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Ontogenetic behavior, migration, and social behavior of pallid sturgeon, *Scaphirhynchus albus*, and shovelnose sturgeon, *S. platyrhynchus*, with notes on the adaptive significance of body color

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Synopsis

We conducted laboratory studies on the ontogenetic behavior of free embryos (first life interval after hatching) and larvae (first feeding interval) of pallid and shovelnose sturgeon. Migration styles of both species were similar for timing of migration initiation by embryos on days 0 after hatching and cessation by larvae on days 12–13 at 25–29°C cumulative temperature (degree units), migration distance (about 9 km), life interval when most distance was moved (embryo), and diel behavior of embryos (diurnal). However, the species differed for two behaviors: movement characteristics of embryos (peak movement rate of pallid sturgeon was only one-half the peak rate of shovelnose sturgeon, but pallid sturgeon continued the lower rate for twice as long) and diel behavior of larvae (pallid sturgeon were diurnal and shovelnose sturgeon were nocturnal). Thus, the species used different methods to move the same distance. Migrating as poorly developed embryos suggests a migration style to avoid predation at the spawning site, but moving from spawning habitat to rearing habitat before first feeding could also be important. Migrants of both species preferred bright habitat (high illumination intensity and white substrate), a behavioral preference that may characterize the migrants of many species of sturgeon. Both species were remarkably similar for swimming height above the bottom by age, and day 7 and older migrants may swim far above the bottom and move far downstream. A migration of 12 or 13 days will probably not distribute larvae throughout the population's range, so an older life interval likely initiates a second longer downstream migration (2-step migration). By day 2, individuals of both species were a black-tail phenotype (light grey body with a black-tail that moved conspicuously during swimming). Aggregation behavior suggests that black-tail is a visual signal used for group cohesion.

Introduction

Pallid sturgeon, *Scaphirhynchus albus*, inhabits the Missouri and lower Mississippi rivers and is one of the rarest riverine fish species in North America (Kallemeyn 1983). The species is listed as federally endangered because of population declines during

the 20th Century that occurred during dam building (Dryer & Sandvol¹). Little information exists on any aspect of the early life-history of pallid sturgeon

¹ Dryer, M.P. & A.J. Sandvol. 1993. Recovery plan for the pallid sturgeon (*Scaphirhynchus albus*). U.S. Fish & Wildl. Serv., Reg. 6, Denver. 55 pp.

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(Kallemeyn 1983, Carlson et al. 1985, Duffy et al.²). In this long-lived species with 40-year-old individuals common (Keenlyne et al. 1992), year class strength is likely established early in life. During culture of many sturgeon species, the greatest mortality occurs within the first 30 days of life, i.e., during migration and initial foraging (B. Kynard personal observation). It is likely this situation also occurs in wild populations; thus, understanding the behavior and life-history styles of early life intervals is critical to management of sturgeon.

Shovelnose sturgeon, *S. platyrhynchus*, is a smaller, sympatric sibling species that is abundant and harvested commercially (Helms³, Carlson et al. 1985, Morrow et al. 1998). Spawning occurs over rocky substrate in river mainstems directly downstream of dams or along wing dams (Helms³), and pallid sturgeon may be similar (Dryer & Sandvol¹). River temperature during spawning in June is 20°C or slightly higher (Moos 1978, June 1977). ~~Also free embryos (first life interval after hatching, Balon 1999) and larvae (first feeding life interval) of pallid sturgeon, shovelnose sturgeon, or both were captured by netting in the Yellowstone River at a river temperature of 20°C (Gardner⁴). No other information is available on behavior of early life intervals of pallid or shovelnose sturgeon.~~

Studies of sturgeon behavior recently revealed that some species of *Acipenser* have saltatory behavioral changes during ontogenetic development. After hatching, free embryos of shortnose sturgeon, *A. brevirostrum*, and Atlantic sturgeon, *A. oxyrinchus*, are photonegative and seek cover and dark substrate. Then, as embryos develop into larvae, their preferences change and they avoid cover, prefer bright habitat (illumination and white substrate), and initiate downstream migration (Buckley & Kynard 1981, Richmond & Kynard 1995, Kynard & Horgan 2001). The migratory and diel styles of shortnose and Atlantic sturgeon embryos and larvae may reduce predation risk and enhance feeding (Kynard & Horgan 2001).

² Duffy, W.G., C.R. Berry & K.D. Keenlyne. 1994. The pallid sturgeon: biology and annotated bibliography through 1994. Tech. Report No. 5, S. Dakota Coop. Fish & Wildl. Res. Unit, S. Dakota State University, Brookings. 32 pp.

³ Helms, D.R. 1974. Shovelnose sturgeon, *Scaphirhynchus platyrhynchus* (Rafinesque) in the navigational impoundments of the Upper Mississippi River. Iowa Cons. Comm. Tech. Ser. 74-3. 68 pp.

⁴ Gardner, W. 1995. Yellowstone River paddlefish spawning study. Prog. Report on Project No. F-78-R-1, Montana Dept. Fish, Wildl. & Parks, Helena. 18 pp.

With few changes in methods of Kynard & Horgan (2001), we studied free embryos (hereafter, termed embryos) and larvae of pallid and shovelnose sturgeon. We observed the daily behavioral response of fish to illumination intensity and substrate color (brightness), determined the swimming height of fish above the bottom and their use of cover, and monitored migration. The response of sturgeon to bright or dark habitat and swimming height above the bottom give clues to habitat selected in a river, and behavior during migration shows migration style and gives clues to migratory distance.

Comparative behavior of species can reveal important ecological and phylogenetic relationships (McLennan 1999). Pallid and shovelnose sturgeon are similar, but they can be distinguished using morphological characters (Carlson et al. 1985, Keenlyne et al. 1994). The two species are so similar that early genetic analysis could not separate them (Phelps & Allendorf 1983). However, the two species may differ for innate behaviors that reveal alternative life-history styles (Bruton 1990).

