stream tube tests after mixing rearing tank fish by stirring and using beaker brailing to remove fish. Test fish for each replicate were held in a 2-liter bucket until tested, then after testing and draining the tube, fish were returned to the rearing tank. While many of the fish were injured during removal from the tube and died immediately or died later, if a fish survived, there was a chance it could be selected later for another test.

During tests, we captured a single fish from the bucket with a beaker, and then water plus fish was poured into the top of the introduction tube, which carried fish to the bottom of the stream tube. Only upward swimming and cover seeking were noted for the first 1 min (acclimation period). Then at 11-12 min, we recorded swimming height of fish above the bottom each 10 s for 60 s (total measurements = 7). Height of fish off the bottom was determined visually using a depth scale (1-cm marks with 0 = bottom) inscribed on the outside circumference of the tube. We calculated the mean of the seven measurements for each fish and present the grand mean for five day and five night fish as a time series.

We also conducted preliminary tests to determine if the swimming height of fish at 11-12 min accurately represented fish swimming for an extended time period. Earlier tests found no significant difference in swimming height of fish between 5-6 min and 9-10 min, and no difference in swimming height between individuals or pairs of fish except on one day (Kynard et al. 2002-a). However, observations at 9-10 min or 11-12 min are short compared to the long time wild fish may swim in the water column. To begin to examine the affect of test time on swimming height, we tested five day-4 fish (late-embryo stage) and five day-6 fish (early-larvae stage) in the stream tube. We recorded the swimming height of each fish at 1 and 2 h for the day-4 fish and swimming height after 1 h for the day-6 fish.

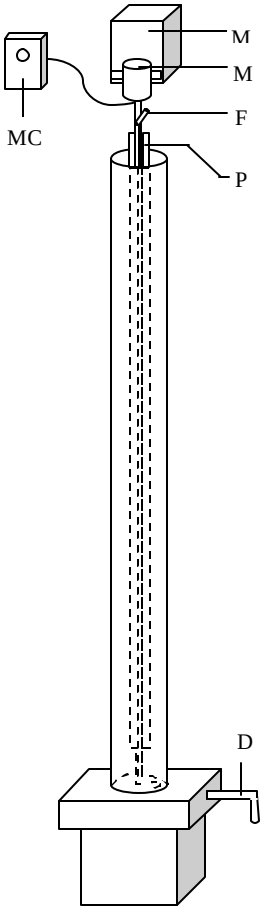

Figure 2. Side view of the clear stream tube (water depth, 300 cm; diameter 15 cm) used to determine swimming height above the bottom of pallid sturgeon free embryos and larvae. Key to components: M = motor, MM = motor mount, MC = motor control, F = fish introduction tube, P = paddlewheel, and D = drain. The rotating paddlewheel created a water current circling the tube at a velocity of 2 cm/s.

Results

Velocity vectors in test tanks

Plots of velocity vectors in the slow, medium, and fast velocity treatment tanks at 5 cm and 0.6 depth are shown in Figures 3, 4, 5. In all three treatments, velocity was highest along the outside wall of the tank (channel habitat) and on the narrow ramp. Although mean channel velocities were different among the three treatments, there was a distinct channel and eddy habitat, the area with zero or reversing (negative) velocity. These two habitats were distinctly different, yet they were separated by only a few centimeters, so a fish in the eddy that swam-up only a short distance could be entrained

into the channel flow. This was especially likely in the fast velocity treatment because the eddy was smallest there.

The velocity environments in the three velocity treatments were very different (Table 1). The mean velocities for the three treatments in the channel at 0.6 depth showed the slow treatment was close to the medium treatment, but the fast treatment was much faster than the medium treatment (mean velocity: slow = 17.3 cm/s, medium = 21.1, and fast = 30.1 cm/s. For each treatment group, mean velocity in the channel at 5 cm above the bottom was similar to the mean 0.6 depth velocity, showing velocity was similar throughout the water column in the channel habitat (Table 1). The mean velocity in the eddy at 5 cm above the bottom in the slow treatment was much slower than the mean velocity in either medium or fast velocity eddies, i.e., slow = - 2.8 cm/s, medium = -5.0 cm/s, and fast = -5.6 cm/s (Table 1). At 5 cm above the bottom, both the size and shape of the eddy varied with velocity treatment. Eddy habitat was largest in the slow treatment tank, medium sized in the medium treatment, and smallest in the fast velocity treatment. The outside edge of the eddy in the slow velocity treatment was evenly curved up- to downstream, but the eddy in the medium and fast velocities had upstream and downstream lobes (Figures 3, 4, 5).

Table 1. Mean (maximum and minimum) velocity at 5cm above the bottom and 0.6 depth for slow, medium, and fast velocity treatments.

	Eddy						Channel					
	0.6 Depth			5 cm			0.6 Depth			5 cm		
Velocity Treatment	mean	max	min	mean	max	min	mean	max	min	mean	max	min
Slow	-3.3	1.0	-8.0	-2.8	6.0	-7.0	17.3	25.0	1.0	13.8	31.0	-1.0
Medium	-4.7	-1.0	-9.0	-5.0	0.0	-10.0	21.1	53.0	1.0	20.3	56.0	1.0
Fast	-4.8	1.0	-9.0	-5.6	0.0	-10.0	30.1	82.0	-2.0	27.7	79.0	2.0

