Environmental Biology of Fishes **70:** 43–55, 2004.
© 2004 *Kluwer Academic Publishers. Printed in the Netherlands.*

Ontogenetic behavior and migration of Gulf of Mexico sturgeon, *Acipenser oxyrinchus desotoi*, with notes on body color and development

Boyd Kynard[a] & Erika Parker[a,b]
[a]*S. O. Conte Anadromous Fish Research Center, Leetown Science Center, U.S. Geological Survey, One Migratory Way, Turners Falls, MA 01376, U.S.A. (e-mail: kynard@forwild. umass.edu)*
[b]*Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA 01003, U.S.A.*

Received 28 January 2003 Accepted 5 August 2003

Key words: larva, dispersal, rearing habitat, feeding, early life history, Acipenseriformes

Synopsis

We observed Suwannee River Gulf sturgeon, *Acipenser oxyrinchus desotoi*, in the laboratory and found free embryos (first interval after hatching) hid under rocks and did not migrate. Thus, wild embryos should be at the spawning area. Larvae (first interval feeding exogenously) initiated a slow downstream migration, and some juveniles (interval with adult features) continued to migrate slowly for at least 5 months, e.g., a 1-step long larva-juvenile migration. No other population of sturgeon yet studied has this migration style. A conceptual model using this result suggests wild year-0 sturgeon have a variable downstream migration style with short-duration (short distance) migrants and long-duration (long distance) migrants. This migration style should widely disperse wild fish. The model is supported by field studies that found year-0 juveniles are widely dispersed in fresh water to river km 10. Thus, laboratory and field data agree that the entire freshwater reach of river downstream of spawning is nursery habitat. Foraging position of larvae and early juveniles was mostly on the bottom, but fish also spent hours holding position in the water column, an unusual feeding location for sturgeons. The holding position of fish above the bottom suggests benthic forage in the river is scarce and fish have evolved drift feeding. The unusual migration and foraging styles may be adaptations to rear in a river at the southern limit of the species range with poor rearing habitat (low abundance of benthic forage and high summer water temperatures). Suwannee River Gulf sturgeon and Hudson River Atlantic sturgeon, *A. o. oxyrinchus*, are similar for initiation of migration, early habitat preference, and diel migration. The two subspecies differ greatly for migration and foraging styles, which is likely related to major differences in the quality of rearing habitat. The differences between Atlantic sturgeon populations show the need for geographical studies to represent the behavior of an entire species.

Introduction

Atlantic sturgeon, *Acipenser oxyrinchus*, is a large, anadromous species found in rivers, estuaries, and coastal marine ecosystems on the Atlantic coast and the Gulf of Mexico, North America (Vladykov & Greeley 1963). There are two allopatric subspecies: Atlantic coast Atlantic sturgeon, *A. o. oxyrinchus*, occur in coastal rivers from the St. Lawrence River, Canada to northern Florida; Gulf of Mexico sturgeon (hereafter, Gulf sturgeon), *A. o. desotoi*, occur in northern rivers of the Gulf of Mexico (Stabile et al. 1996, Smith & Clugston 1997). Zoogeographic barriers associated with geologic creation of the Florida peninsula have existed since the Pleistocene period and are believed responsible for the allopatry and biological differentiation within Atlantic sturgeon (Rivas 1954, Bowan & Avise 1990).

Decline and extirpation of individual river stocks of Atlantic sturgeon during the 20th century resulted in recent protection of both subspecies (Waldman 1995, Waldman & Wirgin 1998, Secor 2002). River populations of *A. o. oxyrinchus* are federally protected as Special Concern and are also protected by most states (Smith & Clugston 1997). The federal Endangered Species Act protects Gulf sturgeon, which was listed as Threatened in 1991.

Gulf sturgeon spawning in the Suwannee River, Florida occurs during April at 17–23 EC (Sulak & Clugston 1999). Spawning of Suwannee River Gulf sturgeon occurs in discrete areas with rock and gravel substrate found at river km 202–221 (particularly, river km 215; Sulak & Clugston 1999, K. Sulak pers. comm.). Spawning of *A. o. oxyrinchus*, has only been studied in the Hudson River, where spawning occurs in June at river km 132–184 (Van Eenennaam et al. 1996, Bain 1997).

Early life history of Gulf sturgeon has been primarily studied in the Suwannee River where capture of eggs and a few year-0 juveniles during many years led to the following conceptual model of movement. Suwannee River Gulf sturgeon begin life in April at one of four discrete gravel bottom spawning areas between river km 202–221. Year-0 fish spend the first summer and fall in fresh water distributed from river 237, which is slightly upstream of any known spawning site, downstream to river km 10. After about 10 months, juveniles migrate downstream in late January–early February and join older juveniles in the estuary at the river mouth (Clugston et al. 1993, Sulak & Clugston 1998, 1999).

Field studies on Suwannee River Gulf sturgeon have not revealed the behavior or migration style of early life stages. Hundreds of eggs were collected to locate spawning areas (Marchant & Shutters 1996, Sulak & Clugston 1998, 1999), but massive field sampling during day and night with diverse gear types captured only 51 year-0 life stages (one larvae captured within a known spawning area, 4-month 2–4 juveniles, and 46-older juveniles). The few fish are insufficient to reveal migration style, but the capture locations of same-age juveniles show they are annually dispersed widely in fresh water (Carr & Carr 1996, Sulak & Clugston 1998, 1999). The dispersed capture locations of year-0 juveniles <350 mm TL provide excellent information to test predictions on migration gathered in the present laboratory study.

Behavior of early life stages of Hudson River Atlantic sturgeon has been studied mostly in the laboratory. Ontogenetic behavior and migration of free embryos (hereafter, embryos, Balon 1999) and larvae was studied using an artificial stream and aquaria (Kynard & Horgan 2002). Hatchling, free embryos did not migrate, but remained concealed under rocks and avoided bright habitat (bright illumination and white substrate). Larvae preferred bright habitat, left cover, and initiated a 1-step long downstream migration that lasted 12 days (peak, first 6 days). Bath et al. (1981) captured larvae in bottom nets, so most larvae likely migrate near the bottom.