Limited information is available on body color of embryos and larvae. The bodies of shortnose and Atlantic sturgeon embryos and larvae are dark (blackish) and these species depart the spawning area as well-developed larvae (Richmond & Kynard 1995, Kynard & Horgan 2001). However, some species migrate as embryos with light grey bodies and black-tails. Examples of this combination of body color and behavior are Siberian sturgeon, *A. baeri* (Gisbert et al. 1999) and white sturgeon, *A. transmontanus* (Brannon et al.⁵). In the present study, we describe the body color and behavior of young *Scaphirhynchus* and review body color and migration of several sturgeon species to explore the adaptive significance of body color.

Methods

We conducted tests with 500 Missouri River pallid sturgeon that hatched on 25 June 1997 and 400 day-2 pallid sturgeon received the following year on 16 June 1998. Tests were conducted during 2 years with shovelnose sturgeon of Yellowstone River stock: in 1997, 200 fish that hatched on 18 June and 350 fish that hatched on 20 June; and in 1998, 400 fish that hatched on 24 June.

⁵ Brannon, E., S. Brewer, A. Setter, M. Miller, F. Utter & W. Hershberger. 1985. Columbia River white sturgeon (*Acipenser transmontanus*) early life history and genetics study. Final Report. Bonneville Power Administration, Portland. 68 pp.

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The shovelnose sturgeon tested in 1997 and 1998 were from different parents. Eggs were fertilized at a federal hatchery (see Acknowledgements) then shipped to us. The number of days after hatching was used to characterize age of fish, not the number of days after fertilization, because early rearing varied before we received eggs. Fish hatching in the first 24 h were termed day-0 fish, i.e., in 1997 pallid sturgeon were day 0 on 25 June and day 1 on 26 June.

We reared fertilized eggs in hatching jars that passed embryos in overflow water into 18 or 30-l circular rearing tanks. Temperature of dechlorinated city water from Montague, MA, was similar in rearing and experimental tanks. Water temperature in the oval migration channel in 1997 was 19.0–21.0°C for pallid sturgeon and 18.0–20.0°C for shovelnose sturgeon; and in 1998, temperature was 16–18°C for pallid sturgeon and 18–18.5°C for shovelnose sturgeon. All test and rearing water temperatures were within the range of temperatures experienced by wild fish (USGS data). The natural photoperiod for the Turners Falls location was maintained at all time. Early larvae were fed 6–8 times daily using a timed feeder and four times daily with live *Artemia* nauplii. In 1998, larvae were fed a sturgeon starter diet (see Acknowledgements), whereas 1997 larvae were fed commercial BioKyowa.

Illumination, substrate color, height above bottom, and cover

The year and test (species and test in parentheses) were: 1997 (both species – illumination, substrate color, and use of cover); 1998 (pallid sturgeon – height above bottom; shovelnose sturgeon – illumination, substrate color, height above bottom, and cover).

Aquaria used in illumination and substrate choice were 20-l rectangular glass tanks with black plastic covering the four vertical sides to exclude outside light. Two 0.3 m long, 20 watt fluorescent lights were placed 0.3 m above the test tanks, and with barrier partitions underneath the lights, provided the final light intensity for test aquaria. A black cover over one-half of the illumination aquarium's top divided the tank into almost equal areas of illumination (8.2–5.0 lx), dark (0.7–0 lx), and transition in the center (5.5–2.2 lx). The bottom of the illumination aquarium was clear glass and the aquarium sat on a tan table. The bottom of the substrate color aquarium was also clear, but underneath the bottom, the area was divided equally between black and white by two square pieces of white and

black plastic. Illumination intensity above the substrate was: white (4.3–2.6 lx) and black (3.3–3.0 lx). During illumination and substrate tests, aquarium position was reversed after each fish to prevent recording side bias of fish. Water was replaced in aquaria between tests to keep water temperature within 1°C of rearing water.

Five pallid sturgeon and four to ten shovelnose sturgeon were tested daily for preference of illumination intensity and substrate color. Before each test, actively swimming fish were removed from a rearing tank using beaker brailing and placed together in a 1–3 l bucket. During each test, a single fish was removed from the bucket by beaker brailing and placed at the water surface in the center of the aquarium. Without acclimation, fish movement was visually recorded as a continuous time series relative to habitat (illumination test – dark, transition, and illuminated; substrate test – white or black bottom). We used an arcsine-transformation of percent data and the percentage of time sturgeon occurred on white substrate or on the illuminated side in all data analyses and calculated 95% confidence intervals to find differences from 50% (no preference).

In 1998 we daily tested eight pallid and shovelnose sturgeon for swimming height above the bottom in an artificial stream tube that simulated a vertical section of stream (Figure 1). The stream tube was a clear plexiglass cylinder 153 cm long × 15 cm inside diameter with water 150 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⁻¹. 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 drained after each test to remove fish and replace water and maintain water temperature within 1°C of rearing tanks.

Sturgeon for stream tube tests were obtained after mixing rearing tank fish by stirring and using beaker brailing to remove fish. Test fish for each replicate were held in a 2 l bucket, and during tests, a single fish was beaker brailed and poured into the top of the introduction tube, which carried fish to the bottom (Figure 1). Only upward swimming and cover seeking were noted for the first 60 s (acclimation period). At 1–2 min, 5–6 min, and 9–10 min, we continuously recorded up and down movements and the vertical distance of each move. Height of fish off the bottom was determined visually using a depth scale (5 cm marks

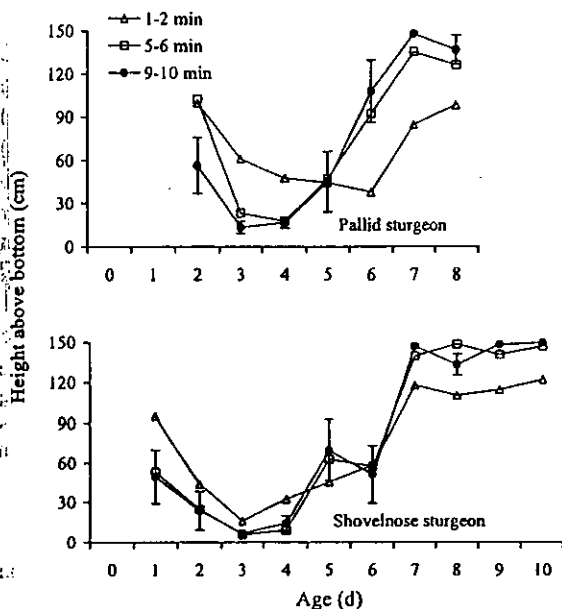


Figure 5. Swimming height of pallid and shovelnose sturgeon above the bottom in the stream tube (water depth = 150 cm) by age. Each point is the grand mean for all fish during one of three 60 s periods. Standard error bars are provided for the 9–10 min period only.