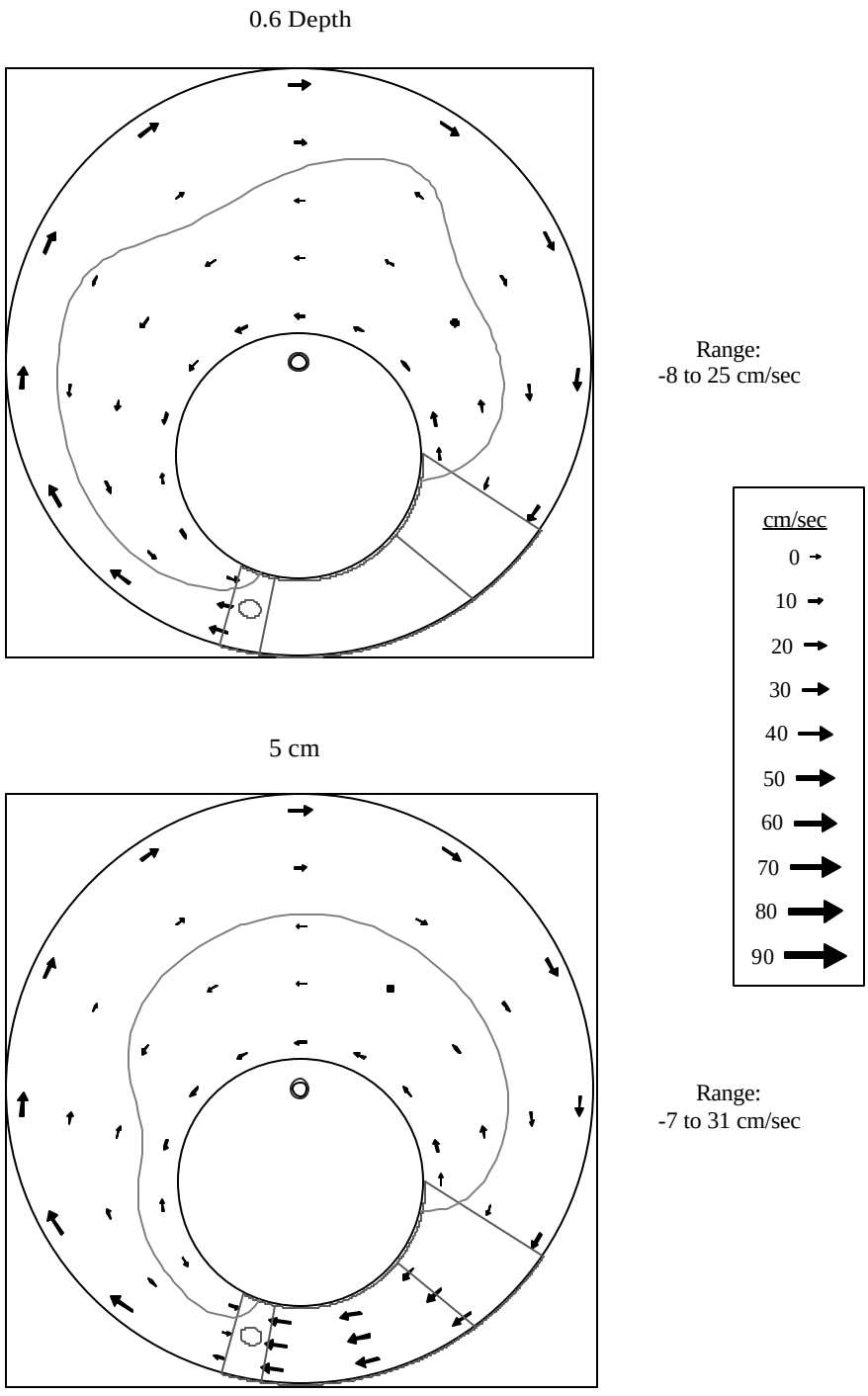

Figure 3. Velocity vectors at 0.6 depth and 5 cm above the bottom in the slow velocity tank. Configuration of the eddy (zero and reversing velocities) shown by the faint dotted line. Range of velocity for each water depth regime shown at right side along with the velocity vector scale.

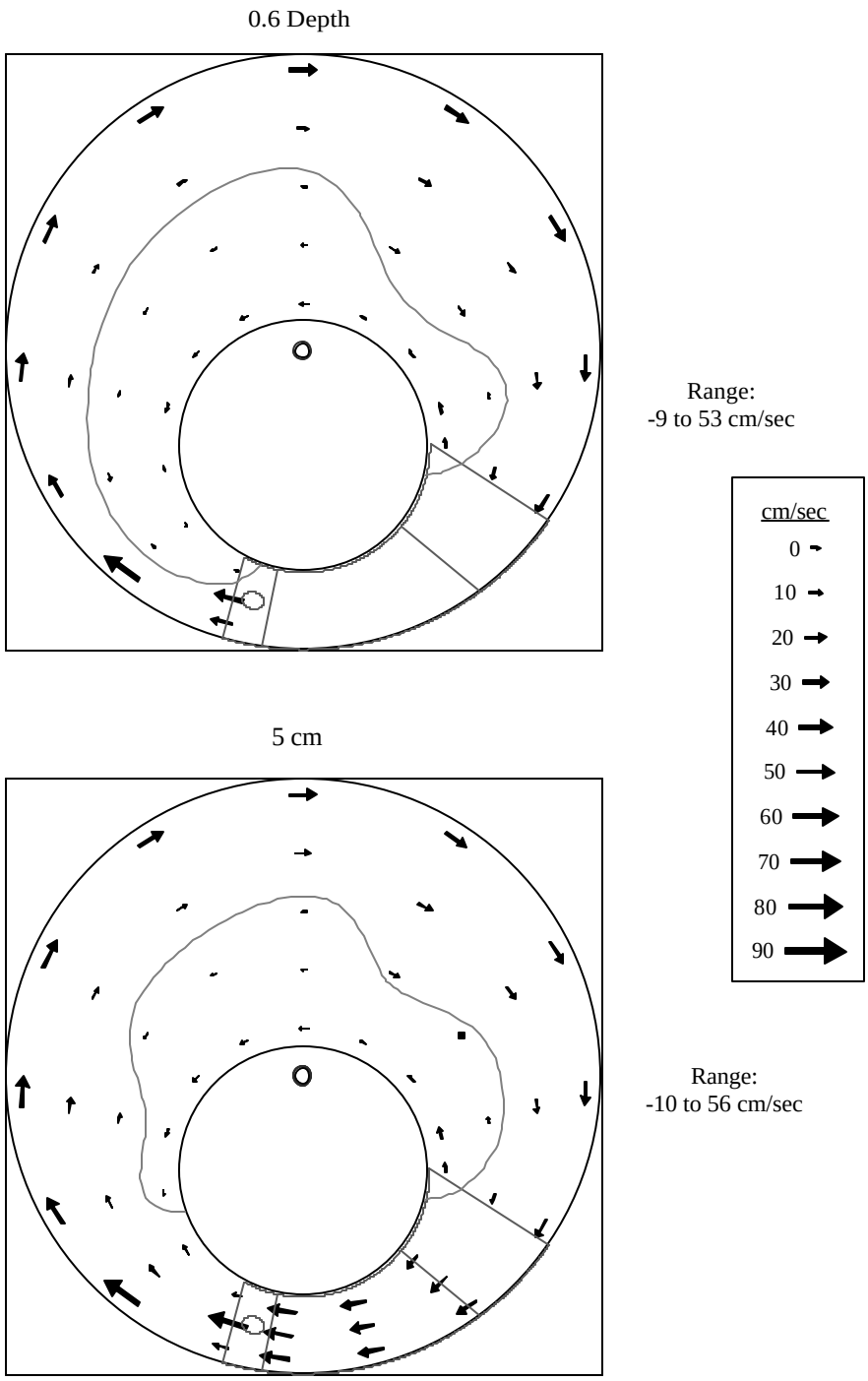

Figure 4. Velocity vectors at 0.6 depth and 5 cm above the bottom in the medium velocity tank. Configuration of the eddy (zero and reversing velocities) shown by the faint dotted line. Range of velocity for each water depth regime shown at right side along with the velocity vector scale.