With few changes in methods of Kynard & Horgan (2002), Kynard et al. (2002a,b, 2003), we examined the early life stages of Suwannee River Gulf sturgeon for ontogenetic change in preference for bright habitat (bright illumination intensity and white substrate color) and cover, swimming height above the bottom, foraging habitat, up- and downstream movement, and aggregation. Habitat preferences give clues to the habitat used by wild sturgeon. Swimming height above the bottom, diel behavior, and up- and downstream movements (particularly movement duration) give insight into foraging and migration styles. This information can provide behavioral explanations for the field distribution of fish and expand the conceptual model of year-0 fish movement (Sulak & Clugston 1998). Movements of sturgeon in our endless stream have repeatedly been confirmed by field data as similar to the movements of wild sturgeon (Kynard & Horgan 2002, Zhuang et al. 2002, Kynard & Parker unpubl. data).

Hudson River Atlantic sturgeon and Suwannee River Gulf sturgeon represent almost the entire north–south latitudinal distribution of Atlantic sturgeon (coastal Atlantic sturgeon occur farther north than the Hudson River to the St. Lawrence River, Canada). The Hudson and Suwannee Rivers represent very different physical and biological environments that could select for different migration and foraging styles of early life stages. Comparing the innate behavior of early life stages from populations at the extremity of a species' range can provide insight into the ecology and life style of the entire species.

Recent information indicates that body color of sturgeon early life intervals is related to migration style (Kynard & Horgan 2002, Kynard et al. 2002a,b, 2003). Body color of migratory embryos is light (usually light gray or tan) with a light-colored or a black tail, whereas migratory larvae have a dark body and tail. We observed body and tail color of Suwannee River Gulf sturgeon during the migration period to compare with Hudson River Atlantic sturgeon.

Methods

We conducted tests with 200 Suwannee River Gulf sturgeons that hatched on 22 March 2001. Eggs were fertilized by University of Florida personnel (see Acknowledgements) then shipped to us. 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 varied before we received the eggs. Fish hatching in the first 24 h were termed day-0 fish. Sturgeon were day-0 on 22 March and day-1 on 23 March. 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 was 17–21°C, an acceptable range of temperatures for early life intervals of Gulf sturgeon (Chapman & Carr 1995, Sulak & Clugston 1999). The natural photoperiod for the Turners Falls location was maintained at all time. Early larvae were fed a sturgeon starter diet (see Acknowledgements) 6–8 times daily using a timed feeder and four times daily with live *Artemia nauplii.*

To link behavior to development, we scaled sturgeon development to age and cumulative temperature. Water temperature in the oval migration channel was recorded hourly with a data logger and these data were used to calculate daily thermal degree units and cumulative temperature degree units (CTU) in degree-days after hatching. Cumulative degree-days were calculated for each day (beginning at 24:00 h) and used the mean hourly temperature (°C) for each day. For example, day-0 fish accumulated 0 degree-days, day-1 fish accumulated the mean temperature for day 1, and fish on day 2 accumulated the degree-days of day 1 plus the mean temperature of day 2.

We identified the free embryo interval (hereafter, embryo) that began on day-0 (hatching) and lasted to the first day of exogenous feeding, and larva interval, which began the first day of feeding and lasted until fish developed into juveniles. We were unsure of when the juvenile interval began. The morphological transition from larva to juvenile is subtle and in Hudson River Atlantic sturgeon is complete by days 55–65 (60–70 mm SL; Snyder 1988). Nothing is known about characteristics of the behavioral transition to juvenile. We did not examine Gulf sturgeon to determine when larvae developed morphologically into juveniles, but we recognized this transition period by referring to fish that were >day-70 (>42 mm SL) as late larvae or presumed juveniles.

Illumination, substrate color, swimming 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-W 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 (8.2–3.0 lx), and dark (2.2–0 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 black and white 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 sturgeons were tested daily for preference of illumination intensity and substrate color. Before each test, we removed actively swimming fish from a rearing tank using beaker brailing and placed them 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. After 1 min acclimation, we visually recorded fish movement for 1 min as a continuous time series relative to habitat (illumination test – dark and illuminated; substrate test – white or black bottom). To evaluate fish preference for bright illumination and white substrate, we calculated the percentage of time fish spent daily in these habitats and plotted these as a daily time series. We transformed the daily percentages to arcsine values and calculated binomial 95% confidence intervals to determine if the percent of fish preferring each habitat was significant (confidence intervals that included 50% were not significant).

We daily tested eight sturgeons for swimming height above the bottom in an artificial stream tube that simulated a vertical section of stream with horizontal velocity (see Figure 1, Kynard et al. 2002a). The stream tube was a clear plastic cylinder 153-cm long × 15 cm

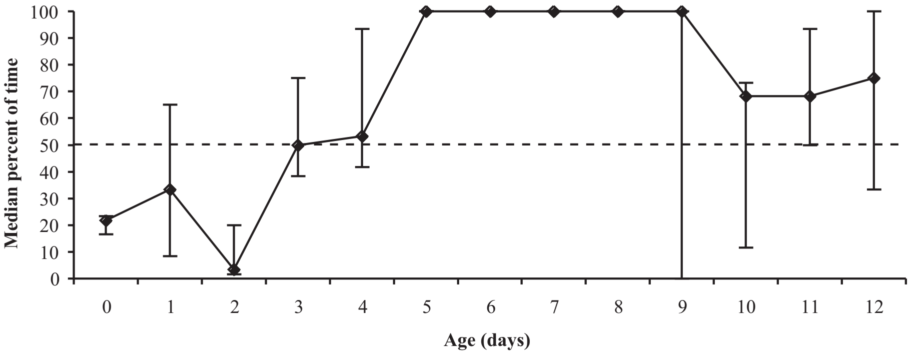

Figure 1. Median percentage of time (±quartile range) sturgeon were on the bright side of illumination choice tank by age. N = 5 fish tested daily. Dashed line is at 50% choice.

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, replace water, and maintain water temperature within 1EC of rearing tanks.

Sturgeon for stream tube tests was 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. Only upward swimming and cover seeking were noted for the first 60 s (acclimation period). Then at 5–6 min, we recorded 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 means of the seven measurements for each fish and presented the grand means for eight fish as a daily time series.

One-half of the stream tube's bottom was covered with two layers of gray rocks (5 cm diameter) to create cover habitat and the other one-half of the bottom was open (without cover). Use of cover was recorded only when fish stopped on the bottom under the rocks or in the open.

In all substrate, illumination or stream tube tests, fish were randomly selected from 200 fish, and after testing, all were returned to rearing tanks. While the probability of selecting any fish a second time increased with the number of days tested, we believe the haphazard selection process should provide a group of fish with a set of random tests.

