

Ontogenetic behavior of Kootenai River White Sturgeon, *Acipenser transmontanus*, with a note on body color: A laboratory study

Boyd Kynard · Erika Parker · Brian Kynard

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Abstract Laboratory studies indicated the following ontogenetic behavior and body color of wild Kootenai River White Sturgeon, *Acipenser transmontanus*, (hereafter, Kootenai Sturgeon), a landlocked population in the Kootenai River, a major tributary of the Columbia River (United States) and Kootenay Lake (Canada). Hatchling free embryos (hereafter, embryos) are photonegative and hide under cover at a spawning site, and have a grey body. Late-embryos are photopositive and weakly prefer white substrate, use cover less with age, and develop a black tail. Day 13 larvae forage in the day on the open bottom, use cover less with age, prefer bright habitat, have a light-grey body and black tail, and initiate a mostly nocturnal dispersal for about 21 days, and then, continue a weaker dispersal. As they age, the entire body and tail of larvae is a dark-grey color when they develop into juveniles (about 66 days). The

common body and tail color of larvae from the Kootenai, Columbia, and Sacramento rivers indicate a common adaptation to signal conspecifics or avoid predators. Juveniles are variable for foraging height, do not hide in bottom cover, and continue a weak nocturnal downstream movement. Movement of larvae and juveniles in the artificial stream suggests wild Kootenai Sturgeon have a long slow dispersal style (disperse for months). The long dispersal style of young Kootenai Sturgeon may adapt larvae to dispersing all summer in a 100–200 km long reach with a low abundance of food. The final destination of Kootenai Sturgeon during their first rearing season is unknown, but the long dispersal suggests fish could easily move to the lower river or to Kootenay Lake. Ontogenetic behavior of Kootenai Sturgeon is slightly different from Columbia River White Sturgeon, which has a weak embryo dispersal, but both populations have a similar major dispersal by larvae. However, both of these populations differ qualitatively from Sacramento River White Sturgeon, in which juveniles initiate the major dispersal. Thus, major geographic behavioral variation exists among populations and should be considered in restoration programs.

B. Kynard · B. Kynard
BK-Riverfish LLC,
28 Echo Hill Road,
Amherst, MA 01002, USA

B. Kynard · E. Parker
Leetown Science Center (U. S. Geological Survey),
S. O. Conte Anadromous Fish Research Center,
One Migratory Way,
Turners Falls, MA 01376, USA

B. Kynard (✉) · B. Kynard
Department of Natural Resources Conservation,
University of Massachusetts,
Amherst, MA 01003, USA
e-mail: drboyd@nrc.umass.edu

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Introduction

Common garden experiments have observed ontogenetic behavior of sturgeon early life stages, i.e., free

embryos (hereafter embryos), larvae, and juveniles, from many species in the same artificial environments. These studies found differences in habitat preference and downstream movement style among species (Kynard and Horgan 2002; Zhuang et al. 2002; Kynard and Parker 2004, 2005; Kynard et al. 2007).

Similar experiments in the artificial environments also revealed geographic differences in ontogenetic behavior between river populations of the same species. Qualitative differences in downstream movement style were found between northern and southern populations of shortnose sturgeon, *Acipenser brevirostrum* (Kynard and Horgan 2002; Parker 2007) and between Atlantic coast Atlantic sturgeon, *A. oxyrinchus oxyrinchus*, and Gulf of Mexico sturgeon, *A. oxyrinchus desotoi* (Kynard and Horgan 2002; Kynard and Parker 2004). Quantitative differences have been found between river populations of Lake Sturgeon (Kynard and Parker unpublished data).

Despite the decline in abundance of many White Sturgeon populations, early life history of most populations is poorly studied. A laboratory study provides the best behavioral information on White Sturgeon embryos and larvae from the free-swimming lower Columbia River population (Brannon et al. 1985). This study found a weak dispersal by embryos and a major dispersal by larvae. Later, a field study by McCabe and Tracy (1994) verified the early dispersal by capturing larvae far downstream from the spawning site. A recent study by Kynard and Parker (2005) on Sacramento River White Sturgeon (hereafter, Sacramento Sturgeon) found an initial weak downstream movement by embryos (like that found in Columbia Sturgeon), and later, no downstream movement by larvae, and instead, an intense downstream movement by juveniles.

Kootenai River White Sturgeon (hereafter, Kootenai Sturgeon) is a federally protected land-locked population that occupies Kootenay Lake, British Columbia, Canada, and spawns in the Kootenai River, a headwater tributary of the Columbia River (Duke et al. 1999). A few wild larvae have been captured dispersing from spawning sites, so larvae and juveniles must rear somewhere in the Kootenai River. Recruitment failure in this population is believed related to spawning failure, the inability of one or more early life stages to survive, or both. This situation may be related to alterations of the river ecosystem (Paragamian et al. 2001; Anders et al. 2002).

Like the previous common garden experiments with young sturgeons (Kynard and Horgan 2002; Kynard and Parker 2004, 2005), we studied ontogenetic behavior of Kootenai Sturgeon as fish developed from hatchling embryos, to larvae, and to juveniles. The following behaviors were observed, but not all life stages were observed for each behavior: (1) swimming height, (2) preference for illumination vs. darkness, (3) preference for white vs. black substrate, (4) selection of bottom habitat, including cover use, and (5) downstream movement. To test the null hypothesis of no behavioral difference among Kootenai, Sacramento, and Columbia sturgeons, we compared their ontogenetic behaviors, particularly dispersal styles. We also review the implications of Kootenai Sturgeon dispersal on population restoration.

Methods

Laboratory methods generally follow those used for Sacramento Sturgeon (Kynard and Parker 2005). We obtained fertilized eggs from the artificial spawning of a pair of wild Kootenai Sturgeon captured in the Kootenai River in the spring, 2005. Fertilized eggs were placed in ambient river water and shipped overnight to us. We received eggs on 15 June 2005.