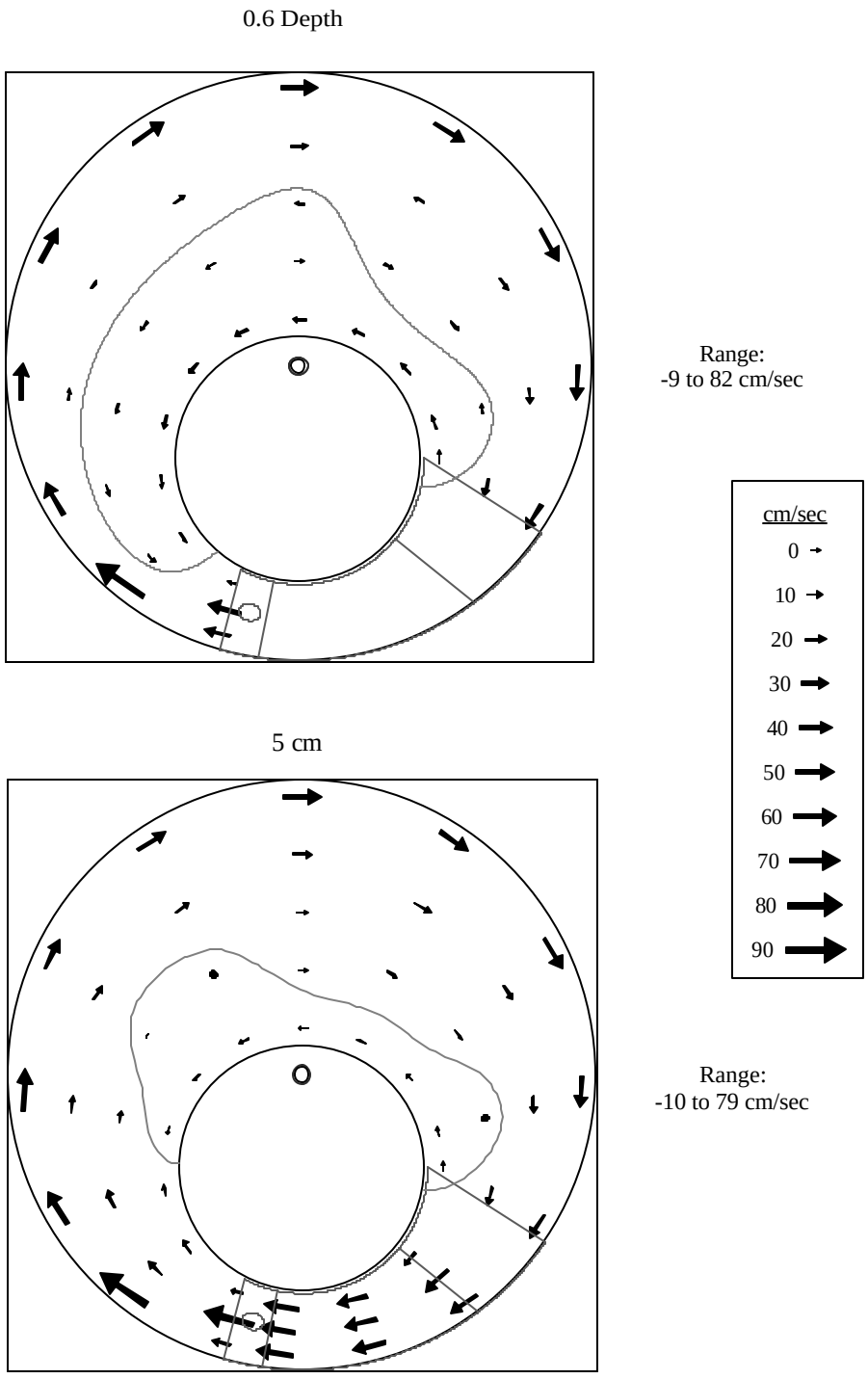

Figure 5. Velocity vectors at 0.6 depth and 5 cm above the bottom in the fast velocity tank. Configuration of the eddy (zero and reversing velocities) shown by the faint dotted line. Range of velocity for each water depth regime shown at right side along with the velocity vector scale.

CTU and fish development

Daily CTU experienced by fish in the rearing stream and in the velocity treatment tanks were very similar (Table 2). This similarity of temperature in rearing tank and velocity test tanks made it possible for us to replace fish that died in a velocity treatment with a rearing tank fish. That is, when a fish died and we replaced it with a fish from the rearing tank, the rearing tank fish was at the same stage of development as the test fish.

Few fish were attracted to introduced food on day 5 (83.5 CTU), but most fish were attracted to food on day 6 (100 CTU). Thus, day 6 was the day fish began transforming into larvae and initiated feeding. All fish should be larvae by day 7 (118 CTU), when all fish responded to food placed in the rearing tank. Based on observation of fish in the stream tube and velocity treatments, dispersal for most fish ended on day 14 (239.5 CTU).

Table 2. Cumulative temperature units for each day. Fish became larvae on day 6 after approximately 100 CTU and dispersal ceased at about 239.5 CTU.

	Cumulative Temperature Units	
Age (days)	Rearing tank	Migration tanks
0	0	0
1	16.1	17.0
2	32.5	34.0
3	49.4	51.0
4	66.5	68.0
5	83.5	85.0
6	100.7	102.0
7	117.9	119.0
8	135.4	136.0
9	152.6	153.0
10	169.8	170.0
11	187.0	187.0
12	204.5	204.0
13	221.9	221.0
14	239.5	238.0

Velocity treatments

On day 0, all fish in the high velocity tanks drifted passively with the current. We visually observed that fish in all tanks swam-up into the water column and drifted

downstream with the current. Day-0 embryos had no ability to resist the current, even in the slowest velocity treatment. The current carried fish around the tank perimeter until eventually they were entrained into the eddy, usually at the upstream edge of the eddy at the entrance to the ramp. Entrained fish remained in the eddy for a variable amount of time (seconds) before their constant swimming movements eventually returned them to channel flow.

Within a few hours, all day-0 fish in the three fast velocity tanks were impinged on the wall of the tank insert and died. Impingement occurred on the insert wall by the head of the eddy. Fish were caught by flow going into the small holes in the tank insert caused by water moving from the test arena (eddy and channel) through the insert holes into the insert and to the pump. Because day-0 fish could not survive in the fast velocity treatment, we collected no information on dispersal (number of loops) of day-0 fish in high velocity. To obtain data on embryos in the fast velocity treatment, we altered test protocol. Beginning at 1200 hours on day 1, and continuing every 3 h for 24 h/day until day 4 at 0600 hours, five fish were introduced by an observer (EP) into each of the three fast velocity tanks, then after a 2 min acclimation, fish were observed for the number of downstream passes during 5 min. After testing, we removed and returned fish to the oval rearing channel.

We collected video data on days 0-3 embryos, but during review of the tapes, we found that the fish were too small and moving too fast to count accurately, even during the day. Thus, we collected no information on loop rate of days 0-3 embryos in the slow or medium tanks. We visually observed these fish were dispersing downstream, used swim-up and drift movement, showed no ability to control movement, and were entrained into the eddy for short periods of time before they eventually returned to channel flow. We also found during review of the tapes that we could not accurately count the number of fish at night for the three medium velocity tanks and for two of the slow velocity tanks. Fish were too small and moving too fast for the red light system and light colored background for us to count fish. Because we only had accurate counts of fish passes in the slow and medium velocity treatments during the day, all data analysis only used day counts of fish.

We collected information on diel behavior of fish in the three fast velocity tanks (daily visual counts of fish passes day and night) and limited data from video in one slow tank. Fish had similar diel behavior in both of these very different water flow conditions–a higher number of fish passes in the day than at night. In the fast velocity tanks, the mean number of fish passes by days 1-10 fish in the day was 21.0 (95% CI=18.5-23.6) and at night the mean was 12.7 (95% CI=10.7-14.7). These confidence intervals did not overlap, so there was a significant difference between the number of fish passes during the day and night. In the slow velocity tank, days 3-5 embryos had about the same number of fish passes day or night (maximum of 20% fewer passes at night compared to the day). For days 6-10 larvae in the slow velocity tank, the daily number of passes at night was 18-65% less than the number of passes in the day. However, days 12-14 larvae had similar number of fish passes day and night. We interpret the fewer number of fish passes at night as related to reduced swim-up behavior at night and more

passive drifting, which would keep fish in the eddy longer and result in fewer fish passes around the tank at night.