Migration, diel activity, habitat, and aggregation

Up- and downstream movements of sturgeon were observed in an oval endless channel of green–blue color whose circumference was divided into 12 sections each 62-cm long (see Figure 1, Kynard & Horgan 2002). The channel was 7.3 m in circumference, 32-cm wide, with water 20-cm deep. A continuous flow-through water system supplied 1.0 l min^{-1} of dechlorinated city water. The only change in the channel from the figure of Kynard & Horgan (2002) was the addition of a plastic ramp in section 2 (the video viewing area) that reduced the depth of water to 13 cm and forced fish to pass close to the camera, making it easier to see fish on the videotape at night. This smooth ramp caused a slight increase in velocity (from 3 to 4 cm s^{-1}) in section 2. A small, submerged pump created a clockwise flow around the channel. Velocity measured at mid-width and 3 cm above the bottom in each of the 12 stream sections was a mean of 3.5 cm s^{-1} (range, 1–9 cm s^{-1}). Water velocity was fast in sections 5 and 6 (respectively, 5 and 9 cm s^{-1}) near the pump, 3–4 cm s^{-1} in the other sections, except for 1 cm s^{-1} in section 4 (downstream of the ramp) and section 10. The bottom was smooth except for six large rocks (each 10–15 cm diameter) placed across the 180° channel turns, which provided cover and reduced velocity. Light level in the channel was low ($\leq$ 20 lx).

We initially introduced 15 hatchlings into the oval channel to observe migration. A Cohu video camera with infrared light was placed over the oval channel to observe the fish passing during the day and night. Silver reflective tape covered the ramp and channel sides in the video field of view to enhance seeing the small fish at night. The video system recorded fish passing up- or downstream for 5 min h^{-1} for 24 h. We reviewed the videotape and counted the number of up- and downstream fish passes per 5 min. Because fish could not be marked individually to determine if all fish were moving up- or downstream, once daily we visually followed individual fish and estimated the number of fish that were moving up- or downstream. If a test sturgeon died, we did not replace it with a rearing tank fish until all 15 fish were dead. Because there were days when less than 15 fish were present, the net count of downstream fish passes (number downstream – number upstream) was scaled to the mean net number of passes per fish. After day 16, we periodically taped fish for 24 h until day 82 to determine if migration continued. We visually observed fish movement until day 171 (7 September).

In conjunction with migration observations during days 69–75, we conducted an experiment to determine if exposure of juveniles to weak salinity was the cue that stopped migration. On days 69 and 70 (29–30 May), we acclimated 10 juveniles to the stream channel using a closed system of fresh water. We created several vegetated areas in the tanks using clumps of plastic plants. We observed fish for 5 min h^{-1} for 24 h using the video system described previously. After 48-h acclimation, on day 71 we gradually introduced a saline solution (salt + sea salt mixture) during 2 h to create 5 ppt salinity in the stream channel. Fish were exposed to 5 ppt for 48 h (until day 73). Then, we increased salinity to 10 ppt and monitored fish during an additional 48 h (days 74–75). We recorded up- and downstream fish passes with video as described previously, and daily visually observed fish behavior, feeding, and fish mortality.

To determine daytime habitat use, we visually observed fish in the stream channel five times daily. We observed 15 fish on days 0–7 and 3–15 fish on days 8–47 for distribution in four habitats: under rocks, on the open bottom, in the water column (>3 cm above the bottom), and at the water surface. For each day, we determined the grand total of fish using each habitat, converted this number to percent, and present the daily percent of fish using each habitat as a time series. For days 69–171 juveniles, we used videotapes to determine the body orientation of fish as they swam downstream (head upstream, head downstream, or body lateral to water flow).

We examined the aggregation tendency of Gulf sturgeon using five daily visual counts of the number of fish in each of the 12 channel sections. However, we were not able to use many days because some early larvae persisted in using rocks and numbers of fish in the stream channel were not constant. We used Monte Carlo simulation ($n = 10\,000$) to find the expected distribution of sturgeon numbers in the 12 channel sections if sturgeon selected their location randomly and independently. We analyzed day-27 larvae ($n = 4$), day-28 larvae ($n = 3$), and days 40–42 larvae ($n = 8$) for a random spatial distribution in the 12 channel sections.

Results

Body and tail color of day-0 hatchling embryos on 22 March was a medium gray (Grey 41, RGB 156 156 156). On days 2–4, color was a light gray body (Gray 41, RGB 105 105 105) and blackish tail. When embryos developed into larvae and began feeding exogenously on day 5, body color was a dark gray (Gray 21, RGB 54 54 54) and the tail was black. This body and tail color was present during the larva interval. Day-27 larvae were a mean of 18.8 mm TL ($n = 8$) and still had a dark gray body and black tail. Tail color gradually became the same as body color as the dark gray body color spread over the tail by day 85 (June 15; juvenile interval).

Embryos developed into larvae on day-5 after 110.3 CTU. The mean TL of day 5 larvae was 14.7 mm TL ($n = 5$). The CTU per mm of day-5 larvae TL was 7.5 (110.3 CTU ÷ 14.7 mm = 7.5 CTU mm^{-1} TL).

Illumination, substrate color, and swimming height

Early embryos avoided illumination, late embryos had no preference, and early larvae preferred illumination (Figure 1). The avoidance of bright illumination on day 0 was significant ($p < 0.05$). Larvae spent most of the time in bright illumination beginning on day 5, and the preference was significant on days 5–8 ($p < 0.01$). Days 9–12 larvae spent most of the time in bright illumination, although preference was not significant.

Embryos spent most of the time on dark substrate and larvae spent most of the time on white substrate (Figure 2), but the preference was not significant on any day ($p > 0.05$). Days 0–3 embryos weakly used black substrate. Day-5 and older larvae weakly used white and days 6 and 9 fish spent 80% or more of the time on white substrate. The lack of a significant preference on any day was likely due to the lack of a strong preference and the small sample of fish observed.

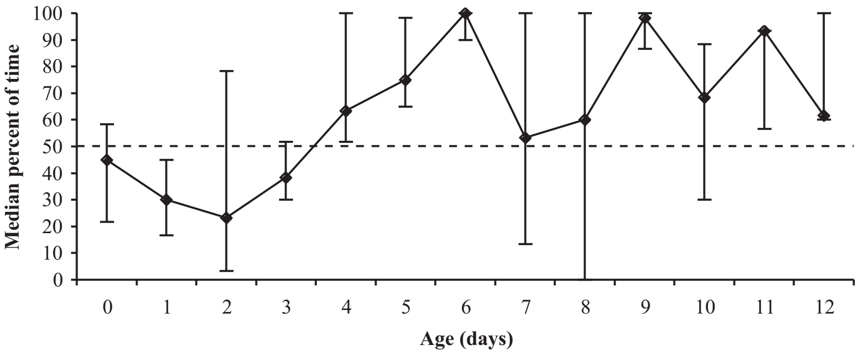

Figure 2. Median percentage of time (±quartile range) sturgeon were on the white side of the white–black substrate choice tank by age. N = 5 fish tested daily. Dashed line is at 50% choice.