All rearing and experiments were done in facilities at the S.O. Conte Anadromous Fish Research Center, Turners Fall, MA. We used dechlorinated city water (Montague, MA) for all rearing and experiments. Temperature in rearing and test tanks was similar ($\pm 1^\circ\text{C}$). Fish experienced the natural photoperiod for Turners Falls, MA.

We reared eggs in a McDonald hatching jar and hatchling embryos swam from the hatching jar in over-flow water into two 18-L circular flow-through rearing tanks, which had several rocks on the bottom for cover. We reared fish in these tanks until fish were larvae and had been feeding for about 2 weeks, and then, we moved them to a larger 50-L circular rearing tank and maintained the same feeding regime. Rock cover was removed in the large tanks because larvae did not use cover and keeping tanks clean was easier without it.

We fed larvae and juveniles a commercial food (Bio-Oregon, Inc., Longview, WA) beginning with starter size and increasing food size as fish grew. Fish were fed six–eight times day and night using a timed

feeder. Early-larvae were also fed four times daily with live *Artemia* nauplii for 10 days. Except for long-term observations on fish for downstream movement, we did not feed fish during any behavioral test.

To link daily behavior and development, we scaled fish development to daily cumulative water temperature (CTU). We recorded temperature (°C) every 2 h and determined the mean daily temperature to the final day of observation. Daily temperatures were sequentially added to obtain the total cumulative temperature units (CTU) for each day. The starting time for the 24-h cycle used to calculate CTU was 2400 h (the estimated time of first hatching).

We characterized body and tail color of embryos, larvae, and juveniles using Hype's Color for Netscape v. 3. We were particularly interested in whether fish developed into the black-tail phenotype like Sacramento Sturgeon (Kynard and Parker 2005). The black tail color of black-tail phenotypes remain on fish that die. Kootenai Sturgeons examined for body and tail color were not sacrificed. We used the first day that the stomachs of five fish contained food (began foraging) as the beginning of the larval interval. We examined fins of five larvae every few days to determine the approximate day and CTU when fish developed into juveniles (fish with the adult number of fin rays).

In all daily experiments, we mixed about 800 rearing tank fish and randomly selected fish for tests, then after tests, returned fish to the rearing tank. No individual was tested twice in the same day, but there was a small chance a fish could be captured and used in later tests. The random selection and capture process using a suction tube or small net provided a non-selected group of test fish for daily experiments.

Swimming height and cover use

Vertical stream tank, 150 cm high × 15 cm diameter

On each test day, we tested eight fish in a tank that simulated a vertical section of water with a horizontal low-speed water velocity ($2 \text{ cm}\cdot\text{s}^{-1}$; Fig. 1a). Illumination level (top to bottom) was 300–50 lux to 30–5 lux depending on time of tests, so we tested fish at the same time each day to have a similar illumination regime. Previous tests found no effect of illumination level on swimming height of ELS in the tank (Kynard et al. 2002). To give fish a choice of bottom habitat,

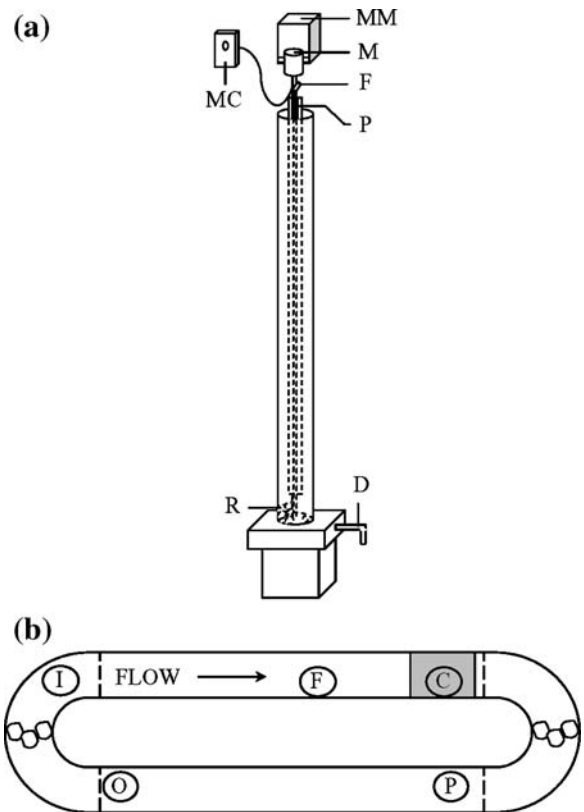


Fig. 1 Panel **a** shows the small vertical stream tank (water depth, 150 cm; diameter, 15 cm) used to observe swimming height of Kootenai Sturgeons. Component key: M = motor, MM = motor mount, MC = motor control, F = fish introduction tube, P = paddlewheel, R = rocks, and D = drain. A rotating paddlewheel created clockwise horizontal water current (velocity, $2 \text{ cm}\cdot\text{s}^{-1}$). Fish were introduced through the long tube that ended 8 cm above the bottom. Fish using the bottom had a choice of rock cover on one-half of the bottom or open habitat on the other one-half. Panel **b** shows the oval artificial stream (32 cm wide \times 7.3 m circumference; water 20 cm deep; and mean velocity 2.5 cm above the bottom = $7 \text{ cm}\cdot\text{s}^{-1}$) used to observe downstream movement and habitat use. Three rocks at each end of the tank provided cover. Tank features follow: *arrow* = flow direction, *I* = water inflow, *O* = water outflow, *P* = submerged pump, *F* = feeder, *C* = video camera + infrared light, *shaded area* = field of view

cover (a 10-cm high pile of 5-cm diameter gray pebbles) covered one-half of the bottom and the other one-half of the bottom was open.

During tests, we poured a single fish and water into the top of the introduction tube, which carried fish down to 6 cm above the bottom. After a 5-min acclimation period, we visually recorded swimming height of each fish for 60 s, recording a fish's location each 10 s (total measurements = 7). We used a depth

scale (1-cm marks with 0 = bottom) inscribed on the outside of the tank to determine fish height. For analysis of swimming height, we calculated the mean of the seven samples and present the grand mean (\pm SE) for all fish as a daily time series. We compared the mean daily swimming height of Kootenai vs. Sacramento Sturgeon embryos (Kynard and Parker 2005) using *t*-tests.