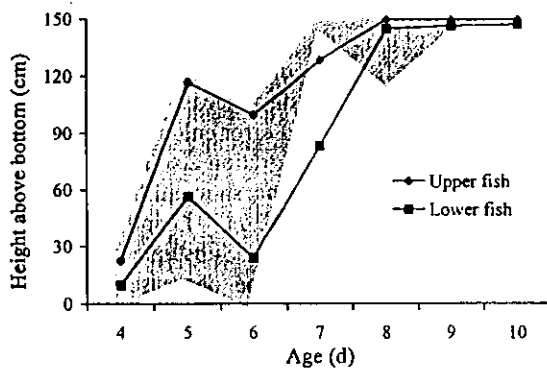


Figure 6. Swimming height above the bottom in the stream tube of shovelnose sturgeon tested in pairs. Data are for the 9–10 min period only. Shaded area encompasses the 95% confidence interval for the mean of solitary shovelnose sturgeon of the same age.

In 1998, days 4–10 shovelnose sturgeon were also tested in pairs. The mean heights for upper and lower fish were within the 95% confidence intervals of solitary fish height on days 4–6, but near the extremes of the confidence interval (Figure 6). However, solitary day-7 fish immediately went to the surface and remained there, while paired fish only went to a mean height of

83 and 128 cm for lower and upper fish, respectively. This distribution was outside the solitary fish confidence interval. Within each fish pair, distance between fish was consistent, but among pairs, the mean height difference on days 5–7 was highly variable (1–130 cm).

Both species swam-up with or against the current, then drifted motionless head-down at a 45° angle with the current, then resumed swim-up to remain in the water column. Swimming-up with the current was typical on days 0–1; older fish swam-up with or against the current. Swimming against the current greatly increased the rate of ascent.

Cover

Both species used only open habitat. None sought cover under rocks in the stream tube or in the migration tank and fish that swam under rocks did not stop, but quickly emerged. Even fish which swam on the bottom in the stream tube (Figure 5), did not stop under cover.

Migration and diel behavior

Daytime visual observations show that 100% of the pallid sturgeon migrated daily from days 0 to 7 (except for two fish on day 6; Figure 7, top panel). After day 7 (140 CTU), the percent migrating daily declined about 20% per day and migration ceased on day 12 (243 CTU). (The one fish migrating on days 12 and 14 is explained in the following paragraph.) The peak of migration, as indicated by days with the largest numbers of fish moving downstream past the video camera, was on days 0–3 (60 CTU). Migrant numbers decreased daily after fish developed into larvae on day 4 at 79 CTU (Figure 7, top panel). Video tapes of days 9–15 were accidentally erased and were not available for analysis.

Pallid sturgeon moved up- and downstream during the day and night, although there was much more downstream than upstream movement (Figure 7, top panel). There were no days for which day and night downstream movement were significantly different (unpaired *t*-tests, all >0.10). Although the trend was toward increased nocturnal behavior, the trend was not significant to day 8 when migration was about over (paired *t*-test, 0.16).

We replaced single pallid sturgeon that died on days 9, 11, 12, and 13 with replacement fish from the rearing tank. In the rearing tank, fish moved with the flow like they were attempting to migrate downstream;

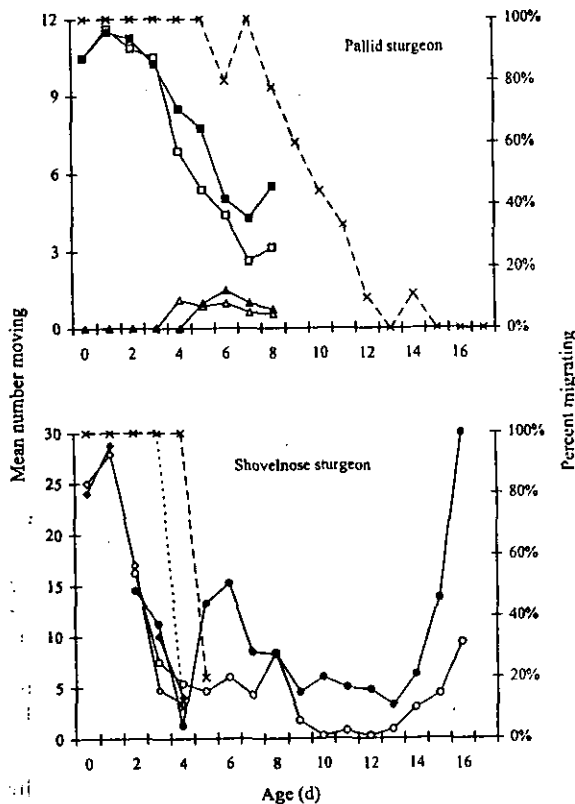


Figure 7. Migration of pallid sturgeon by age in the oval endless channel during 1997 ($n = 10$) and by shovelnose sturgeon (1997, $n = 10$; 1998, $n = 15$). Migrant counts were of two types: daily visual counts of percent total fish moving downstream and video counts of fish moving up- or downstream past a stationary camera with infrared light (hourly observations for 5 min, 24 h per day). The mean number of fish is the net downstream number (downstream number minus upstream number). Lines with \times indicate the percent of fish moving downstream by visual counts (1997 shovelnose sturgeon indicated by short dashes, 1998 shovelnose sturgeon by long dashes). Open and filled symbols indicate day and night counts, respectively. Symbols used are squares (pallid sturgeon), diamonds (1997 shovelnose sturgeon), circles (1998 shovelnose sturgeon); and triangles (upstream migrants). For clarity of shovelnose sturgeon, data on upstream migrants are not included, but are presented in the text.

however, they were crowded, grew slower, and could not maintain small aggregations like oval channel fish. Because replacement fish were slightly smaller, we could identify them. On day 12, the eight surviving oval channel sturgeon had stopped migrating, as had replacement fish introduced on days 9 and 11 (Figure 7, top panel). The day 12 replacement fish stopped migrating after < 1 day and the day-13 fish stopped on day 14.