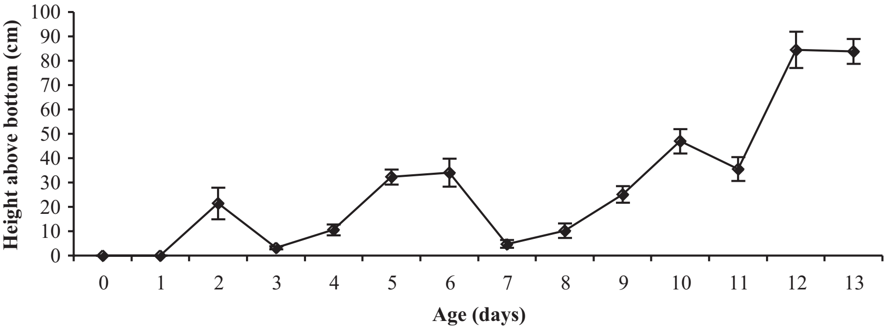

Figure 3. Swimming height of sturgeon above the bottom in the 150-cm high stream tube by age. Each point is the grand mean (±standard error) of 8 fish. Each fish was observed at 10 s intervals (7 times) between 5 and 6 min after introduction.

In the swim tube, days 0–4 embryos swam on or within 25 cm of the bottom (Figure 3). Days 5–6 early larvae initially swam a mean of 30–40 cm above the bottom, and after a brief decrease in swimming height on days 7–9, swam higher with age to a mean of 90 cm on days 12–13, when observations ceased. Variation within a day for swimming height among the eight fish was very small.

Migration and diel behavior

During video and visual observations of sturgeon in the stream channel to day 171, we rarely observed any upstream movement and never observed sustained upstream movement that lasted for hours. Typically, fish moved downstream, stopped and held position for minutes or hours, then resumed downstream movement.

After introduction of day-0 embryos at mid-day into the stream channel, some fish moved downstream for several hours (0.4 passes per fish in the day, then zero passes at night; Figure 4). Video observations showed downstream movement ceased at night (zero passes). Downstream movement of days 1–4 embryos was slight and only occurred at night, i.e., ≤ 0.1 passes per fish at night and zero during the day (Figure 4). All observations indicate embryos did not migrate, although some movement occurred at night, possibly a fish or two seeking different cover.

The number of downstream passes per fish increased gradually at night after day 5 to day 22, except for the decrease on day 14 (Figure 4). Larvae initiated a weak downstream migration that was continued throughout the observation period. Downstream passes of days 6–16 early larvae were 0.4–0.6 passes per fish at night and 0.2 or less (often zero) passes during the day. The passes at night of day-21 larvae to day-51 (late-larvae or early juveniles) ranged widely between 0.3 and 1.7 passes per fish, but was usually 1.0 passes per fish. The number of night passes of these older fish was also higher than the number of day passes, but there was a clear trend with increased age for movement during the day as well as at night (Figure 4).

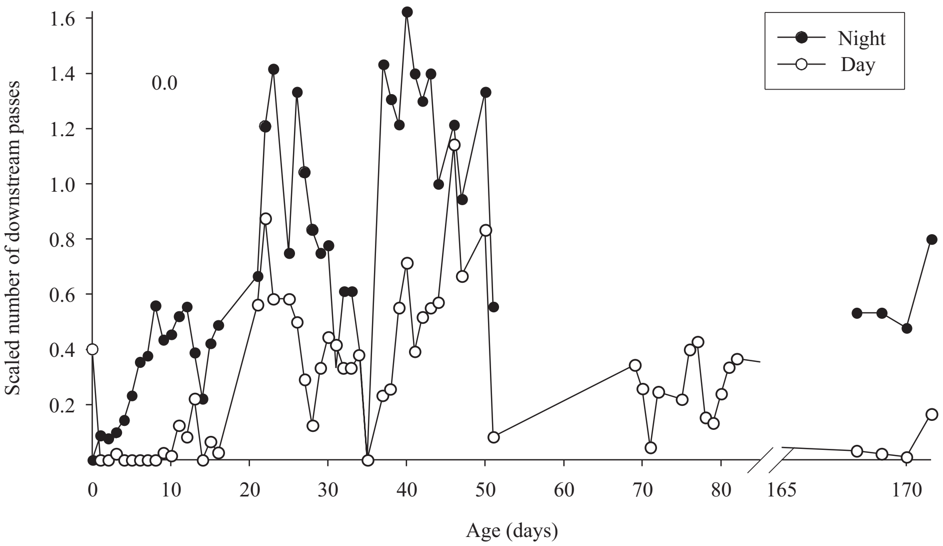

Figure 4. Downstream migration of sturgeon during day and night in the stream channel by age. A video camera with infrared light observed the number of up- and downstream fish passes past one location for the first 5 min of each hour for 24 h per day. The net number of downstream fish passes (total downstream passes – total upstream passes) was determined for day and night periods of each day, then scaled to the mean net number of passes per fish present. The number of fish was 15 for days 0–7 and 3–15 fish for days 8–47.

Video observations of days 69–82 presumed juveniles showed they continued a low level migration mostly at night, but some also moved downstream during the day (Figure 4). As these juveniles moved downstream at night, some continued to move out of the IR light field, but some turned quickly, swam upstream, and remained in the illuminated area. Although there were many more fish passes at night than during the day, the mixing of fish at the camera made it impossible to accurately count the number of fish passes at night. Thus, we have only presented the day fish passes (Figure 4). The number of passes per fish during the day on days 69–82 was <0.4 passes per fish, which was usually less than the number of daytime passes of days 38–50 fish (Figure 4). Video and visual observations on days 168–171 juveniles showed that a low level of downstream movement continued and most movement was at night.

Downstream movement by early larvae was almost entirely nocturnal, but as larvae aged, they also moved in the day, but at a lower level than at night (Figure 4). During visual daytime counts of days 6–16 larvae, about 30% were migrating during any observation time.

Days 69–171 juveniles observed by video actively swam downstream headfirst, day and night, and did not drift passively. The number of observations each hour varied from 1 to 17 and the number of hours observed per day varied from 5 to 12.