For use of the bottom and bottom cover, we counted the number of fish each day that used the bottom and the number of these fish that used cover. We present the data as a daily time series of the percent of all fish that used the bottom and the percent of these fish using cover.

Vertical stream tank, 175 cm high \times 60 cm diameter

We observed days 42–79 larvae and juveniles in a large vertical stream tank (not shown, but the same design as the tank in Fig. 1a). Six 10-cm diameter rocks provided bottom cover.

We introduced five fish and water into the top of the tank by pouring from a 1-L bucket. After 1 h acclimation, we recorded the swimming location of each fish as (1) on the bottom, or (2) above the bottom. We also measured the swimming height of each fish to the nearest centimeter (scale on outside of tank). We characterized fish that swam above the bottom as (1) in the water column—fish oriented with ventral surface of body away from wall and body not contacting the wall, or only the tips of pectoral fins touching the wall, or (2) along wall—fish swimming along the wall with their ventral body toward wall, either contacting or close to wall.

We observed the point location (centimeters above the bottom) of each fish at 30 sec intervals for 5 min (total measurements = seven per fish). Fish were not individually marked, so two observers visually followed individual fish at the same time. We did two replicates (ten fish total) each test day. Illumination in the tank during tests was ≤ 400 lux.

Illumination and bottom color preference

We tested 10 single fish each day for preference of illuminated vs. dark habitat and for preference of white vs. black bottom color. We used two 20-L rectangular glass tanks with overhead light provided by two 20-W fluorescent lights and black plastic

around the tanks to exclude other light. We tested illumination preference using a tank with a black cover over one-half of the aquarium's top to divide the tank into equal areas of bottom illumination (8.2–3.0 lux) and dark (2.2–0 lux). The bottom color tank gave fish a choice of white vs. black bottom. The bottom of the tank was clear glass, and under the glass, black and white plates created equal areas on the length of the tank's bottom. Underwater light intensity on the bottom was similar on both sides, e.g., 4.3–2.6 lux (white side) and 3.3–3.0 lux (black side). In both illumination and bottom color tests, we reversed habitat position after each fish to prevent side bias.

During tests, we placed a fish at the water surface in the center of the aquarium. After 1-min acclimation, we visually recorded fish movement for 60 s as a continuous time series of fish presence on each habitat type (dark vs. illuminated side or white vs. black bottom). We calculated the percent of time the fish spent in each habitat and the daily mean percent of time all fish spent in each habitat, and plotted the percent as a daily time series. We transformed the daily percentages on one of the two habitats to arcsine values and calculated binomial 95% confidence intervals to determine if the percent of time fish spent in the selected habitat was significant (confidence intervals that included 50% were not significant).

Downstream movement and diel activity

We daily observed up- and downstream movements of 15 fish (introduced as day-0 embryos) in an oval, endless stream tank colored light green-blue (Fig. 1b). The tank was 7.3 m circumference \times 32 cm wide with water 20 cm deep. Underwater light intensity was ≤ 20 lux. In- and outflow of water was $1 \text{ l}\cdot\text{min}^{-1}$. Three rocks (each 10–15 cm in diameter) in the two turns of the channel provided cover (structure, low light, and a slower velocity). Current velocity measured each 50 cm in the center around the tank was $3\text{--}9 \text{ cm}\cdot\text{s}^{-1}$ (mean, $7 \text{ cm}\cdot\text{s}^{-1}$).

Fish were observed each hour, 24 h per day from hatching (day 0) using a video camera and infrared (IR) light over the stream (Fig. 1b). White Sturgeons do not see IR light until they are several months old (Loew and Sillman 1993), so fish should not be affected by the IR light at night. If a fish died, it was replaced with a fish from the rearing tank. Fish were

not identified individually, so we counted the number of fish passes around the tank at one site as a measure of downstream movement intensity. Silver reflective tape covered surfaces in the video field-of-view to enhance observing the small fish at night. We observed fish movement for 5 min per hour for 24 h and reviewed videotapes counting the number of up- and downstream fish passes for every other hour. We scaled the number of fish passes to the number of fish in the tank each day, usually 15, but sometimes 14, as a fish that died was not replaced until after live observations on habitat use. We show the data in two daily time series with age: one showing the number of daily fish passes and one showing the day vs. night trend in daily fish passes.

Habitat selection

In the oval stream during five daytime observation periods each day, we visually determined the number of the 15 fish that were in four habitat types: on the bottom under rocks, on the bottom in the open, in the water column (>3 cm above the bottom), and at the water surface. At the same time, we counted the number of fish that were moving downstream. We calculated the grand total of fish in each habitat type (including moving downstream) on each day and present the percent in each category as a daily time series. The same method was used to characterize habitat use by young Gulf of Mexico and Sacramento Sturgeons (Kynard and Parker 2004, 2005).

Results

CTU and body color

Body and tail color of day-0 hatchling embryos was a light gray (gray 81). Body color of day-7 embryos (CTU 104) was still a light gray, but 3–4 mm of the tail tip was black, i.e., the black-tail phenotype. Days 8–12 embryos also had light bodies and black tails.

Body color of day-13 larvae (CTU 230) was a darker medium gray (gray 51) and the black on the tail had expanded to cover the posterior 7–8 mm of the body. Body color of larvae gradually became darker (body of day-19 larvae was a darker gray, gray 11), but the tail tip remained black. The black tail was most evident during the late-embryo and early-larva

stages, although the tail tip remained black during the entire larval stage.

Larvae developed into juveniles on about day 66 (1266 CTU). Body color of juveniles was a medium (gray 51) or dark gray (gray 11) except for the tail tip, which was still black.

Not all larvae developed into the black-tail phenotype. The body of some fish remained light gray (even lighter than same-age black-tail morphs). Thus, there were two body-color morphs (black tail and gray). Eventually, the number of gray fish decreased either due to mortality or to fish gradually developing a dark body.