There was general agreement for the daily number of fish passes among the three tanks in the medium and fast treatments, but one tank in the slow treatment was different from the other two tanks. Grand mean number of passes in the three slow tanks was 13.1, 15.9, and 4.8, which were significantly different (one way ANOVA, normality and equal variance passed, $F=7.356$, $P<0.005$). We do not know why fish in the one tank had fewer passes than the other two tanks. We included the data from this tank in calculating grand mean number of daily passes for the slow treatment. The daily mean number of fish passes among the three tanks in the medium or fast treatments were not different from each other (one way ANOVA, normality and equal variance passed, medium treatment – $F=2.063$, $P=0.156$; fast treatment – $F=1.862$, $P=0.184$).

The number of downstream passes observed visually for the fast treatment tanks and by video for the slow and medium treatments is shown in Figure 6. The five fish in the fast velocity tanks during days 1-13 always drifted and there was no trend to reduce the number of loops with age like fish in the medium and slow velocity treatments. We often visually observed larvae in the fast velocity tanks attempting to hold position on the bottom in the eddy, but they could not hold position for more than a few seconds. Pair-wise comparison of the three treatment groups (all tanks in each treatment lumped) for differences in the daily mean number of fish passes during days 4-10 showed fish in the slow and medium treatments were not different, but fish in the fast treatment were different from both slow and medium treatments (Student-Newman-Keuls Method, slow vs. medium ($q=0.320$, $P>0.05$), slow vs. fast ($q=9.525$, $P<0.05$), and medium vs. fast ($q=6.589$, $P<0.05$). In the fast velocity treatment, variability for the daily number of fish passes was very small on all days, except for day 1, indicating fish behaved similarly each day, and that holding behavior in the eddy was never fully expressed, i.e., velocity dominated fish behavior. The highest number of passes by embryos in the fast velocity treatment was during days 1-2, and for larvae, during days 6-8.

Days 4-13 fish in the slow and medium treatments behaved similarly with a peak in the number of fish passes during days 6-7, then a gradual decline in number of passes with age (Figure 6). Although the slow and medium velocity environments were quite different (Table 1), the reduction in number of passes by fish in each group was similar after day 7, showing a general decline in dispersion of fish in both groups by day 13, the end of dispersion. The decline in number of fish passes likely indicates fish were spending more time holding position in the eddy. By day 8 and on later days, the number of fish passes decreased, likely because fish held position in the eddy in the slow and medium velocity tanks (Figure 6).

Dispersal speed of fish in the three treatment groups was much slower than the speed of water in the channel (Figure 6). Because we used the number of fish passes per 5 min to calculate dispersal speed, the relationship among the three treatment groups was the same for dispersal speed (cm/s) as for the number of fish passes per 5 min, i.e., fish in the slow treatment were not different than fish in the medium velocity treatment, but fish

in the fast velocity treatment were different than fish in slow or medium treatments (one-way ANOVA, normality and equal variance passed, $F=22.607$, $P<0.001$), and Tukey pair-wise comparisons- slow vs. medium ($q=0.028$, $P>0.05$), fast vs. slow ($q=8.22$, $P<0.05$), and fast vs. medium ($q=8.25$, P0.05). Dispersal speed of fish was always much less than the mean velocity of the channel flow in any of the three treatments. For example, in the fast velocity treatment, fish speed was 5-10 cm/s for embryos or larvae and the mean velocity of channel flow was 30.1 cm/s. So, fish speed was about 1/3-1/5 times slower than water speed. In the slow and medium velocity treatments, speed of day-4 embryos was 1-3 cm/s, and mean velocity in the slow treatment channel was 17.3 cm/s and in the medium treatment channel was 21.1 cm/s (Table 1). Thus, day-4 embryos were moving much slower than the channel velocity. In the slow and medium velocity treatments, dispersal speed was highest for larvae on days 6-7 when they moved 5-6 cm/s, still about 1/3 to 1/4 of the channel velocity. At other times, they moved even slower than channel velocity. We included an expansion of fish dispersal speed to km/d to provide scale of the test environment with river flows (Figure 6).

The percent of fish (N=5) that occurred in the eddy each day during the observation period is shown in Table 3. High percentages of fish (60% or greater) occurred in the eddy beginning on day 2 in the slow and medium treatments, and in the slow treatment, during at least one observation period every day after day 2, 80% or more of the fish occurred in the eddy. The percentages of fish in the eddy in the medium velocity treatment were similar to the data from the slow treatment suggesting a common cause: the similar channel velocities in both treatments. The percent of fish in the eddy in the fast velocity treatment was slightly less than in the slow or medium velocity treatments, showing more fish were in the channel flow in the fast velocity treatment. There was no clear trend in any velocity treatment for an increasing number of fish to occur in the eddy. The possible exception is in the slow velocity treatment where 100% of the fish were in the eddy during at least one observation period on days 13-14, the end of dispersal (day 14, CTU=238; Table 2).

The percent of fish (N=5) that held position in the eddy each day is shown in Table 4. No fish in any velocity treatment held position until day 8, and then some fish in all velocity treatments held position. In the slow velocity treatment, all fish (100%) held position during one period on days 13-14, indicating the end of dispersal. In the medium velocity treatment, there was no trend for increasing percent of fish to hold position with age and the percent typically varied from 20-60%. The percent holding position never reached 100%, even on days 13-14, when the percent varied from 20 to 60%. In the fast velocity treatment, the highest percentages of fish holding position occurred on days 12-14 when 80% occurred once, 60% occurred three times, and 20%-40% occurred one time each. Fish could not hold position in the fast velocity treatment during days 0-10, when a maximum of 40% holding position occurred only on two observation periods.

Perhaps, the number of fish holding position as a percent of the total number of fish in the eddy gives the best example of the differences among fish in the three treatments (Table 4). In the slow velocity treatment, there was a trend with age of fish for increasing percentages of fish to hold position, i.e., 100% of the fish in the eddy held

position on day 10 (one period), day 12 (one period), day 13 (one period), and day14 (two periods). Fish in the medium velocity treatment showed slightly less ability to hold position with 100% of the fish in the eddy holding position only on day 12 (two periods) and day 14 (one period). One hundred percent of the fish in the fast velocity treatment only held position in the eddy during one period on day 11 (Table 4).