Habitat use and foraging

In the stream tube, 100% of the days 0–2 embryos sought cover under rocks and as fish aged to day-13 larvae, there was a trend for fish to occur more frequently in the water column (Figure 3). Some days 5–9 larvae also sought cover under rocks in the tube in the daytime. Days 10–13 larvae did not use the rocks, and many preferred the water column or open bottom.

Visual observations five times per day in the stream channel found days 1–4 embryos and early larvae to day 6 were mostly under rocks (Figure 5). During the larva period, habitat use went through four phases: days 5–10 larvae used rock cover and open bottom, days 11–16 larvae used the open bottom, days 28–32 larvae used the water column, and days 38 larvae to day 47 presumed early juveniles used the open bottom, and to a lesser extent, the water column.

Daytime visual observations of larvae and presumed juveniles to day 72 in the stream channel showed fish moved downstream using a move-pause foraging style. Fish moved downstream, then stopped (paused), faced into the current, and held position for minutes to hours. Afterward, fish turned head downstream and slowly drifted or swam to another area, then turned head upstream, paused again, and resumed foraging. Larvae and presumed early juveniles held position on the bottom and in the water column.

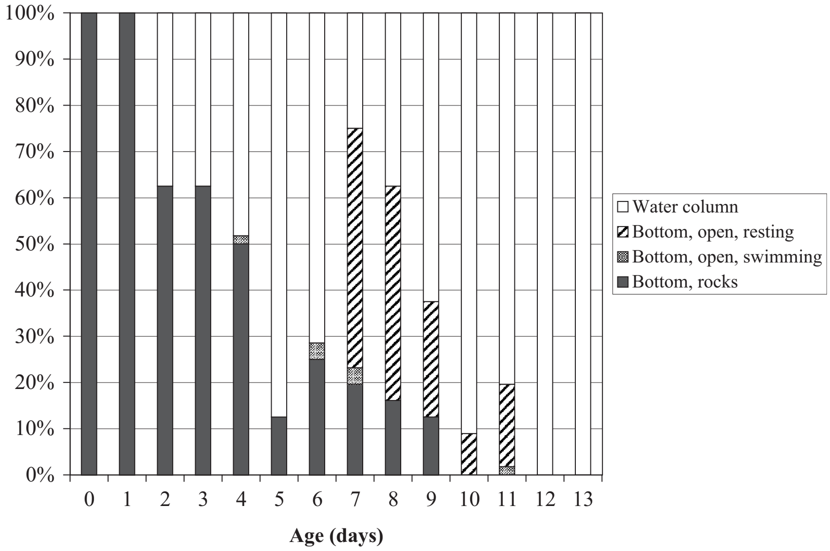

Figure 5. Habitats used by sturgeon in the 150-cm high stream tube during days 0–13. Each bar shows the percentage of fish (n = 8) in four habitats (water column, swimming on bottom, resting on bottom in open, and on bottom in rocks) between 5 and 6 min after introduction.

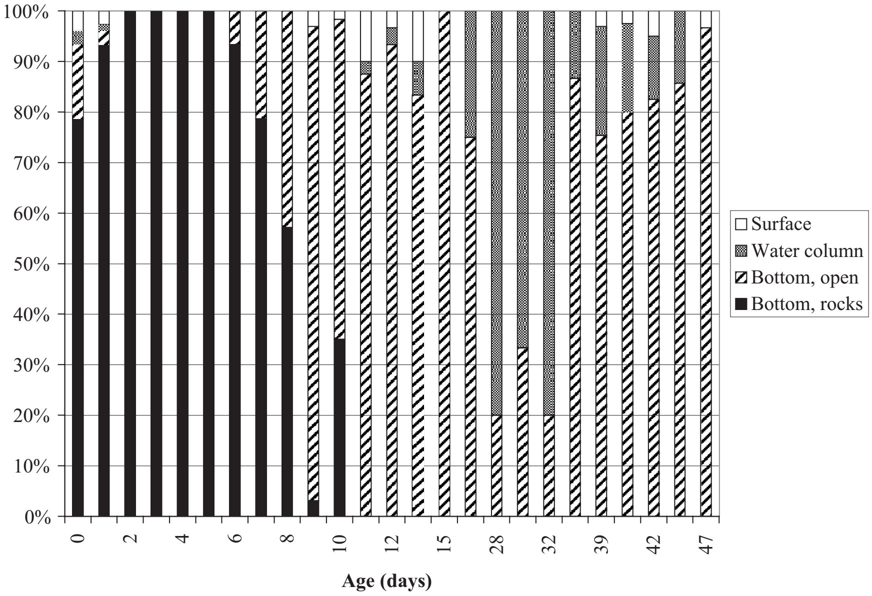

Figure 6. Habitats used by sturgeon in the stream channel by age. Each bar is the daily mean percentage of fish (n = 15 for days 0–7, n = 3–15 for days 8–47) in four habitats (water surface, water column (>3 cm above bottom), bottom, and under rocks) during five daily visual observations.

Of the 15 fish introduced into the stream channel on days 0, 15, and 38, survival was best for day-38 late larvae. The initial 15 test fish were alive on day 10 (5 days after initiation of feeding), but all had died by day 15. During the day, these fish were feeding mainly on the bottom on days 10–15 (Figure 6). The prepared sturgeon food floated for a short time, but eventually sank to the bottom. Thus, food was available in the water column for a short time and on the bottom for a long time. This should not be a problem for fish feeding on the bottom, but could create a mismatch of food and feeding style for fish feeding in the water column.

As larvae aged, day observations in the migration channel found fish occurred less frequently in the water column and more frequently on the bottom (Figure 6). The switch may indicate fish were switching entirely to benthic feeding as they developed into juveniles. Mortality of larvae was low in the rearing tank where fish at high density foraged mainly on the bottom or trapped food on the vertical walls of the tank. This foraging was a striking contrast to fish at low density in the stream channel, which often foraged in the water column on drift.

Salinity test

The 10 presumed early juveniles acclimated in the stream channel on day 69 held position briefly, then started a move-pause downstream movement. After a 48 h acclimation to fresh water at 14:20 h on day 71, salinity was added during 2 h to create 5-ppt salinity. After 24 h (14:20 h on day 72), no fish were dead or showed signs of stress and fish continued the slow downstream migration. Thus, exposure to weak salinity of 5 ppt for 24 h did not stop the downstream migration of fish. Temperature during acclimation was 20.2°C and temperature during the salinity test was 19.6–19.8°C.