Swimming height and use of cover in vertical stream tanks

Embryos swam low, swam high, swam low, and swam high with age (Fig. 2a). However, most fish also used the bottom and most of these fish used cover (Fig. 3). The up and down pattern of fish using cover with age was similar to the up and down pattern for swimming height in Fig. 2a.

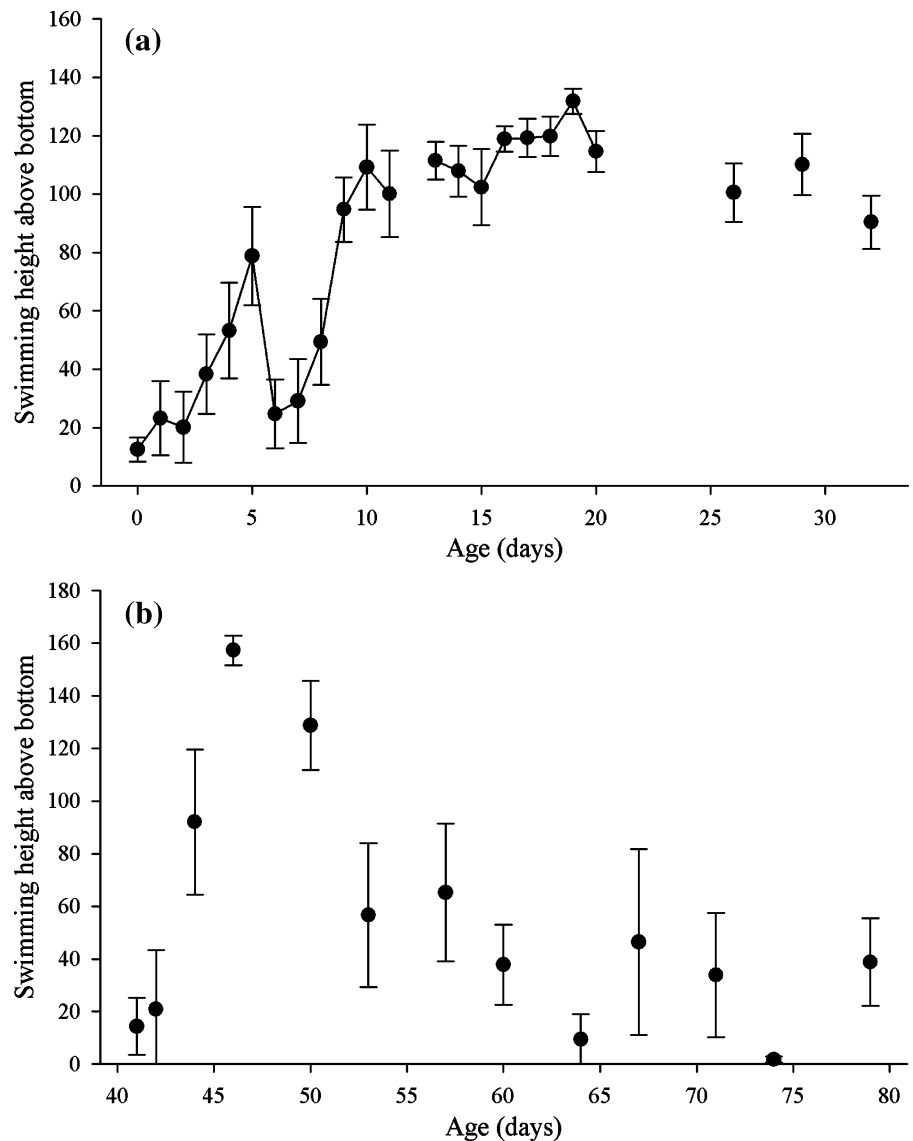
Days 9–12 embryos increased swimming height to 100 cm or higher (Fig. 2a). All day-8 embryos used bottom cover (Fig. 3), so the change to swim high occurred quickly.

Days 13–32 larvae swam a mean height of 111.5 cm (SE = 3.4 cm; daily mean range, 90–132 cm; Fig. 2a). Swimming was not fast at the water surface, indicative of escape behavior; instead, each day's fish, regardless of age, swam-up to about the same height and remained swimming there. Of the 88 larvae observed during the 11 days, none swam near the bottom.

Swimming height in the large vertical stream tank by days 41 and older fish, using only fish swimming in the water column (daily mean swimming height for 13 days) was 64.7 cm (SE = 17.4; range, 9–160 cm; Fig. 2b). Swimming height of days 41–64 larvae showed a trend to decrease swimming height, except on days 41 and 42, when fish swam low (20 cm above the bottom). Fish did not use rock cover even when swimming on the bottom.

Swimming height of larvae and juveniles was of two types: 1) bottom fish—fish that swam on the bottom or along the lower tank wall, and 2) variable-height fish—fish that swam on the bottom and also along the walls and in the water column. Larvae

Fig. 2 Panel **a** shows the mean ($\pm 95\%$ CI) swimming height of embryos and larvae in the small (150 cm high \times 15 cm diameter) vertical stream tank. Panel **b** shows the mean ($\pm 95\%$ CI) swimming height of late-larvae and juveniles in the large (175 cm high \times 60 cm diameter) vertical stream tank. N = daily number of fish swimming in the water column not in contact with the side of the tank



swimming in the water column swam with and against the current. Except when days 44, 46, and 50 larvae swam a mean of 90, 160, or 130 cm high, the mean daily swimming height of fish was <70 cm above the bottom.

During 4 days of observations on days 67–78 juveniles, all fish swam near or on the bottom (<50 cm high; Fig. 2b). Although many fish swam on the bottom, none used rock cover.