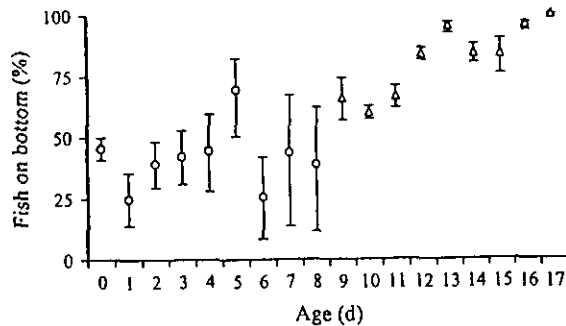


Figure 8. Percentage of pallid sturgeon (\pm SE) observed on the bottom of the oval channel by age. Data were collected using two methods: days 0–8, each fish was observed multiple times and error is among-fish (circles); days 9–17, a group of fish was observed simultaneously and error is among-observations (triangles).

During days 0–8, except for day 5, pallid sturgeon occurred more than 50% of the time in the water column (Figure 8). After day 8, the percent of fish on the bottom increased and this change reflected the gradual decrease in the number of downstream migrants after day 7 (Figure 7, top panel). Because the aggregated movements of day 8 and older fish prevented us from observing individual fish, we changed from multiple observations of one fish to multiple simultaneous observations of the entire group. Thus, within-age variation for bottom use is not directly comparable between early (to day 8) and later days because of the different observational methods and error calculations.

Shovelnose sturgeon migration also began at hatching and daytime visual counts show all fish were moving downstream on days 0–3 (1997) and on days 0–4 (1998; Figure 7, bottom panel). Subsequently, the number migrating in the daytime decreased sharply to 10% on day 4 (1997) and to < 20% on day 5 (1998), so we discontinued daytime visual observations. The switch from diurnal to nocturnal movement occurred on day 4 each year after similar periods of development: 1997 – 78 CTU and 1998 – 72 CTU.

Video counts of the number of shovelnose sturgeon moving downstream show the migration peaked during days 0–1 in 1997, then declined sharply to almost zero by day 4, when observations stopped (Figure 7, bottom panel). In 1998, a mechanical failure delayed video taping until day 2, then on days 2–4, the mean number moving downstream was similar to the mean number moving in 1997. This suggests that the 1998 migration, like the 1997 migration, peaked earlier on days 0–1, but data are missing. Migration

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almost stopped both years on day 4 when embryos developed into larvae and began feeding. In 1998, downstream migrant counts increased on days 5–6 (108 CTU), then gradually declined until day 13 (236 CTU). The increased number of fish moving downstream on days 14–16 (Figure 7, bottom panel) was not a renewed downstream migration because movement was also upstream. The mean number moving upstream (not shown in Figure 7 for clarity) was 1–5 fish each day for days 0–14, except for 7 fish on day 8. However, the number of upstream moving fish increased to 15 fish on day 16. The up- and downstream movements on days 14–16 were not related to any known change in the oval channel environment (water velocity was stable and temperature was unchanged at 18–18.5°C). All test fish were dead by day 18 with no food in their stomachs, so movement on days 14–16 was likely abnormal behavior of fish searching for acceptable food. Migration had almost stopped by day 13, but some fish may have migrated for another day or so.

Shovelnose sturgeon migration in 1997 was diurnal during days 0–2 and on day 4 (no night data for day 3; Figure 7, bottom panel). Migration was also diurnal in 1998 on day 2, suggesting a similar diurnal pattern for days 0–1 (as in 1997), but data are missing. On day 4 when feeding began, day migrants dominated in 1998, but on days 5–6, night migrants dominated (unpaired *t*-tests, <0.05) and the trend was toward nocturnal behavior. Considering days 2–10, movement was significantly higher at night (paired *t*-test, 0.046).

Water temperature increase or decrease of 1.5°C and variation in water velocity had no obvious effect on migrant behavior. During the pallid sturgeon migration, water temperature was 20–21°C, except for a decrease from 20.5°C to 19.0°C on days 1–3 and a return to 20.5°C on days 3–5. During the period when temperature decreased or increased 1.5°C, 100% of the pallid sturgeon moved downstream each day (Figure 7, top panel). Water temperature during the 1998 shovelnose sturgeon migration was almost constant (18.0°C during days 0–6 and 18.0–18.5°C during days 7–16, the period when migrant numbers greatly decreased, then increased). Also, the percent of shovelnose sturgeon migrating during days 0–3 in 1997, when water velocity was fast (153 s water loop time) and for the same period in 1998, when water velocity was slower (221 s water loop time), was the same – 100% were migrating (Figure 7, bottom panel). Water velocity was also unchanged during the decrease in numbers of migrants that occurred on day 4 of both years at 72–78 CTU and the increase in number of migrants on day 16.

Migration rate

Both species were good swim-up and drift swimmers and some day-0 fish (particularly, shovelnose sturgeon) had loop times similar to or faster than water speed (Table 1). Fish actively swam headfirst downstream for up to several minutes, then rested and drifted with the current for a short time, and resumed swimming

Table 1. Time (mean and range) required for sturgeon to complete one loop of the oval channel by age. Loop time of only water by test was pallid sturgeon (1997) 221 s, shovelnose sturgeon (1997) 153 s, and shovelnose sturgeon (1998) 221 s.