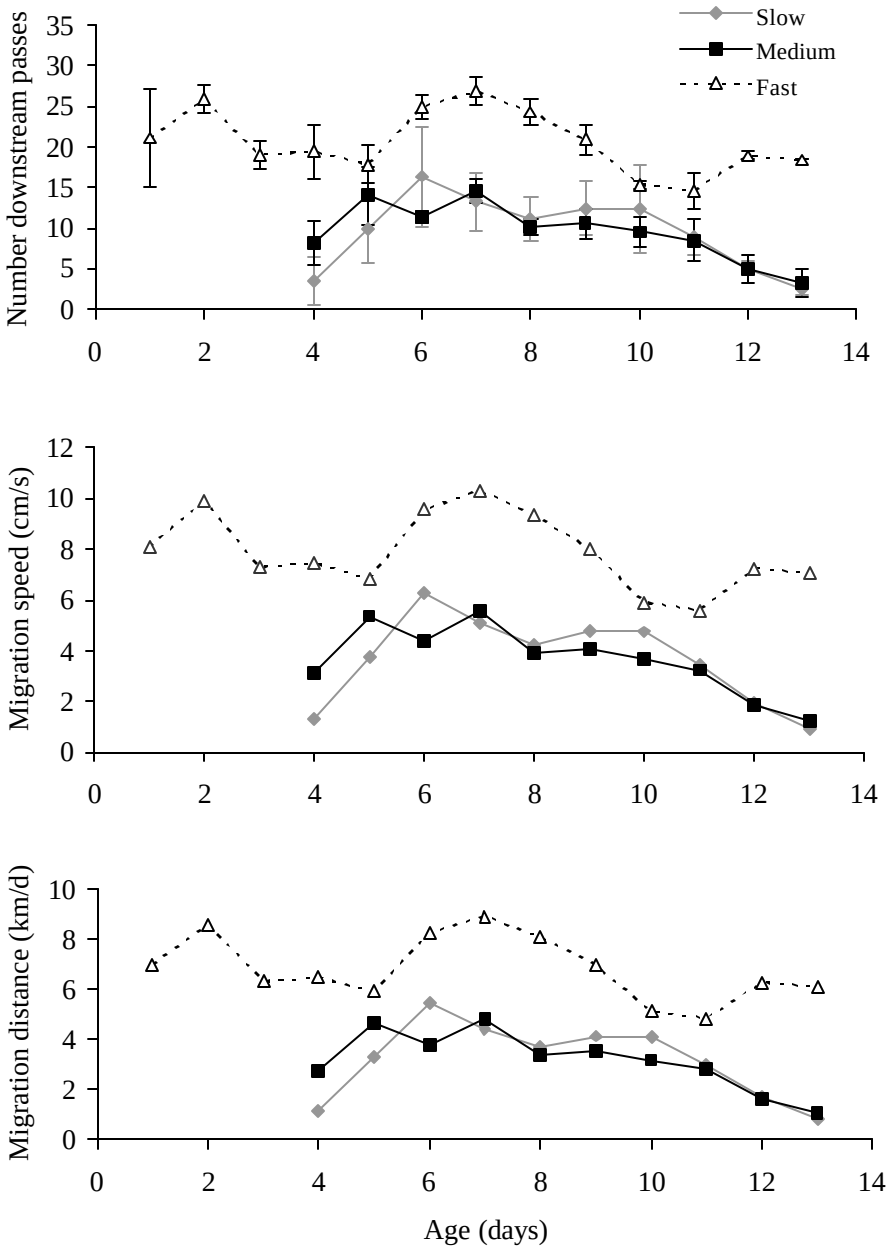

Figure 6. Number of loops in 5 min, dispersion speed, and distance estimated from the number of loops for each of the three velocity treatments. Number of loops was counted on video for slow and medium velocities and by live observation for fast velocity. Data for each velocity treatment represent the mean of three replicate tanks.

Table 3. Percentage of fish in the eddy each day. Observations were made twice a day, once during daylight hours and once in the dark .

		Velocity treatment		
Age (days)	Time	Slow	Medium	Fast
1	night	20%	40%	
1	day	40%	20%	
2	night	60%	80%	
2	day	80%	60%	
3	night	60%	80%	
3	day	80%	100%	
4	night	80%	40%	
4	day	80%	40%	60%
5	night	80%	60%	20%
5	day	60%	60%	40%
6	night	80%	80%	60%
6	day	80%	60%	60%
7	night	40%	60%	20%
7	day	80%	80%	40%
8	night	60%	80%	40%
8	day	60%	60%	60%
9	night	60%	40%	20%
9	day	80%	60%	60%
10	night	80%	80%	0%
10	day	80%	60%	60%
11	night	80%	100%	60%
11	day	60%	80%	60%
12	night	60%	80%	20%
12	day	80%	60%	60%
13	night	60%	80%	60%
13	day	100%	40%	20%
14	night	100%	60%	0%
14	day	60%	60%	60%

Table 4. Percent of fish holding position, displayed as a percent of the total number of fish in the tank and then as a percent of the total fish in the eddy. Fish only held position when they were in the eddy.

		Percent of total fish			Percent of fish in eddy		
		Velocity treatment			Velocity treatment		
Age (days)	Time	Slow	Medium	Fast	Slow	Medium	Fast
1	night	0%	0%	0%	0%	0%	
1	day	0%	0%	0%	0%	0%	
2	night	0%	0%	0%	0%	0%	
2	day	0%	0%	0%	0%	0%	
3	night	0%	0%	0%	0%	0%	
3	day	0%	0%	0%	0%	0%	
4	night	0%	0%	0%	0%	0%	
4	day	0%	0%	0%	0%	0%	0%
5	night	0%	0%	0%	0%	0%	0%
5	day	0%	0%	0%	0%	0%	0%
6	night	0%	0%	0%	0%	0%	0%
6	day	0%	0%	0%	0%	0%	0%
7	night	0%	0%	0%	0%	0%	0%
7	day	0%	0%	0%	0%	0%	0%
8	night	0%	40%	20%	0%	50%	50%
8	day	40%	20%	20%	67%	33%	33%
9	night	0%	20%	0%	0%	50%	0%
9	day	60%	40%	40%	75%	67%	67%
10	night	60%	40%	0%	75%	50%	0%
10	day	80%	20%	40%	100%	33%	67%
11	night	60%	60%	60%	75%	60%	100%
11	day	40%	40%	40%	67%	50%	67%
12	night	60%	80%	0%	100%	100%	0%
12	day	60%	60%	0%	75%	100%	0%
13	night	20%	60%	20%	33%	75%	33%
13	day	100%	20%	0%	100%	50%	0%
14	night	100%	40%	0%	100%	67%	0%
14	day	60%	60%	40%	100%	100%	67%

Swimming height

Swimming height of individual fish during days 0-14 is shown in Figure 7. Days 0-2 embryos swam within 25 cm of the bottom, day or night. Days 3-5 embryos swam within 50 cm of the bottom, except for three fish (one on day 4 and two on day 5). Variation in swimming height of days 0-5 embryos was small, except for a rare fish, all fish swam <50 cm high, most < 25 cm high.

Most fish developed into larvae on day 6 and 6 of 10 fish swam to a height of 100 cm or 300 cm (Figure 7). During days 6-9, fish were dispersed throughout the water column, top to bottom. After day 6, a greater proportion of fish each day swam far above the bottom, so that by day 8, some fish were swimming at all water depths. We selected all fish randomly, and all seemed healthy and swam actively. Thus, the fish that swam near the bottom were not different, to our level of examination, from fish that swam far above the bottom. The time of fish being dispersed throughout the water column was brief, and by day 10, 8 of 10 fish swam <50 cm above the bottom. Day-14 fish only observed in the day were like the day-10 fish, with 4 of 5 fish on the bottom, but one fish swam an average height of 228.1 cm. We tested no fish on days 11, 12, or 13 because there were no healthy swimming larvae in the rearing stream to test. The fish we tested on day 14 were healthy fish removed from a velocity treatment that we discontinued. The remainder of the fish tested in the stream tube were rearing tank fish. We observed no fish at night on day-14 because there were no healthy fish available.