Illumination preference

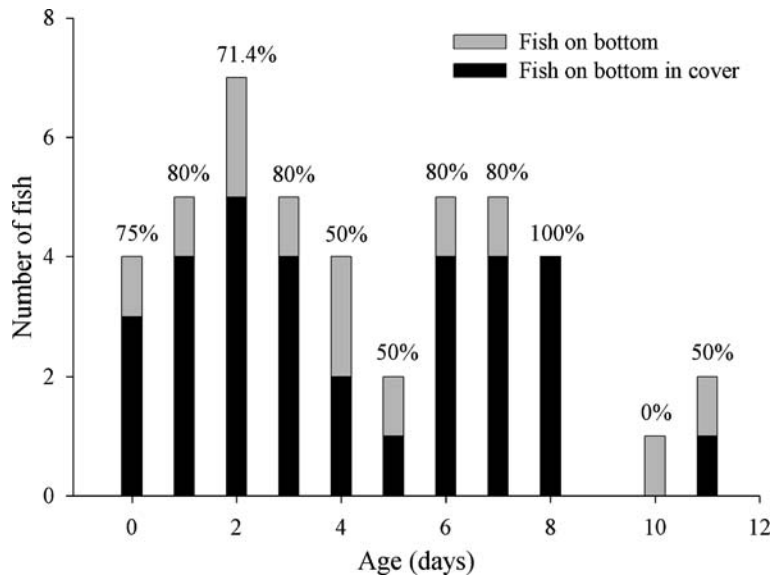
Days 0–7 embryos were strongly photonegative, avoiding illumination on all days, except on day 4,

when fish had no preference (Fig. 4). The time spent on the illuminated side with age follows: a short time (days 0–2), the longest time on day 4, and decreasing to a short time on day 7. These changes with increasing age were similar to the timing of changes in swimming height by embryos (low–high–low–high; Fig. 2a).

Days 8–12 embryos changed from no preference on day 8 to a strong photopositive response on day 9, which continued on the following days (Fig. 4). This change in photo-response in 24 h shows how quickly a major response to the environment can switch during early development.

Days 13–38 larvae strongly preferred illumination on most days (Fig. 4). With increasing age,

Fig. 3 Number of fish using the bottom and cover during the daily observations of swimming height of eight fish. Percent of fish using cover is shown above each bar

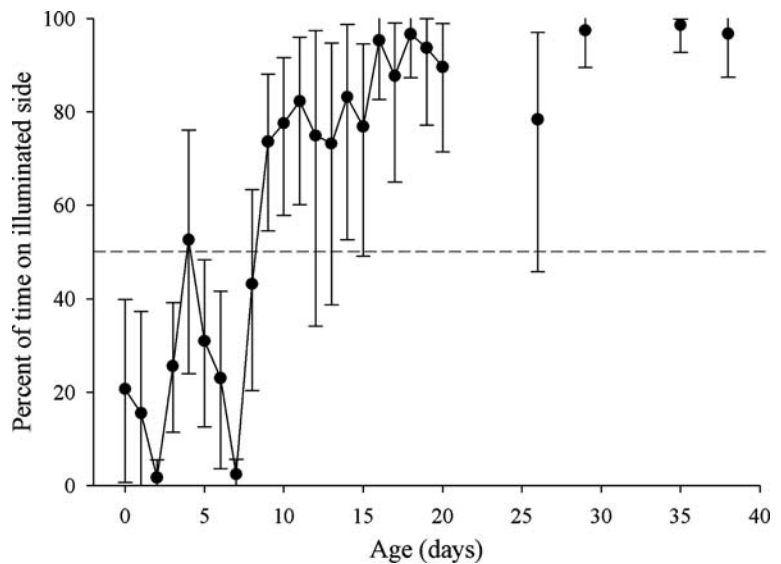


there was less variation among test fish for illumination preference.

Bottom color preference

Days 0–7 embryos weakly preferred black bottom, with the strongest preference on day 3 (when preference was significant) and day 4, when preference was not significant (Fig. 5). Days 8–12 embryos weakly preferred white bottom, but preference was only significant on day 8.

Fig. 4 Means and 95% CI of percent time fish spent on the illuminated side of the illumination intensity choice tank. Confidence intervals that include 50% (indicated by dashed line) show preference is not significant

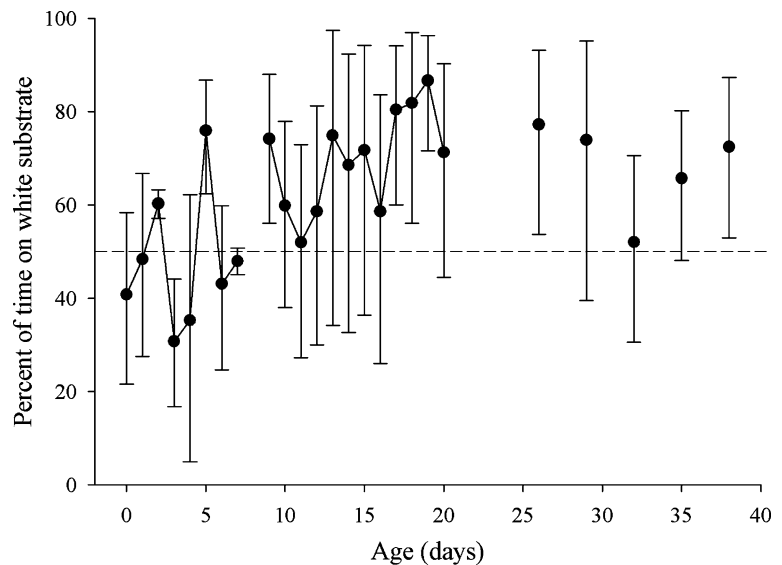


Larvae observed periodically from days 13–38 always spent more time on the white bottom (Fig. 5). However, the preference was weak and not significant on most days.

Downstream movement and diel activity

We observed up- and downstream movements (net number of fish passes per fish) from 19 June (day-0 embryos) to 4 September (day 77 juveniles; Fig. 6a). Days 0–7 embryos weakly moved downstream in the day

Fig. 5 Means and 95% CI of percent time fish spent on the white side of the bottom color choice tank. Confidence intervals that include 50% (indicated by *dashed line*) show the preference is not significant



and night (weak night peak) and movement decreased daily. Most days 8–12 embryos hid under cover during the day, but twice as many downstream passes occurred at night compared to days 0–7 embryos, particularly near the end of the embryo stage on days 11–12.