On day 72 at 12:20–14:20 h, salinity was increased to 10 ppt during 2 h. Temperature was 20.3°C. On day 73 at 14:20 h, eight fish were dead, and the two others were swimming erratically and had rapid gill ventilation. Fresh water was added at 14:20–16:20 to reduce salinity to 0.1 ppt, but on day 74 at 14:20, the remaining two test fish were dead. The 24-h exposure to 10 ppt killed 100% of the 10 juveniles. Final water temperature was 20.1°C. Sturgeon did not selectively use the clumps of plants scattered around the channel.

Aggregation

The spatial distribution of larvae on days 27, 28, and 40–42 in the 12 sections of the stream channel differed from a random distribution on all days. On days 27 and 28, the majority (80% and 87%, respectively) of fish were in sections 6–8, i.e., the faster water downstream of the pump. On days 40–42, fish also aggregated more than expected, with 30% of the observations occurring in section 9. We observed fewer sections than expected with 0 or 1 fish in them and more sections than expected with 3 and 4 fish in them on all days. Aggregated fish were not close enough to use each other for cover; they just used the same general area.

Discussion

Juvenile Suwannee River Gulf sturgeon aggregated in the stream channel more than would be expected by chance. Chan et al. (1997) also observed aggregation by Gulf sturgeon juveniles in an artificial stream. Is aggregation an artifact of individuals being closer together than would occur naturally in the wild, or do wild individuals aggregate? The few captures of year-0 juveniles have almost always been of solitary fish (K. Sulak pers. comm.), so field evidence does not indicate juveniles aggregate. Laboratory data show that juveniles have the potential to form a social group, and will if close to other individuals. Shortnose sturgeon, *Acipenser brevirostrum*, and likely Hudson River Atlantic sturgeon, has a size-based dominance hierarchy in artificial streams (Kynard & Horgan 2002). This may be important for population regulation and emigration of fish from rivers at high population density (Kynard 1997).

Larvae and juveniles in the artificial channel never sustained an upstream movement more than a few hours, suggesting that wild fish should be downstream of spawning areas. During one year, a few year-0 juveniles were captured 16 km upstream of the most upstream known spawning site (Sulak & Clugston 1998). This suggests that some fish move upstream. In previous studies, other species moved upstream in the stream channel (Zhuang et al. 2003, Kynard & Parker, unpubl. data), so we believe that Gulf sturgeon should also move upstream if they had the behavioral drive. It is likely that all fish movement is downstream and the upstream juveniles resulted from an unmonitored spawning upstream or that some juveniles moved upstream in an up-current eddy along the shoreline (K. Sulak pers. comm.).

A conceptual model of year-0 migration that integrates the present laboratory results with field captures of year-0 juveniles indicates that fish have a variable downstream migration style. After eggs hatch, free embryos remain hidden under cover at the spawning site. Larvae leave cover and move slowly downstream with no early peak in intensity that is characteristic of migrant larvae of other species. Migration duration by each individual was not determined because fish were not individually marked, but all observations show some larvae and juveniles moved for months, while others either slowed or stopped moving downstream, e.g., a 1-step long larva-juvenile migration. Larvae and juveniles actively swam headfirst downstream, clearly indicating their directional preference. These observations in the stream channel indicate juveniles of similar size (and age) should be widely dispersed downstream of the spawning area. Field captures support this prediction and show month 2–10 juveniles are widely dispersed in fresh water downstream of spawning sites, except as noted previously (Sulak & Clugston 1998, 1999). Salinity tolerance is poor (present study), so juveniles do not contact salinity and have not evolved avoidance of deleterious concentrations. Hudson River Atlantic sturgeon juveniles (9 month, 100 mm TL) tolerate direct exposure to 15 ppt seawater (S. McCormick unpubl. data), which may be similar to Gulf sturgeon. Field captures show that when Suwannee River sturgeon is age 10–12 months, they move downstream to the estuary and join older juveniles. A variable migration style within one life interval is also found in year-1 juveniles of Connecticut River shortnose sturgeon, where some individuals migrate far downstream (100+ km), while others do not migrate (Kynard 1997, Kynard et al. unpubl. data). In this case, two life intervals are variable – larva and juvenile intervals.

A discrete rearing reach downstream of spawning areas occurs for larvae and year-0 juvenile Hudson River Atlantic sturgeon (Dovel & Berggren 1983), Connecticut River shortnose sturgeon (Kynard & Horgan 2002), and Yangtze River Chinese sturgeon (Zhuang et al. 2002). The rearing locations are consistent with predictions from migration duration in the stream channel and river velocity during the migration period. Suwannee River Gulf sturgeon is very different from these species and has no discrete rearing reach.

The absence of a discrete rearing reach for sturgeon in the Suwannee River may be the result of the low abundance of benthic invertebrates, so fish must forage widely. In the middle reach of the Suwannee River (downstream of sturgeon spawning areas), benthic invertebrate abundance is low during the summer, which is typical of brown water, acidic, oligotrophic–mesotrophic, southeastern rivers (Mason 1991). No information on foraging by larvae and early juveniles is available (Mason & Clugston 1993), but the mid-water position of sturgeon larvae in the stream channel during their travel-pause feeding (MacKenzie & Kiorboe 1995) strongly suggests that drift feeding occurs in the river. The small variation among larvae for swimming distance above the bottom shown in Figure 3 is the strongest response for this behavior we have seen in any sturgeon population and suggests a strong selection for position above the bottom, which could be related to drift feeding. If the drift-feeding hypothesis is correct, then benthic forage is limited and sturgeon have evolved drift feeding to supplement benthic feeding. Gulf sturgeon larvae may have a more flexible foraging style (and mouth morphology?) than other sturgeon yet studied. When the larvae in our study developed into presumed juveniles, use of the water column decreased, so the switch from benthic-drift feeding to benthic feeding likely begins at the juvenile interval and is completed by 12 months (Huff 1975, Mason & Clugston 1993).