A few larvae (10-33% of the test fish) swam to the surface of the 300 cm tube during the three days fish swam the highest (days 6-8; Figure 7). One fish reached 290 cm on day 4; day 6 was the first day a fish swam to 300 cm. Fish that swam to the surface swam in circles around the top of the tube, suggesting they would have moved higher, if possible.

Diel behavior of embryos and larvae was quite different. Except for the one day 4 embryo that swam high during the day, embryos swam on the bottom day or night (Figure 8). Day 6 and day 8 larvae swam higher during the day than at night, but day 7 larvae were different, swimming low in the day and high at night. We cannot explain this seemingly spurious result of the day 7 daytime fish. Older larvae were similar day or night.

Test duration and the mean swimming heights (in parenthesis) for five day-4 embryos observed for swimming height after 1 h, then after 2 h, follow: 1 h test from 1720 to 1820 hours (swimming height = 0, 5, 5, 10 and 285 cm; 2 h test from 1820 to 1920 hours (swimming height = 0, 5, 10, 18 and 290 cm). Thus after 1 or 2 h, 4 of 5 fish were on the bottom, but one was far above the bottom, like day-4 fish observed at 11–12 min (Figure 7). (The same fish likely swam high during both observation periods.) For five day-6 larvae observed after 1 h (1800–1900 hours), the swimming heights were 290, 255, 230, and 15 cm. Data was available on only four fish because one fish swam back into and up to the top of the introduction tube and was omitted from analysis. This fish would likely have swum far above the bottom. Thus, the day-6 fish observed for 1 h

showed similar variation in swimming height as day-6 fish observed for 11-12 min (Figure 7). Water temperatures during prolonged tests were similar, i.e., 18–22°C for embryo tests and 19–22°C for larval tests. Temperature was lowest at the start of tests and warmed to room temperature by the end of tests.

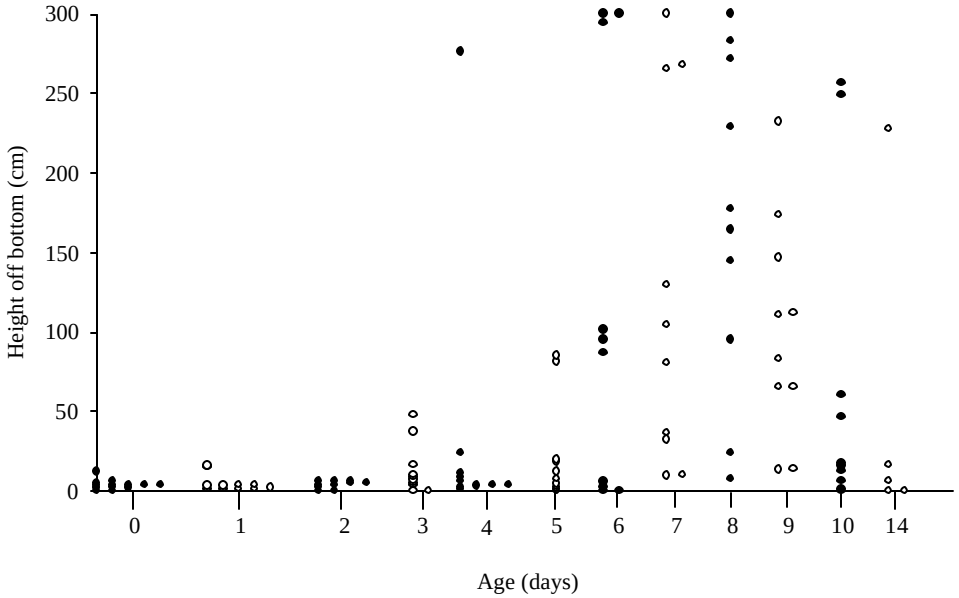

Figure 7. Swimming height off the bottom of all individuals tested in the 300 cm high stream tube. The color of the points is for visual distinction of days only (i.e., every other day has filled symbols). Ten fish were tested each day except for day 0 (n = 13), day 1 (n = 11), and day 14 (n = 5). The data represent fish tested both day and night, except on day 14 when fish were only tested during the day.

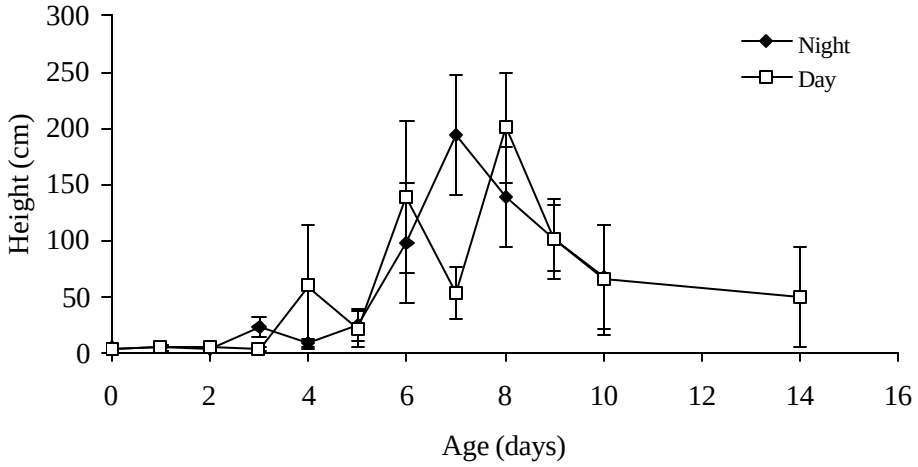

Figure 8. Mean (± SE) swimming height above the bottom in the stream tube of pallid sturgeon tested during the day and at night.

Discussion

The present study confirmed the results from the 1997 study that found ontogenetic changes in behavior occur with development of fish from embryo to larva (Kynard et al. 2002-a). Data from velocity tests on dispersal (number of fish passes) and percent of fish holding position and from stream tube tests on the decrease in swimming depth with age show that the dispersal ends at about day 14 (238-239.5 CTU). The tests in 1997 and 2003 observed progeny from different parents and were tested different years, yet they behaved similarly. This is strong evidence for the innate nature of the dispersal, the ontogenetic changes in behavior, and habitat preferences of embryo and larva life intervals.

The changes in swimming depth as embryos develop into larva may be partly related to foraging. Embryos have only one drive, to disperse downstream, but larvae have to incorporate a second drive with dispersal, the drive to forage. Larvae must forage or they will die within a few days, and the most critical period for their survival is the initial few days after feeding begins. We do not know how dispersing throughout the water column on days 6-9, likely the most critical days for foraging, relates to foraging or dispersal success, but it could be critical for the success of both behavioral drives.