Days 13–42 larvae initially continued the same level of downstream passes as late-embryos, and then, exhibited a 21 day period (days 21–32) of increased downstream movement (Fig. 6a). Within this period, the first peak was slightly greater than the second peak. Most movement was nocturnal, but during the peak period, the level of daytime fish passes was the highest for all days. Days 43–65 larvae and days 66–78 juveniles continued a weak downstream movement. There was a strong drive by larvae and juveniles to move downstream, not upstream. The only upstream movement was the weak daytime movement that increased with age of late-larvae and early-juveniles (Fig. 6a). This movement was likely related to foraging (as determined by observing fish feeding on drifting food).

The level of daily activity (combined scaled numbers of up- and downstream fish passes for day vs. night) increased with fish age (Fig. 6b). The greatest level of activity was always at night, but during the movement peak (days 21–42), activity in the day reached its highest level. Days 66+ juveniles also moved mostly at night.

During daytime visual observations in the oval stream on days 0–8 embryos, 5–65% of the 15 fish (1–10 fish) were moving downstream (Fig. 7). When

fish developed into larvae, downstream movement in the day slowed greatly (movement was at night), so counting the number of downstream migrants was not possible during our brief daytime observation period. Fish appeared to be foraging during the day. The increasing percent of larvae we observed swimming in the water column or at the surface with increasing age (5–20% of the 15 fish; Fig. 7) were likely the same few fish the camera recorded as moving downstream in the day.

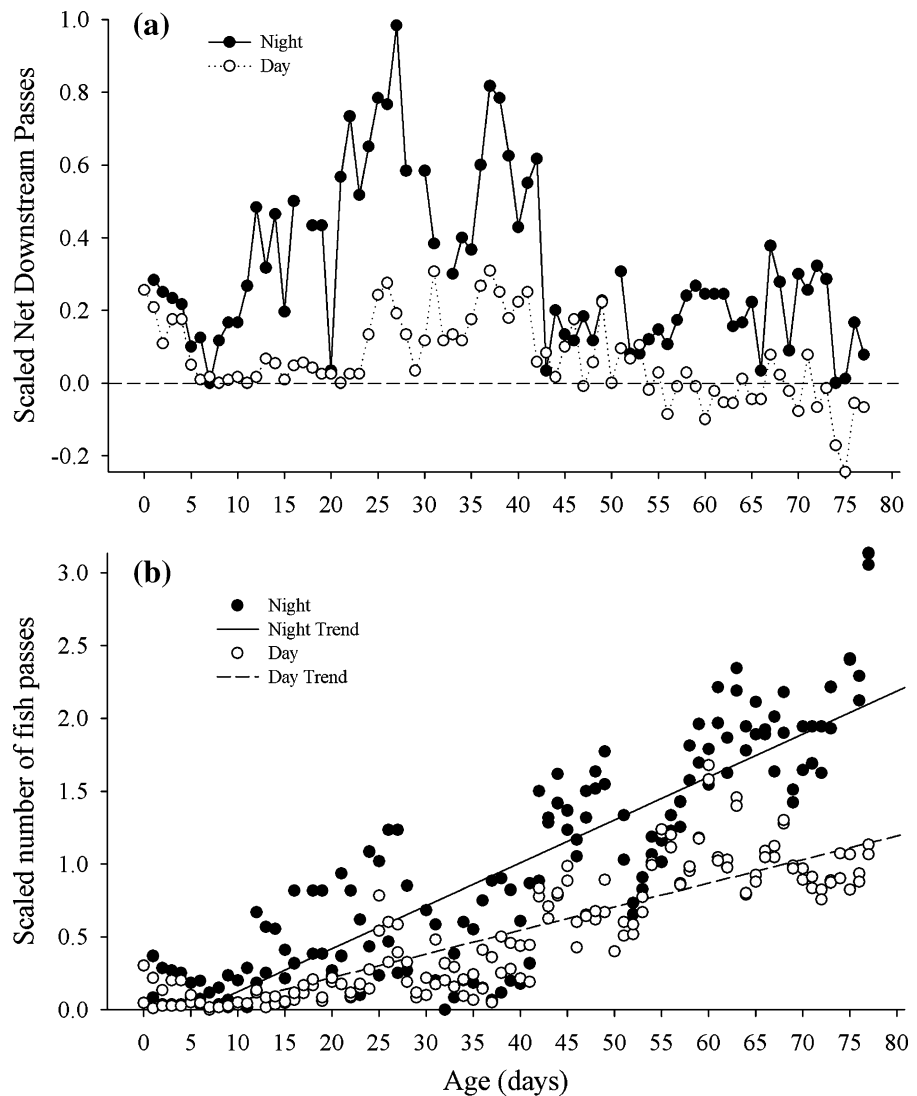
Habitat selection

In addition to a decreasing percent of fish moving downstream with age, there was a strong trend with increasing age of fish (to day 20) for the following habitat selection: (1) a decreasing use of rock cover, and (2) an increasing use of the open bottom, the water column, and the surface (Fig. 7). The percent of fish hiding in rocks decreased daily as embryos developed into larvae.

The percent of larvae (days-13 and older fish) using cover decreased to zero by day 19 (Fig. 7). Most larvae ($\geq 80\%$) were on the open bottom and foraging during the daytime, but a few swam in the water column, even to the surface.

During daytime observations in the oval stream tank and in the large vertical stream tank, larvae and juveniles used the open bottom, not rock cover. Although fish swam around and over rocks, none stopped under rocks.