Age (day)	Pallid sturgeon		Shovelnose sturgeon			
	1997		1997		1998	
	Loop time (s)	Range	Loop time (s)	Range	Loop time (s)	Range
0	296	(252–365)	111	(105–126)	256	(222–273)
1	298	(243–412)	138	(121–154)	315	(190–493)
2	229	(176–291)	109	(95–124)	266	(186–533)
3	247	(213–266)	210	(146–285)	1547	(197–4044)
4	274	(227–339)	383	(256–448)	636	(595–657)
5	853	(369–1320)				
6	2436	(590–6000)				
7	1517	(609–3665)				
8	1332	(195–4800)				
9	428	(380–466)				
10	577	(410–748)				
11	298	(276–335)				

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upward before reaching the bottom. After fish began feeding on days 4–5, loop time slowed as fish spent more time holding position or moving upstream on the bottom or along the channel walls, particularly at the water surface. On the last day that 100% of pallid sturgeon were migrating (day 7), mean loop time was seven times slower than water speed.

We compared the loop times for all three experiments for days 0–3 (day 4 excluded because fewer fish were evaluated, Table 1). In order to compare among tests with different water loop times, we corrected fish loop times by subtracting the average time for the surface float to complete a loop of the channel (153 s for 1997 shovelnose sturgeon tests and 221 s for tests with pallid sturgeon and 1998 shovelnose sturgeon). Shovelnose sturgeon in 1998 had the longest corrected loop times ($p < 0.05$). Pallid sturgeon in 1997 had slightly longer corrected loop times than 1997 shovelnose sturgeon ($p > 0.05 < 0.10$; Table 1). Age and age \times experiment interaction terms were also significant ($p < 0.05$) due mostly to the long loop times of day-3 shovelnose sturgeon in 1998. The fast loop times of pallid sturgeon observed on days 9–11 (Table 1) were replacement fish that replaced dead original fish.

The daily daytime mean number of pallid sturgeon counted passing downstream each 5 min during video counts closely agreed with the expected number that should complete a circuit of the channel based on migration rate determined from visual observations of the mean time for fish to move 7.3 m or one loop around the oval channel. The video counts were 10.88–2.63 fish (>10.00 for days 0–3, then decreasing daily to day 8), and the expected numbers for the same days were 13.10–1.23 fish (>10.07 for days 0–4, then decreasing daily). Mean ground speed of pallid sturgeon varied little during days 0–4 (2.5 – 3.2 cm s^{-1}). After day 4, ground speed decreased to 0.9 cm s^{-1} on day 5, and on days 6–8, ground speed was only 0.5 cm s^{-1} .

The ontogenetic pattern of movement rate differed widely between species (loop time of all fish corrected to a water speed of 221 s for one loop, Figure 9). Pallid sturgeon embryos moved at a rate of about 300 loops per fish per day during days 0–4, then as fish began feeding, movement of larvae slowed gradually to about 100 loops per fish per day by day 8. Shovelnose sturgeon embryos in 1997 moved very fast during days 0–1 (500–575 loops per fish per day), a rate almost twice that of days 0–1 pallid sturgeon. The 1997 and 1998 shovelnose sturgeon movement rates were similar for days 2–3 and identical for day 4, when movement

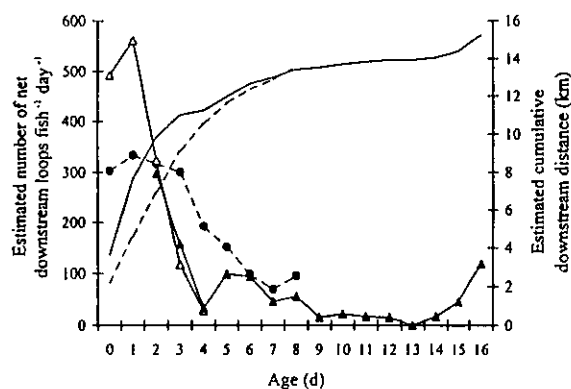


Figure 9. The estimated number of net downstream loops per fish per day and the cumulative distance moved in the oval channel in 1997 by pallid sturgeon ($n = 10$) and by shovelnose sturgeon (1997, $n = 10$; 1998, $n = 15$). Cumulative distance analysis used twice the number of daytime as nighttime hours for each 24 h, 7.3 m as the distance for one loop, and the 1997 shovelnose sturgeon loop speed was corrected to the water loop speed (221 s per loop) of the others. Pallid sturgeon are indicated by dashed lines and filled circles. Shovelnose sturgeon are indicated by solid lines and triangles: open for 1997 (days 0–4) and filled for 1998 (days 2–16).

declined to almost zero. These results were obtained when 10 shovelnose sturgeon were observed in 1997 in fast velocity flow, and when 15 were observed in 1998 in slow velocity flow. Because these early movement rates were the same between years, it is likely that 1998 shovelnose sturgeon also had high movement rates on days 0–1, like 1997 shovelnose sturgeon, but data are missing. After day 4, movement rate of shovelnose sturgeon larvae was slow (≤ 100 loops per fish per day), while pallid sturgeon moved at a slightly faster rate than shovelnose sturgeon on days 3–5. The cumulative distance curves for each species show the distance moved to day 8 was 13.6 km for pallid sturgeon and 13.4 km for shovelnose sturgeon.