Velocity and dispersal

The velocity experiment showed that embryos went with the flow in all velocity treatments, spending time in the channel flow and in the eddy, when current carried them there. They showed little ability to control movement. The same situation likely occurs in rivers. Data were missing on days 0-3 embryos in the slow and medium velocity treatments, but we visually observed these embryos behaved similarly to day 4 embryos on which we collected data. The day-4 embryos were large, more developed, and better swimmers, yet the current still moved them around the test tanks almost like passive particles. No fish held position in the eddy until day 8 (larval stage), even in the slow or medium velocity treatments (mean bottom velocity, -3.3 and -4.7 cm/s, respectively). The data on number of daily fish passes and numbers of fish holding position indicate that wild embryos should move less than the mean velocity because all embryos are bottom-oriented and some will be moved by currents into areas of low velocity or eddies. The continuous swim-up movements of embryos will eventually return them to the main flow, just as it did in our test tanks, but these embryos will not be moving at the speed of the main flow. Additionally, embryos in the stream tube were on the bottom for much of the time, thus would be moving less than the water velocity even measured at 25 or 50 cm above the bottom.

The decrease in daily number of days 0-5 embryos passing the observation area in the fast velocity tanks indicates a gradual trend for embryos to remain longer in the eddy with age. The number of embryos passing was highest on day 2 and lowest on day 5 (Figure 6). This suggests that dispersal rate of wild days 1-2 embryos should be high, then slower for older days 3-5 embryos. The pattern for the highest dispersal rate to occur in the early period of a life stage continued during the larva stage, i.e., after the

peak dispersal by days 6-9 larvae, the number of larvae moving downstream during days 6-14 gradually declined (Figure 6).

Fish did not move at the velocity of channel flows in our tanks, but instead, embryos and larvae were frequently entrained into the eddy, which slowed their total dispersal rate. Dispersal rate of embryos was always slower than the channel velocity and slowed from 8-10 cm/s to about 5 cm/s during the embryo stage. In the fast velocity treatment, speed of fish was 1/6 to 1/3 water speed. Speed of day-4 embryos was 1/17 water speed in the slow velocity treatment and 1/7 water speed in the medium velocity treatment. Travel rate of larvae slowed as they began to hold position in the eddy. Larvae (days 6-7) had the highest speed in the slow and medium velocity treatments and moved about 1/3 channel velocity (Figure 6).

The dual environments in the velocity test tanks were more complex hydraulically and structurally than the artificial stream tank used by Kynard et al. (2002-a), but the environment was not as complex as, nor did it correctly represent, all environments present in the river environment. However, the basic behavioral drive and swimming ability of embryos and larvae provide a reasonable interpretation of likely fish movements in the riverine environment. Embryos are somewhat like a passive particle drifting near the bottom (< 50 cm) in that they have little ability to resist currents, even weak ones. However, they are not completely passive drifters. Their constant short bouts of swim-up and drift returned them to the main flow if they entered an eddy. This movement is likely highly adaptive for dispersing sturgeon embryos downstream as all species that migrate as embryos show this behavior (Kynard et al. 2002-a, b; Zhuang et al. 2002-a, b).

Swimming height above the bottom

The 1997 data and the present data on embryos agree that swimming height of embryos is near the bottom. Swimming height of embryos in the 300 cm stream tube was < 30 cm above the bottom, except for a few rare fish that swam 50 cm high or higher. In rivers, some embryos will be carried farther above the bottom by turbulence and bottom current; however, embryos displaced farther above the bottom than they prefer likely have a strong drive to return to the bottom. Stream tube tests were conducted at a slow velocity (2 cm/s) to determine depth preference of fish without introducing velocity effects. All fish, even day-0 embryos, could easily swim upward with the 2-cm velocity (Kynard et al. 2002-a).

The study in 1997 failed to obtain information on swimming depth of days 0-2 embryos and on day 9+ larvae, but the data in this study provided information on swimming depth of days 0-14 fish. This data support and extend to the entire embryo period the general pattern of swimming depth suggested by the previous partial data, i.e., that embryos of all ages swim < 50 cm above the bottom, then as fish develop into larvae, they swim far above the bottom. The present study shows that days 6-9 larvae swim throughout the water column; and some (10-33%) swam to the surface on days 6-8. So, the behavior of larvae in the previous study that swam to the top of the 150 cm tube, then swam in circles at the top, did correctly show intention movements to swim higher. Also,

in the previous study, all larvae swam 150 cm to the surface on days 7-8, suggesting all fish would swim higher if possible. However, the present study shows that not all days 7-8 fish prefer to swim 150 cm or higher (Figure 7). Days 6-9 larvae in the present study were widely dispersed throughout the water column, showing these larvae have great diversity in swimming height.

The difference in results of swimming height between days 7-8 larvae tested in the 150 cm and 300 cm stream tubes suggests that water depth affects swimming height. Days 6-9 larvae may regulate swimming depth depending on depth of the water, swimming to the surface when water is 150 cm deep (or shallower) and dispersing throughout the water column when water depth is 300 cm deep or deeper. This phenomenon has been observed in downstream dispersing juvenile American shad Alosa sapidissima in the Connecticut River that are at the surface in shallow water (2 m deep), but disperse deeper in water 10 m deep (Kynard et al. In Press). Avoidance of benthic predators may be the selective factor in this case. The results strongly suggest larval pallid sturgeon change swimming depth depending on water depth. Additional tests should be conducted to fully understand this important aspect of larval dispersal.

The present study provided a positive answer to the question of whether the days 6-8 larvae that swam to the top of the 150 cm tube in the tests of Kynard et al. (2002-a) would swim higher if the tube was higher – many did swim higher in the 300 cm high tube. Thus, frantic swimming around the top of the tube is a clear behavioral intention movement. All observations indicate that the few fish that swam to the top of the 300 cm tube would swim even higher if the tube were longer.

The preliminary tests of 1-2 h duration on five embryos and five larvae provide additional insight into the likely swimming height of both life intervals for a prolonged time. Swimming height of 4 of 5 day-4 fish after 1 h was a maximum of 10 cm, which was similar to their behavior after 2 h (maximum swimming height=18 cm). Further, both prolonged swimming heights were like the nine day-4 embryos observed at 11-12 min (mean, 5.5 cm). One fish in both the prolonged and short-term tests swam high above the bottom (276 cm in the short-term test, 285-290 in the prolonged tests); so a few fish (estimated at 10% or less) swim high even during the embryo interval. Although the prolonged tests were only preliminary, swimming height of embryos at 11-12 min and 1-2 h were similar, indicating that 11-12 min observations were sufficient to describe swimming height of embryos.

The prolonged observations on day-6 larvae are the first to show this life stage is physically capable and prefers to swim high above the bottom for 1 h. If tests had been done for longer, fish would likely have remained far above the bottom, because at the end of the 1-h test, fish showed no movement toward the bottom. Mean swimming height of the three day-6 fish that swam above the bottom at 1 h and the three day-6 fish that swam high above the bottom at 11-12 min were similar, respectively, 258 cm and 232.0 cm. Thus, the one prolonged test on larvae support the observations on larvae at 11-12 min, but the data are too limited to fully verify the swimming height of fish for a prolonged time.