Summer water quality in the Suwannee River may also create poor rearing conditions and contribute to a long fish migration. Daily maximum temperatures in the Suwannee River during summer are 25–28°C with brief increases to 32°C (Mason 1991, Chapman & Carr 1995, Sulak et al. unpubl. data). Laboratory data indicates that some Gulf sturgeon embryos, larvae, and early juveniles cannot tolerate these temperatures, i.e., embryos and early larvae have high mortality at 25°C (Chapman & Carr 1995). Also, we found that some day 70–80 juveniles were hyperactive, ceased feeding, lost equilibrium, and a few died when rearing temperature was increased from 21°C to 23°C during 5 h. Chapman & Carr (1995) speculated that early life intervals of Suwannee River Gulf sturgeon seek refuge from high temperature in cooler springs, which are 20–21°C. However, intensive sampling and diving in springs for years found no juveniles (Sulak & Clugston 1999, K. Sulak pers. comm.). Also, most springs are unsuitable due to low dissolved oxygen levels (<3–$4\ \mathrm{mg\ l^{-1}}$; Sulak et al. unpubl. data). During June–September of many years, the mean water temperature at the capture sites of year-0 juveniles ($n = 11$) was 25.4°C (range, 22.9–28.0°C; K. Sulak pers. comm.). Thus, some juveniles tolerate mainstem temperatures. However, summer mid-day river temperatures may increase 3–4°C (Sulak et al. unpubl. data), and fish may seek a temporary daily thermal refuge. In Sonoran Desert streams where summer temperatures are 39–41°C for several hours each mid-day, desert pupfish, *Cyprinodon macularius*, seek daily thermal refugia (5–6 h) along shorelines where cool groundwater enters (B. Kynard unpubl. data). High summer temperature may affect year-0 sturgeon rearing, survival, and structure of the population.

Suwannee River Gulf sturgeon is similar to Hudson River Atlantic sturgeon for response to bright habitat and diel movement, but differ greatly for migration style. Avoidance of bright habitat by embryos in both populations is adaptive because the behavior keeps non-migrants under cover to complete development and avoid predation. The switch by larvae to preferring bright habitat is likely related to swimming-up into the water column during migration, and perhaps, to enhancing visual detection of small prey (Kynard & Horgan 2002). Diel behavior was similar in north and south populations: early larvae were nocturnal, but within a few days, fish moved day and night (Kynard & Horgan 2002, present study). The major activities of larvae are foraging and migrating. When larvae initiate feeding is a critical period, and in the laboratory, many fish do not survive the transition to exogenous feeding. The changes in diel behavior with age suggest early larvae may not migrate during the day so they can optimize foraging using vision. With increased age, foraging ability improves and fish can simultaneously forage and migrate during the day. The similar response to bright habitat and diel movement by fish from northern and southern populations of Atlantic sturgeon suggests these behaviors have a high fitness value throughout the geographic range of the species. The two populations differed for migration style with Hudson River Atlantic sturgeon having a 1-step long larval migration (12-day migration, with a strong peak the first 6 days; Kynard & Horgan 2002). Dispersal of larvae ceases just upstream of the fresh water: salt water interface where yearlings are also found (Dovel & Berggren 1983). Thus, Hudson River Atlantic sturgeon larvae stop migrating and remain in a permanent rearing reach. Suwannee River Gulf sturgeon continue migrating throughout the larva and juvenile intervals for a much longer migration, dispersing widely and using the entire river downstream of spawning for rearing. The qualitative differences between the Hudson River and Suwannee River populations show the importance of examining populations throughout a species' range to correctly characterize the entire species.

The CTU required to develop from embryo to larva was much higher for Hudson River Atlantic sturgeon than for Suwannee River Gulf sturgeon. Hudson River Atlantic sturgeon developed into larvae on day 8 after 181 CTU (Kynard & Horgan 2002). First feeding larvae were 15.4 mm TL (mean, $n = 3$); thus, the CTU needed per millimeter of larva TL was 11.7. In contrast, Suwannee River sturgeon needed only 7.5 CTU mm^{-1} larva TL to develop into larvae. Thus, Suwannee River sturgeon developed into larvae about 1.5 times faster than Hudson River sturgeon. The development rate of Hudson River Atlantic sturgeon to the larva interval is typical of other *Acipenser* and the development of Gulf sturgeon is faster than any other *Acipenser* species (Kynard et al. 2003). A development rate to the larva interval of about 7–8 CTU mm^{-1} larva TL may be as rapid as *Acipenser* are capable. The fast development of Suwannee River sturgeon may be related to their southerly distribution, but the adaptive significance of variation in development rate is unclear.

Body color of embryos and larvae from the Hudson River Atlantic sturgeon and Suwannee River Gulf sturgeon were generally similar for larvae color, but embryo color differed. Hudson River Atlantic sturgeon embryos have a gray–black body and tail (Snyder 1988), but Suwannee River Gulf sturgeon embryos have a light-gray body with a black tail. In both populations of Atlantic sturgeon, body color of larvae was medium to dark gray–black with a blackish tail. The black tail of early Suwannee River Gulf sturgeon larvae was more distinct from the body color than it was for Hudson River Atlantic sturgeon (Snyder 1988).

Body color and migration of Suwannee River sturgeon is consistent with the pattern found in other species of *Acipenser*. Four species that migrate from the spawning area as embryos have light-colored bodies (Gisbert et al. 1999, Zhuang et al. 2002, 2003, Kynard & Parker unpubl. data). Five species (or subspecies) that migrate as larvae have dark bodies (gray, brown, or black; (Kynard & Horgan 2002, Kynard & Parker, unpubl. data, present study). No *Acipenser* yet found has a dark migrant embryo or light migrant larvae.

Laboratory studies of *Acipenser* found many migration styles of early life stages, number of species in parenthesis, e.g., larva migration (4), embryo migration (3), embryo–larva migration (1), larva-juvenile migration (1 subspecies), and juvenile migration (1; Richmond & Kynard 1995, Gisbert et al. 1999, Kynard & Horgan 2002, Zhuang et al. 2002, 2003, Kynard et al. 2002a,b, 2003, Kynard & Parker unpubl. data). The continuous larva-juvenile 2-step migration style of Suwannee River Gulf sturgeon has not been found in other *Acipenser* species and suggests an unusual adaptation to rearing in marginal habitat at the southern limit of the species range. Migration style of Gulf sturgeon in other rivers is likely similar to Suwannee River Gulf sturgeon, but local variation likely exists due to changes in food supply and water quality. Similar migration and foraging styles may also occur in southern Atlantic coast Atlantic sturgeon and southern shortnose sturgeon, but research is needed.

Acknowledgements

We thank Frank Chapman, University of Florida, for providing fertilized eggs and the Florida Marine Fisheries Department for approving transfer of Gulf sturgeon eggs to Massachusetts. Richard Barrows, U.S. Fish & Wildlife Service, Bozeman Fish Technology Center, Bozeman, MT provided sturgeon starter diet. Brian Kynard reviewed videotapes and processed data. J. Clugston and K. Sulak provided valuable reviews of the manuscript; K. Sulak provided unpublished data and valuable insight into the Suwannee River's ecology. The S.O. Conte Anadromous Fish Research Center provided funding.