Spatial distribution

Days 0–2 fish of both species were solitary, but many day 3 and older fish moved downstream in loose aggregations of 3–5 fish. Individuals were not in schools with similar orientation and spacing, but in shoals that traveled together about 60 cm from lead to trailing fish. Groups typically swam one or more loops around the channel, then stopped at sections 5–7 in the fast water near the pump, the site of the greatest aggregation. Some fish in a group usually continued around the tank with new fish; others remained in the aggregation at

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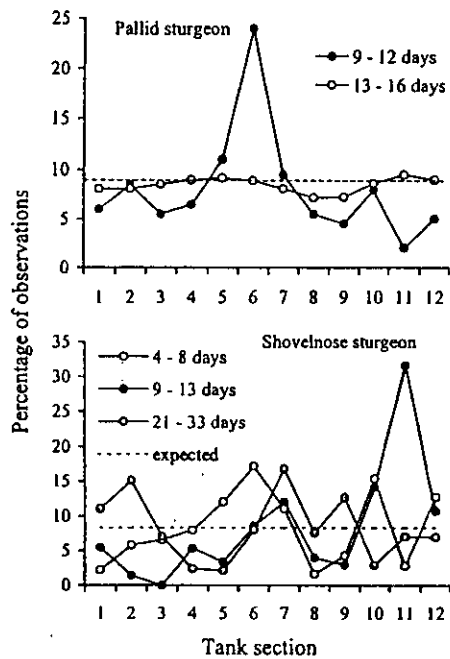


Figure 10. Spatial distribution of sturgeon among 12 sections of the oval channel. Top panel shows pallid sturgeon late migrants (days 9–12) and early residents (days 13–16) in 1997. Bottom panel shows shovelnose sturgeon migrants (days 4–8), late migrants (days 9–13), and residents (days 21–33) in 1998. Dashed lines are at 8.3% which is the level of occupancy expected with random distribution or even spacing. Days 14–18 with dying shovelnose sturgeon were excluded from the analysis.

the pump. We could not identify individuals, but there was no obvious group cohesion, e.g., individuals did not remain in the same group.

Days 9–12 pallid sturgeon late migrants were aggregated, but days 13–16 early residents were evenly spaced (Figure 10, upper panel). On day 6, late migrants aggregated in the fast water of section 6. However, most pallid late migrants, and particularly early residents were spaced evenly.

The spacing pattern of the original shovelnose sturgeon was observed in the oval channel until day 13, then replacement fish were observed, after several days of acclimation, on days 21–33. Many days 4–8 migrants were aggregated in fast velocity (sections 5–7; Figure 10, bottom panel). Days 9–13 late migrants also used section 7, but most stopped in section 11 in the largest aggregation observed. Days 21–33 residents aggregated in sections 1–2 downstream of the feeder and in sections 7–9 (fast velocity).

Late migrant and early resident pallid sturgeon were distributed in the oval channel in a manner

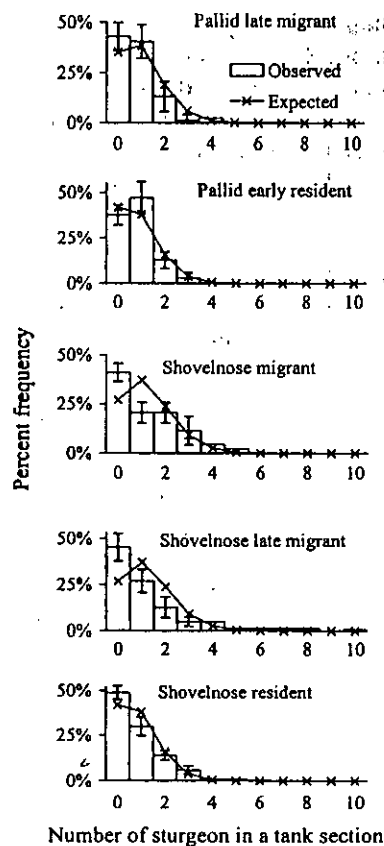


Figure 11. Percent frequency histogram of the number of sturgeon occupying each channel section with values expected if occupancy was random and independent among fish. Expected values were generated from Monte Carlo simulations, $n = 10,000$, for 10 fish (pallid and resident shovelnose) or 15 fish (younger shovelnose). Stages observed in 1997 were pallid sturgeon late migrants (days 9–12) and early residents (days 13–16); and in 1998 were shovelnose sturgeon migrants (days 4–8), late migrants (days 9–13), and residents (days 21–33). Days 14–18 with dying shovelnose sturgeon were excluded from the analysis.

consistent with random and independent selection (Figure 11, upper two panels). The greatest deviation from expected numbers of fish were by late migrants which had a slight excess of 0's and a deficiency of 2's. Early residents had a slight excess of 1's. True even spacing would result in a majority of sections with 1's, because there were fewer fish (10) than sections (12).

Migrant shovelnose sturgeon ($n = 15$) differed strongly from the expected random spatial distribution with an excess of 0's and a deficiency of 1's (Figure 11, middle panel). Late migrants showed the same deviation from expected as migrants and additionally,

2's were also less than expected (Figure 11, next to bottom panel). Resident shovelnose sturgeon were distributed more closely to a random distribution, but 0's were still more abundant and 1's less abundant than expected, indicating a slight continued aggregation (Figure 11, bottom panel).

Shovelnose sturgeon, unlike pallid sturgeon, consistently had an excess of 0 fish sections showing fish were aggregated more than expected by chance. Single and double fish sections were expected if spacing was even, but these were under represented (Figure 11, shovelnose migrant and late migrant panels). Resident shovelnose sturgeon spatial distribution approached the expected distribution, but zero sections were still over represented and sections with 1's were still under represented (Figure 11, bottom panel).

Discussion

The striking similarity of shovelnose sturgeon from different parents for preference of illumination and substrate and for diel behavior of embryos is evidence for the innate nature of the behaviors, and demonstrates the repeatability of the experimental results. Also, migrant numbers were not affected by variation in water temperature and water velocity conditions. All test results indicate that slight variation in these environmental factors between river and laboratory conditions or between laboratory conditions during different tests will not affect expression of behavior during comparative studies of sturgeon ontogenetic behavior.