Fig. 6 Graph of downstream movement intensity and activity with increasing age of fish. Panel **a** shows the daily scaled net number of fish passes for day and night. Positive numbers = downstream movement; negative numbers = upstream movement. Panel **b** shows scaled mean number of daily up- and downstream fish passes (as a measure of activity) for day and night. Linear regression shows trends for day and night activity with age of fish



Discussion

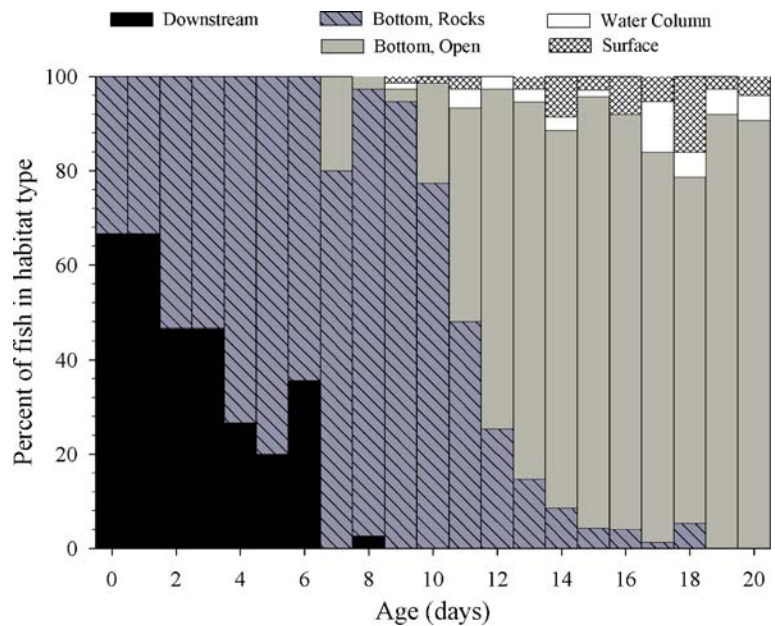
Swimming height

In the small vertical tank with a horizontal current top to bottom of $2 \text{ cm}\cdot\text{s}^{-1}$, embryos spent time on the bottom in cover, but also left the bottom and swam above the 10-cm high rock cover. Swimming above bottom cover was different from embryos in the oval stream, where fish not moving downstream hid in cover. Further, the behavior of embryos in both these tanks was different from embryos in later studies where all fish hid under rocks if abundant cover was present (Kynard et al. 2008). The swimming height of embryos in the small vertical stream tank was

abnormal behavior likely caused by a sensitivity to handling or a short acclimation period. Embryos of some *Acipenser* species quickly hide in rocks in this stream tank after a short acclimation period (Kynard and Horgan 2002; Kynard and Parker 2004), suggesting Kootenai Sturgeon embryos are sensitive to handling.

Our interpretation of larvae swimming day after day to about 100 cm follows: in the small vertical stream tank, the disturbed fish (which would normally be foraging on the bottom in the day) were selecting to swim about 100 cm above the bottom rather than seek bottom cover. The similar swimming height day after day suggests disturbed fish were moving to a position of safety above the bottom. If correct, this swimming height may also reflect the swimming

Fig. 7 Percent of fish by age observed using four habitats (surface, water column, open bottom, or bottom cover) or moving downstream in the oval stream



height of fish at night during dispersal, when safety from bottom predators could also be important. Dispersing late-embryos of Pallid Sturgeon, *Scaphirhynchus albus*, in the same vertical stream tank swam the same swimming height day or night (Kynard et al. 2007). The variable swimming height of Kootenai Sturgeon larvae and juveniles in the large vertical stream could reflect the ability to forage widely on the structurally and vertically complex bottom in the lower Kootenai River (Kynard et al. 2008).

Bright habitat preference

Embryos and larvae had a qualitatively different response to illumination and bottom color. However, whether fish were avoiding or preferring bright habitat, the response to illumination and bottom color was similar, and possibly linked. The strongest preference by embryos or larvae was always to illumination level, not to bottom color.

The preference for high illumination intensity was independent of cover preference by late-embryos. We expected photopositive fish would also always avoid cover, and vice versa, and this was the case for early-embryos and larvae. However, this was not the case for late-embryos because they were photopositive (present study), yet preferred to hide in cover (Kynard et al. 2008).

Downstream movement

A long slow dispersal–rearing style lasting 5 months or more by larval and juvenile Suwannee River Gulf of Mexico Sturgeon (*A. oxyrinchus desotoi*) was observed in the oval stream used in the present study (Kynard and Parker 2004). Further, field captures of year-0 juveniles by K. Sulak (U.S. Geological Survey unpublished data) in the 200 km long rearing reach supported the slow dispersal style observed in the oval stream. Gulf of Mexico sturgeon may have evolved this slow dispersal because it is about 200 km from spawning sites to the estuary (spatial goal of the freshwater dispersal), forage abundance in the river is low, and juveniles cannot move directly downstream and enter the estuary until they develop salinity tolerance after about 10 months.

The 2-month downstream movement by Kootenai Sturgeon larvae and juveniles in the oval stream suggests wild larvae and juveniles have a slow dispersal lasting 2 or more months. This dispersal style indicates no rearing reach with abundant forage exists close to the spawning area, because in this case, other studies on sturgeons found downstream movement in the oval stream stops within 2 weeks (Kynard and Horgan 2002).

Habitat use

Habitat use changed with ontogeny, with embryos using rock cover and larvae and juveniles using the

open bottom. The few embryos moving downstream in Fig. 7 would be hiding in rock cover and not moving downstream if more cover was available (Kynard et al. 2008).

Geographic variation

Body color

Most Kootenai Sturgeon late-embryos and larvae were the black-tail phenotype (gray body with black tail), which is similar to Sacramento Sturgeon (Kynard and Parker 2005) and lower Columbia River Sturgeon (Joel Van Eenennaam Univ. Calif., Mike Parsley U.S. Geol. Survey pers. comm.). Thus, the black-tail phenotype is present in two coastal populations and one land-locked population in very different riverine environments. Also, the black-tail phenotype is adaptive whether larvae are dispersing (Kootenai and Columbia Sturgeons) or not (Sacramento Sturgeon), suggesting the character has a common selective value for signaling conspecifics or avoiding predators.

The presence of two body color morphs (black tail and gray) in Kootenai Sturgeons was unexpected. If the morphs are a genetic polymorphism, perhaps they evolved to avoid predators differently, e.g., a black-tail morph, using wigwag swimming and a black tail to evade a predator's strike (Buskirk et al. 2004), and a gray morph, using camouflage to avoid detection by predators. Body color morphs need study as they may give clues to selective factors on larvae.