References

Bain, M. 1997. Atlantic and shortnose sturgeons of the Hudson River: Common and divergent life history attributes. Env. Biol. Fish. 48: 347–358.

Balon, E. 1999. Alternative ways to become a juvenile or a definitive phenotype (and on some persisting linguistic offenses). Env. Biol. Fish. 56: 17–38.

Bath, D.W., J.M. O'Conner, J.B. Albert & L.G. Arvidson. 1981. Development and identification of larval Atlantic sturgeon (*Acipenser oxyrhynchus*) and shortnose sturgeon (*A. brevirostrum*) from the Hudson River estuary, New York. Copeia 1981: 711–717.

Bowen, B.W. & J.C. Avise. 1990. Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: Influence of zoogeographic factors and life-history patterns. Marine Biology 197: 371–381.

Carr, S.H. & T. Carr. 1996. First observations of young-of-the-year Gulf of Mexico sturgeon (*Acipenser oxyrinchus desotoi*) in the Suwannee River, Florida. Copeia 1996: 44–46.

Chapman, F.A. & S.H. Carr. 1995. Implications of early life stages in the natural history of the Gulf of Mexico sturgeon, *Acipenser oxyrinchus desotoi*. Env. Biol. Fish. 43: 407–413.

Chan, M.D., E.D. Dibble & K.J. Kilgore. 1997. A laboratory examination of water velocity and substrate preference by age-0 Gulf sturgeon. Trans. Amer. Fish. Soc. 126: 330–333.

Clugston, J.P., A.M. Foster & S.H. Carr. 1993. Gulf sturgeon, *Acipenser oxyrinchus desotoi*, in the Suwannee River, Florida, U.S.A. pp 215–224. *In*: Second International Symposium on Sturgeon, Moscow.

Dovel, W.L. & T.J. Berggren. 1983. Atlantic sturgeon of the Hudson estuary, New York. NY Fish Game J. 30: 140–172.

Gisbert, E., P. Williot & F. Castello-Orvay. 1999. Behavioural modifications in the early life stages of Siberian sturgeon (*Acipenser baerii*, Brandt). J. Appl. Ichthyol. 15: 237–242.

Huff, J.A. 1975. Life history of Gulf of Mexico sturgeon, *Acipenser oxyrhynchus desotoi*, in Suwannee River, Florida. Florida Marine Res. Publ. 16, 32 pp.

Kynard, B. 1997. Life history, latitudinal patterns, and status of shortnose sturgeon, *Acipenser brevirostrum*. Env. Biol. Fish. 48: 319–334.

Kynard, B. & M. Horgan. 2002. Ontogenetic behavior and migration of shortnose sturgeon, *Acipenser brevirostrum*, and Atlantic sturgeon, *A. oxyrinchus oxyrinchus*, 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 notes on body color and development. Env. Biol. Fish. 66: 27–36.

MacKenzie, B.R. & T. Kiorboe. 1995. Encounter rates and swimming behavior of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. Limnol. Oceanogr. 40: 1278–1289.

Mason, W.T. Jr. 1991. A survey of benthic invertebrates in the Suwannee River, Florida. Environ. Monitor. and Assess. 16: 163–187.

Mason, W.T. & J.P. Clugston. 1993. Foods of the Gulf sturgeon in the Suwannee River, Florida. Trans. Amer. Fish. Soc. 122: 378–385.

Marchant, S.R. & M.K. Shutters. 1996. Artificial substrates collect Gulf sturgeon eggs. N. Amer. J. Fish. Manage. 16: 445–447.

Richmond, A. & B. Kynard. 1995. Ontogenetic behavior of shortnose sturgeon. Copeia 1995: 172–182.

Rivas, L.R. 1954. The origin, relationships, and geographical distribution of the marine fishes of the Gulf of Mexico. pp 503–505. *In*: P.S. Galtsoff (ed.) Gulf of Mexico, Its Origin, Waters, and Marine Life. Fishery Bulletin 89, Fishery Bulletin of the Fish and Wildlife Service Vol. 55.

Secor, D.H. 2002. Atlantic sturgeon fisheries and stock abundances during the late-nineteenth century. Amer. Fish. Soc. Symp. 28: 89–98.

Smith, T.I.J. & J.P. Clugson. 1997. Status and management of Atlantic sturgeon, *Acipenser oxyrinchus*, in North America. Env. Biol. Fish. 48: 335–346.

Snyder, D.E. 1988. Description and identification of shortnose and Atlantic sturgeon larvae. Trans. Amer. Fish. Soc. Symp. 5: 7–30.

Stabile, J., J.R. Waldman, F. Parauka & I. Wirgin. 1996. Stock structure and homing fidelity in Gulf of Mexico sturgeon (*Acipenser oxyrinchus desotoi*) based on restriction fragment length polymorphism and sequence analyses of mitochondrial DNA. Genetics 144: 767–775.

Sulak, K.J. & J.P. Clugston. 1998. Early life history stages of Gulf sturgeon in the Suwannee River, Florida. Trans. Amer. Fish. Soc. 127: 758–771.

Sulak, K.J. & J.P. Clugston. 1999. Recent advances in life history of Gulf of Mexico sturgeon *Acipenser oxyrinchus desotoi* in Suwannee River, Florida, U.S.A.: A synopsis. J. Appl. Ichthyol. 15: 116–128.

Van Eenennaam, J., S.I. Doroshov, G.P. Moberg, J.G. Watson, D.S. Moore & J. Linares. 1996. Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrinchus*) in the Hudson River. Estuaries 19: 769–777.

Vladykov, V.D. & J.R. Greeley. 1963. Order Acipenseroidei IN: Fishes of the western North Atlantic. Sears Foundation for Marine Research, Memoir 1, Part 3: 24–60.

Waldman, J.R. 1995. Sturgeons and paddlefishes: A convergence of biology, politics, and greed. Fisheries 20: 20–21.

Waldman, J.R. & I.I. Wirgin. 1998. Status and restoration options for Atlantic sturgeon in North America. Cons. Biol. 12: 631–638.

Zhuang, P., B. Kynard, L. Zhang, T. Zhang & W. Cao. 2002. 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. 2003. Comparative ontogenetic behavior and migration of kaluga, *Huso dauricus*, and Amur sturgeon, *Acipenser schrenckii*, from the Amur River. Env. Biol. Fish. 66: 37–48.