The preference of pallid and shovelnose sturgeon embryos for high illumination intensity is among the strongest photopositive responses observed in young sturgeon (Richmond & Kynard 1995, Kynard & Horgan 2001). Yet, day-0 embryos were photonegative or had no preference. Was the visual sense of day-0 sturgeon sufficiently developed for fish to show a behavioral preference, or did we only measure behavior that was the result of incomplete visual development? Unfortunately, no hatchling sturgeon have been examined for visual development, so the question cannot be answered. By day 1, both species were strongly photopositive and they remained photopositive while migration continued, then shovelnose sturgeon gradually became more photonegative after day 11. If observations on pallid sturgeon had continued past day 9, they likely also would have become more photonegative, but data are lacking. Increasing photonegative behavior with age was not found for two species of

Acipenser (Richmond & Kynard 1995, Kynard & Horgan 2001), and this is a major difference between *Scaphirhynchus* and the species of *Acipenser* yet studied.

Kynard & Horgan (2001) suggest that a bright habitat enhances the contrast between the background and small active prey to enhance early foraging of sturgeon larvae. Migrant *Scaphirhynchus* showed this preference and the migrating larvae of two *Acipenser* species (shortnose and Atlantic sturgeon) behave similarly (Richmond & Kynard 1995, Kynard & Horgan 2001). However, as shovelnose sturgeon aged, preference for illumination and white substrate decreased. These changes may reflect a change in habitat, a change to foraging that uses vision less (shovelnose sturgeon larvae switched to nocturnal), or both. Because pallid and shovelnose sturgeon were similar for early preference of bright habitat, a similar change with age likely occurs in pallid sturgeon, but data are lacking.

The distance that early life intervals of sturgeons swim above the bottom is believed to be related to migration distance (Pavlov 1994). For example, most sterlet, *A. ruthenus*, early life intervals were captured near the bottom, and the species is believed to move only a short distance, whereas most beluga, *Huso huso*, were captured far off the bottom (including 3% at the river's surface), and the species has a long distance migration. Laboratory studies support the basic idea of Pavlov (1994). Shortnose sturgeon larvae swam a mean of 0.3 m (maximum, 1 m) above the bottom and they move <20 km downstream (Kynard & Horgan 2001); while *Scaphirhynchus* in the present study migrated 12-13 days and moved as far as they could above the bottom. Swimming height above the bottom was strikingly similar between pallid and shovelnose sturgeon, and late migrants showed the ability to move higher than 150 cm above the bottom. The present data suggest that mid and late migrants of *Scaphirhynchus* in rivers may be far above the bottom, even at the river's surface, and move far downstream. Swimming height seems related in a complex way to fish developmental stage, habitat preference, and migratory style, not only to migratory distance.

Migration of pallid and shovelnose sturgeon was similar for timing of migration (initiation and cessation), migration distance, and movement pattern of life intervals (diurnal embryonic migrants moved the most distance and larvae, whether diurnal or nocturnal, moved less). The species were also similar for the development required to become larva (79 CTU for pallid sturgeon on day 4 and 72-78 CTU for shovelnose

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sturgeon on day 4). However, the species differed for migratory rate (pallid sturgeon moved about one-half the rate of shovelnose sturgeon, but they moved the slower rate for more than twice as long) and diel behavior of larvae (pallid sturgeon remained diurnal, while shovelnose sturgeon switched to nocturnal). Behavioral changes as fish developed into larvae suggest a linkage between development, diel behavior, foraging, and migration rate. The species' differences are interesting because both species coexist in the same rivers, and presumably, are subject to similar selective factors. While the factors responsible for evolution of the species' differences await studies of young sturgeon in rivers, selection has clearly favored moving most of the migration distance before larvae begin feeding and must divide their time between migrating and searching for prey. Separating the activities may better optimize both. Spawning reaches used by shortnose sturgeon (Kynard 1997) and pallid and shovelnose sturgeon are typically rocky, fast velocity reaches (Dryer & Sandoval¹); whereas, feeding reaches of shortnose sturgeon larvae and juveniles typically have slower velocity and smaller diameter substrate (Kynard & Horgan 2001). Thus, one factor that could lead to a rapid migration by embryos may be the need to move to a different habitat before fish must find the first food. It is also interesting that the species differed little for total distance moved in the laboratory, suggesting a similar situation may exist in rivers. Further, the remarkable similarity for migration rates of shovelnose sturgeon in fast (1997) and slow (1998) water velocity suggest that fish may adjust their movement rates to the prevailing water velocity, thus insuring fish migrate about the same distance regardless of water velocity. Could this be the mechanism used by young sturgeon to migrate to the same rearing reach each year regardless of river discharge? Information on migratory distance of early life intervals of riverine sturgeon is rare and no information exists for *Scaphirhynchus*.

The migratory style for the first year of pallid and shovelnose sturgeon may be similar to the style of shortnose sturgeon. Shortnose sturgeon have a 2-step migration: an initial short migration by larvae to the first aggregation area of adults downstream of the spawning area, then a second long migration by yearlings and older life intervals that distributes fish to the far reaches of the population (Kynard 1997, Kynard & Horgan 2001, B. Kynard & E. Henyey unpublished data). Although the distributional ranges of shovelnose and pallid sturgeon populations are not known, all information suggests the distance from

spawning areas to the most distant rearing areas is far (Dryer & Sandoval¹). A 2-step migration for pallid and shovelnose seems to be the correct interpretation because recent laboratory studies found cultured yearling pallid sturgeon migrated downstream during summer and fall (B. Kynard & E. Henyey unpublished data).

Both species of *Scaphirhynchus* initiated downstream migration at hatching and several *Acipenser* species of diverse phylogeny also initiate migration as embryos at hatching, i.e., white sturgeon (Brannon et al.⁵); Chinese sturgeon, *A. sinensis*, amur sturgeon, *A. schrenckii*, and Russian sturgeon, *A. gueldenstaedti* (Zhuang 1999); and Siberian sturgeon, *A. baeri* (Gisbert et al. 1999). Thus, migration timing has little value for comparing phylogenetic relationships.