Swimming height

The pattern of swimming height in the small vertical stream by Kootenai Sturgeon embryos with increasing age (low-high-low-high) was different than the pattern of Sacramento Sturgeon, which swam high-low-high-low with increasing age (Kynard and Parker 2005). Comparison of the daily mean swimming height of embryos found significant differences between the two populations for days 0–2 ($P=0.008$). The difference between the populations for swimming height of early-embryos may be related to the weak drive by Sacramento Sturgeon to move downstream and a lack of this drive by Kootenai Sturgeon (see Dispersal Style under Geographic variation section).

Bright habitat

Kootenai Sturgeon larvae preferred bright habitat (present study), whereas Sacramento Sturgeon larvae did not (Kynard and Parker 2005). This is a qualitative difference between the two populations. A preference for bright habitat indicates vision is important for daytime foraging (Kynard and Horgan 2002); if correct, Sacramento Sturgeon may use olfaction and other senses to locate food.

Cover use

Kootenai Sturgeon larvae ceased using cover by day 19, with few using cover after day 14, when downstream movement increased. In contrast, Sacramento Sturgeon larvae used cover to day 26 (Kynard and Parker 2005). This suggests optimal daytime foraging for dispersing Kootenai Sturgeon larvae is on the open bottom; whereas, optimal foraging for non-dispersing Sacramento Sturgeon larvae involves using cover.

Dispersal style

Kootenai Sturgeon early-embryos lacked a downstream movement and hid in cover, which is a qualitative difference from the weak downstream movement of Sacramento and Columbia Sturgeon embryos (Brannon et al. 1985; Kynard and Parker 2005; present study). Although a few Kootenai Sturgeon embryos moved downstream, this movement did not occur in later studies, when bottom cover was abundant (Kynard et al. 2008). The initial weak dispersal of Sacramento and Columbia Sturgeon embryos is likely a common adaptation to move hatchlings away from spawning sites to avoid predators and reduce density of larvae when they begin to forage. Because this movement is found in two coastal populations, it likely exists in other coastal populations.

Because Sacramento Sturgeon embryos were also observed in the oval tank with few rocks for cover, their weak downstream movement could also be related to scarce rock cover. However, Sacramento Sturgeon embryos had a stronger drive than Kootenai Sturgeon to move downstream (mean, 1 downstream pass for Sacramento Sturgeon vs. 0.2 passes per 5 min for Kootenai Sturgeon). Sacramento Sturgeon embryos are likely similar to Columbia Sturgeon that swam

above the bottom even when rock substrate was abundant (Brannon et al. 1985).

The same life stage (larva) initiates the major dispersal in Kootenai and Columbia Sturgeon populations, which is a qualitative difference with Sacramento Sturgeon, where juveniles initiate the major dispersal (Brannon et al. 1985; Kynard and Parker 2005; present study). Further, McCabe and Tracy (1994) found wild Columbia River Sturgeon larvae were distributed over >200 km 2 months after spawning. This pattern may be similar to wild Kootenai Sturgeon.

A behavior shared by the three White Sturgeon populations is a nocturnal dispersal. No matter whether the major dispersal is by juveniles or larvae, most movement is nocturnal (Brannon et al. 1985; Kynard and Parker 2005; present study). This behavior may be a common response to a common selective factor present in all rivers (perhaps, avoiding predators).

Dispersal timing in river populations of White Sturgeon is subject to strong local adaptation. A similar local adaptation has been found among populations of other sturgeon species (Kynard and Horgan 2002; Kynard and Parker 2004; Kynard and Parker unpublished data). This has great biological implications for stocking of young sturgeons in restoration programs.

Summary and population restoration

The hypothesis that landlocked Kootenai Sturgeon has the same early behavior as coastal White Sturgeon populations is rejected. There is a qualitative difference between Kootenai and Sacramento Sturgeon for the life stage initiating the major dispersal. Although a difference in early-embryo dispersal exists between Kootenai and Columbia Sturgeon, the two populations are similar for the life stage (larva) initiating the major dispersal. Dispersal by juveniles occurs in both the Sacramento and Kootenai Sturgeons (Kynard and Parker 2005; present study), and may also occur in Columbia Sturgeon, but data are lacking.

The study provides the first conceptual model of habitat use and movements by life stage during the first months of life of the federally protected Kootenai Sturgeon. It also identifies for the first time that Kootenai Sturgeon larvae and early-juveniles are not near the spawning reach, and instead, use a long

dispersal-rearing reach. This reach needs study and protection.

We also identified the period of time (about 1 month) that early life stages are present at a spawning site and need protection. Fertilized eggs and embryos can be disturbed by a sudden release of water discharge by a dam (M. Kieffer and B. Kynard unpublished data). Water releases from Libby Dam in Montana control the temperature and river flow where young Kootenai Sturgeon live and deposit sediment in spawning and rearing areas, which can result in the death of eggs (Kock et al. 2005).

Although the present study revealed that larvae move far downstream from the spawning reach during summer, it did not identify the dispersal's spatial goal because fish did not stop moving downstream, even after developing into juveniles. Presently, adults spawn at Kootenai River km 230–245 at the head of the sandy meandering reach, which extends 110–125 km upstream from Kootenay Lake (Paragamian et al. 2001). Although historical details are lacking, adults likely spawned up to 100 km farther upstream (Duke et al. 1999). It seems likely that the long dispersal of larvae and juveniles could easily move fish from the present or historical spawning sites down to the lower river, Kootenay Lake, or both, prior to wintering in the fall.

If wild larvae and juveniles are in the lower meandering reach during summer and fall as the present study indicates, then habitat and forage availability in this reach are critical to their survival. The reach has been highly modified by agriculture, dikes that separate river from floodplain, a raised level of Kootenai Lake, and flow and temperature changes due to Libby Dam (Anders et al. 2002). All of these activities have had a major effect on river ecology and the benthic invertebrate community. Information on the present habitat and forage available for larvae and juveniles in this reach relative to their habitat and forage preferences may be critical to restoring successful recruitment.

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