Larvae varied greatly for swimming height on any day. In the previous tests of swimming height in Kynard et al. (2002-a), we observed 8 fish during each daily test. Interestingly, the greatest variation (SE = 40-50 cm) in swimming height was by days 5-6 fish for both pallid and shovelnose sturgeons, which were developing into larvae. However, by the time fish developed into day 7-8 larvae, the variation for swimming height was small (SE = <10 cm) because all or most fish went to 150 cm. The variation in swimming height of larvae in the tests using the 300 cm tube was great and similar among days (SE about 50 cm). During each group of 10 fish tested on days 6-8, two to four fish swam near the bottom <37 cm high (4 fish on day 6, 4 fish on day 7, 2 fish on day 8). The data on larval swimming height in the present tests is likely a good representation of fish in water 300 cm deep with 2 cm/s velocity. Now that the fish preference is known, it is important to conduct stream tests with embryos, and particularly with larvae, using higher stream tube velocities that better represent stream velocities.

CTU

Water temperature may be the key to modeling dispersal because it is the environmental factor that regulates development rate of pallid sturgeon early life stages. Further, as the results in the present study show, development of fish is tightly linked to ontogenetic changes in fish behavior, such as dispersal initiation, swimming ability, and habitat preference (swimming depth), and to endogenous physiological changes (Kynard et al. 2002-a). Thus, after embryos leave the spawning area, the timing of each sequence of behavior (swimming height, response to light, cessation of dispersal, etc.) is affected by water temperature because temperature is the exogenous factor controlling the rate of development. The CTU provides a measure of what behavior to expect from the fish. For example, pallid sturgeon embryos began to develop into larvae at 100 CTU and this developmental stage initiated feeding and swimming throughout the water column. If spawning location and spawning timing can be estimated, then the origin site and approximate departure date of dispersing embryos could be estimated.

The results in the present study suggest a conceptual model for dispersal speed that integrates fish development and behavior with the river environment (water temperature and velocity). For embryos (CTU 0-85), modeling should predict water temperature and bottom velocity downstream of the spawning area under various discharges to predict drift rate and CTU for embryos drifting < 50 near the bottom. For stream velocities that are similar to the channel velocities in the present study, this adjustment should change depending on speed of the water and age of the embryos (CTU 0-33, 1/3 water speed and CTU 49-84, 1/2 water speed). At a CTU of 100, the modeling of larval dispersal should begin. Larval dispersal should stop after a CTU of 239, when the present tests indicate dispersal ends. For the period of 100-153 CTU when larvae are swimming far above the bottom, the model should distribute larvae throughout the water column to 300 cm, or slightly higher, particularly at CTU 119-135 when the highest percent of larvae swam to 300 cm (and would have swum higher). The mean of velocities at 0.2, 0.6, and 0.8 depth may adequately describe the velocity during this

period of larval dispersal because fish are distributed almost evenly throughout the water column. (A larger sample size of day-6 larvae in the stream tube would likely show fish preferring to swim at all depths, like on days 7-9.) Finally, for fish at 170-239 CTU and the end of dispersal, 80% of the larvae swam < 50 cm high, the remainder between 200 and 250 cm. Dynamic modeling of dispersal by embryo and larval pallid sturgeon should consider using CTU to link fish factors (development stage and correlated swimming behavior) and stream factors (temperature and velocity), and perhaps water depth, if larvae adjust swimming depth with water depth.

Acknowledgments

We thank Rob Holm (Garrison Dam National Fish Hatchery, USFWS), who supplied fertilized eggs of pallid sturgeon, and Rick Barrows (Bozeman Fish Technology Center, USFWS), who supplied sturgeon starter food for larvae. Pat Braaten (Columbia Environmental Research Center, BRD/USGS) provided information and guidance on river temperature. Special thanks go to Brian Kynard for the months he spent viewing videotapes and counting the small fish. The study was funded by the U. S. Army Corps of Engineers, Omaha District (William Miller, Project Manager -- who earned an Oak Leaf Cluster for his Junior Biologist Badge on this project.)

References

Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. Stream hydrology: an introduction for ecologists. John Wiley & Sons, England.

Gross, M. R., J. Repka, C. T. Robertson, D. H. Secor & W. V. Winkle. 2002. Sturgeon conservation: insights from elasticity analysis. Amer. Fish. Soc. Symp. 28:13 -30.

Kynard, B. & M. Horgan. 2002. Ontogenetic behavior and migration of Atlantic sturgeon, Acipenser oxyrinchus oxyrinchus, and shortnose sturgeon, A. brevirostrum, with notes on social behavior. Env. Biol. Fish. 63:137-150.

Kynard, B., E. Henyey & M. Horgan. 2002a. Ontogenetic behavior, migration, and social behavior of pallid sturgeon, Scaphirhynchus albus, and shovelnose sturgeon, S. platorynchus, with notes on the adaptive significance of body color. Env. Biol. Fish. 63:389-403.

Kynard, B., P. Zhuang, T. Zhang & L. Zhang. 2002b. Ontogenetic behavior and migration of Volga River Russian sturgeon, Acipenser gueldenstaedtii, with a note on adaptive significance of body color. Env. Biol. Fish 65:411-421.

Kynard, B., P. Zhuang, T. Zhang & L. Zhang. 2003. Ontogenetic behavior and migration of Dabry's sturgeon, Acipenser dabryanus, from the Yangtze River with a note on body color. Env. Biol. Fish. 66:27-36.

Kynard, B. & E. Parker. Ontogenetic behavior and migration of Gulf of Mexico sturgeon, Acipenser oxyrinchus desotoi, with notes on body color and development. Env. Biol. Fish. (in press).

Kynard, B., E. Parker & T. Parker. Downstream migration of yearling shortnose, pallid, green, and lake sturgeon: an artificial stream study. In: D. Peterson & B. Kynard (eds.) Behavior and life history of Connecticut River shortnose sturgeon and juveniles of other North American sturgeons. Amer. Fish. Soc. (In Review-a).

Kynard, B., D. Pugh, M. Kieffer & T. Parker. Spawning of Shortnose Sturgeon in an Artificial Stream: Adult Behavior and Rearing and Dispersal of Early Life Stages. In: D. Peterson & B. Kynard (eds.) Behavior and life history of Connecticut River shortnose sturgeon and juveniles of other North American sturgeons. Amer. Fish. Soc. (In Review-b).

Kynard, B., M. Horgan, & E. Theiss. Spatial distribution of juvenile alosids during seaward migration in the Connecticut River. Jour. of Ichthyology. (In Press).

Parsley, M. J., P. J. Anders, A. I. Miller, L. G. Beckman, G. T. McCabe, Jr. 2002. Recovery of white sturgeon populations through natural production: understanding the influence of abiotic and biotic factors on spawning and subsequent recruitment. Amer. Fish. Symp. 28:55-66.

Zhuang, P., B. Kynard, L. Zhang, T. Zhang & W. Cao. 2002a. Ontogenetic behavior and migration of Chinese sturgeon, Acipenser sinensis. Env. Biol. Fish. 65: 83-97.

Zhuang, P., B. Kynard, T. Zhang, L. Zhang & W. Cao. 2002b. Comparative ontogenetic behavior and migration of Kaluga, Huso dauricus, and Amur sturgeon, Acipenser schrenckii, from the Amur River. Env. Biol. Fish. 66: 37-48.