What environmental factor(s) would favor pallid and shovelnose sturgeon embryos migrating with poorly developed senses? Information on the comparative predation on embryos from two sturgeon species suggest that risk of predation may be the major factor that determines whether embryos migrate or remain at the spawning site. Studies on Connecticut River shortnose sturgeon indicated that predation on eggs and embryos at the spawning site was negligible, and embryos remain under cover at the spawning site until they develop into larvae and migrate (Kynard & Horgan 2001). However, two species have heavy fish predation on their eggs and embryos, i.e., Chinese sturgeon are preyed on by copperfish, *Coreius* spp., and other benthic fishes (Deng & Yu 1989, Q. Wei unpublished data) and a similar situation exists for white sturgeon (Miller & Beckman⁶), and both species migrate as embryos (Zhuang 1999, Brannon et al.⁵). Although field data suggest that predation is the major factor responsible for migration of embryos, the need to move to feeding areas before first feeding may also be important.

Several studies found that dark spots and dark vertical bars on the body of fishes function as visual signals for aggregation and group cohesion (Guthrie & Muntz 1993). However, only a few studies are on early life intervals. An aggregation response of *Tilapia* spp. and convict cichlid, *Cichlasoma nigrofasciatum*, young was triggered by simple contrasts of body pattern with

⁶ Miller, A.I. & L.G. Beckman. 1993. Predation on white sturgeon eggs by sympatric fish species in Columbia River impoundments. pp. 343-363. In: E. Beamesderfer & A.A. Nigro (ed.) Status and Habitat Requirements of the White Sturgeon Populations in the Columbia River Downstream from McNary Dam, Volume II, Bonneville Power Admin., Portland.

background (Baerends & Baerends-van Roon 1950, Guthrie 1986): A black spot on a conspicuously moving dorsal fin is used by a small characid, *Pristella riddlei*, to signal conspecifics (Keenleyside 1955). Even fish with poor vision use contrasting dark and light features to signal conspecifics. For example, the electrical fish, *Gnathonemus petersi*, has dark vertical bars used for group cohesion (Tayssedre & Moller 1983). Because of the low light level in rivers (Guthrie & Muntz 1993), and limitations of sturgeon vision, young sturgeon should need a large conspicuous signal. The black-tail of young sturgeon may be such a signal.

Body color of pallid and shovelnose sturgeon day-2 embryos was light grey with a black posterior tail, the black-tail phenotype. The contrasting light body and black-tail and the rapid wig-wag swimming movement made fish visually conspicuous. To compensate for the increased risk of predation this conspicuous trait likely brings, there must be strong advantage(s). Two observations suggest the adaptive significance of black-tail may be as a visual signal among conspecifics. First, black-tail migrants aggregated in shoals (groups of fish that remain together for social reasons, Pitcher 1986). Migrants congregated in fast velocity near the pump, then left and moved downstream in small loose aggregations. Shoaling of Siberian sturgeon, *A. baerii*, larvae was reported by Gisbert et al. (1999), which also have black-tail. Second, tests with shovelnose sturgeon pairs indicated that some behaved differently than solitary fish. Because the visual range of sturgeon near the river bottom is limited, there should be strong selection for fish to stay closely aggregated in order to detect the signal of others.

For black-tail to be an effective signal, black and white vision of sturgeon must be well-developed soon after they hatch. The visual sense of day 5 and older shovelnose sturgeon is well-developed (Sillman et al. 1999). Early development of the visual sense (abundant large rods and three types of cones) is consistent with the idea that early visual development could have co-evolved with the black-tail phenotype. Sturgeon formed shoals and black-tail was developed by day 2, so if our hypothesis is correct, the visual sense should be developed by then. It would be interesting to compare visual development of black-tail species with those that are not black-tail.

The available evidence from several sturgeon species suggests that the significance of body color of early life intervals is related to migration timing. Body colors described so far are of three types: dark body, light body with black-tail (black-tail phenotype), and

light body. Three species (shortnose, Atlantic, and lake sturgeon) have dark bodies (black or brownish black) and migrate downstream as larvae (Kynard & Horgan 2001, E. Kynard & E. Henyey unpublished data). Four species (white, pallid, shovelnose, and Siberian sturgeon, *A. baerii*) have black-tail and all migrate as embryos after hatching (Gisbert et al. 1996, B. Kynard & E. Henyey unpublished data, and present study). Further, if the function of black-tail is for group cohesion, then dark-bodied and light-bodied migrants should not aggregate. No aggregation behavior has been observed by dark-bodied migrating larvae (shortnose, Atlantic, or lake sturgeon) or by light-bodied free-embryo migrants of Chinese sturgeon (Richmond & Kynard 1995, Zhuang 1999, Kynard & Horgan 2001, B. Kynard & E. Henyey unpublished data).

Embryos of two species (Chinese sturgeon and green sturgeon, *A. medirostris*) have a light tan body similar to the color of cave fish. The embryos of both species are also much larger than embryos of most other sturgeons, another characteristic that separates them from other sturgeons. Chinese sturgeon migrate at hatching as embryos, like black-tail species (Zhuang 1999). Migration as embryos likely occurs because there is severe predation on eggs and embryos at the spawning site (Deng & Xu 1989, Q. Wei unpublished data), but black-tail would not be adaptive for Chinese sturgeon if the embryos are in darkness. Measurement of light penetration at the 15–20 m deep spawning site of Chinese sturgeon downstream of Gezhouba Dam, Yangtze River, with a Li-Cor photometer in 1995 found natural illumination did not penetrate deeper than 1 m depth (zero lux at 1 m depth, B. Kynard unpublished data). If this illumination condition is typical of historical spawning sites, then a visual signal like black-tail would not be adaptive. The light body of green sturgeon embryos and larvae may, like Chinese sturgeon, be related to rearing in deep water without illumination, but information on spawning sites of green sturgeon is lacking. We identified three types of body color; others may be found.

The discovery of aggregation behavior and a possible adaptation for communication in *Scaphirhynchus* has implications for the life history of other species with black-tail. This phenomenon deserves additional study. Social interaction among cultured shortnose sturgeon competing for food was reported by Kynard & Horgan (2001). Social behavior appears widespread and complex in sturgeons and provides important research opportunities.

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Acknowledgements

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