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Ontogenetic behavior and migration of Chinese sturgeon, *Acipenser sinensis*

Ping Zhuang[a,b], Boyd Kynard[c], Longzhen Zhang[a], Tao Zhang[a] & Wenxuan Cao[b]
[a]*Yangtze River Fisheries Research Institute, Chinese Academy of Fishery Sciences, Jingzhou, Hubei 434000, China (e-mail: zhuang@yfi.ac.cn)*
[b]*Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, Hubei 430072, China*
[c]*S. O. Conte Anadromous Fish Research Center, U.S. Geological Survey, Biological Resources Division, P.O. Box 796, Turners Falls, MA 01376, U.S.A.*

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Synopsis

The Chinese sturgeon, *Acipenser sinensis*, is an anadromous protected species that presently only spawns in the Yangtze River. Using laboratory experiments, we examined the behavioral preference of young Chinese sturgeon to physical habitat (water depth, illumination intensity, substrate color, and cover) and monitored their downstream migration. Hatchling free embryos were photopositive, preferred open habitat, and immediately upon hatching, swam far above the bottom using swim-up and drift. Downstream migration peaked on days 0–1, decreased about 50% or more during days 2–7, and ceased by day 8. Days 0–1 migrants were active both day and night, but days 2–7 migrants were most active during the day. After ceasing migration, days 8–11 embryos were photonegative, preferred dark substrate and sought cover. Free embryos developed into larvae and began feeding on day 12, when another shift in behavior occurred–larvae returned to photopositive behavior and preferred white substrate. The selective factor favoring migration of free embryos upon hatching and swimming far above the bottom may be avoidance of benthic predatory fishes. Free embryos, which must rely on yolk energy for activity and growth, only used 19 cumulative temperature degree-days for peak migration compared to 234 degree-days for growth to first feeding larvae, a 1 : 12 ratio of cumulative temperature units. This ratio suggests that sturgeon species with large migratory embryos, like Chinese sturgeon, which require a high level of energy to swim during migration, may migrate only a short time to conserve most yolk energy for growth.

Introduction

Chinese sturgeon, *Acipenser sinensis*, is an anadromous species that presently only remains in the Yangtze (= Changjiang) River, China (Wu 1963, Hubei Institute of Hydrobiology 1976). Adult Chinese sturgeon, which are a maximum of 400 cm total length (TL) and 452 kg body weight (BW), are one of the largest fish to enter fresh water (Fu 1988a, Chang & Cao 1999). The population supported a historical fishery that was focused in the upper river, particularly the Yibin reach at river km 2800. Eighty percent of the total annual sturgeon landings (combined catch of Chinese sturgeon and Dabry's sturgeon, *A. dabryanus*, a dwarf riverine species) from the 1950s to the 1970s occurred in this reach (Luo & He 1988, Zeng 1990, Zhuang et al. 1997).

As a result of damming and overfishing, populations of both sturgeon species have greatly declined in abundance (Yu et al. 1986, Zen 1990, Cao 1992, Zhuang 1994, Zhuang et al. 1997, Wei et al. 1997, Chang 1999). Construction of Gezhouba Dam in 1981 at Yichang, Hubei Province, 1766 km from the river estuary, blocked the spawning migration of Chinese sturgeon to the Yibin spawning reach. In 1983, commercial capture of Chinese sturgeon was prohibited and in 1988 the species was listed as a Category I protected

species (highest level of protection). Some successful spawning occurs in the short reach below the dam (Gezhouba spawning site) as verified by the capture of early-life stages in 1982 (Yu et al. 1986) and during 1996–1999 by Wei et al. (personal communication). Although commercial fishing for Chinese sturgeon was prohibited after 1983, as many as 100 adults have been removed annually to support a culture and restocking program (Xiao et al. 1999).

Research on Chinese sturgeon has focused on artificial culture, spawning, and population dynamics. Artificial spawning was first carried out in 1972 using adults captured from the spawning site on the Jinsha River located in the upper reaches of the Yangtze River (Ke et al. 1988, Chongqing Fisheries Research Institute unpublished report). Hybrids of Chinese and Dabry's sturgeon were produced in 1976 (D. Xie personal communication, Zhuang et al. 1997). Artificial spawning of adults captured below Gezhouba Dam and stocking of young has also been done almost yearly since 1983 (Fu et al. 1984, Chang 1999, Xiao et al. 1999), and up to 1998, 4.258 million young have been released to the river (Xiao et al. 1999). The population dynamics of pre-spawning adults at Gezouba Dam was investigated by Hu et al. (1985, 1992), Yu et al. (1986), Deng et al. (1991), Wei et al. (1997), Chang (1999), and Yi et al. (1999). Spawning behavior of adults below Gezhouba Dam was studied using acoustic telemetry from 1994 to 1999 (Kynard et al. 1995, Wei et al. 1998, Wei & Kynard unpublished data).

Most aspects of the early life-history of Chinese sturgeon have not been studied. Zhao et al. (1986) and Yi (1994) investigated the distribution and abundance of juveniles from the Yichang reach to the estuary. They found juveniles concentrated at the river estuary during the period of May–September, and almost all of the young fish found in the estuary were younger than 1 year old. Huang et al. (1991) studied feeding habits of 104 wild juveniles (19.0–43.5 cm TL), and observed that the major food was small fish (Gobiidae), worms (Oligochaeta), and shrimp (Crustacea). Deng et al. (1998) characterized the initial feeding response of larvae to artificial diets and successfully fed larvae with commercial food. Growth and rearing methods for yearlings under artificial conditions were investigated by Xiao et al. (1994), who found that the optimum temperature for juvenile growth was 22–23°C. Zhuang et al. (1999) found that larvae started feeding at 12 days after hatching when water temperature was 18–20°C and the point-of-no-return (starvation tolerance) was 12 days after initiation of feeding. However, little is known about migration or behavior and ecology during early development.

Recent laboratory studies on behavior of early-life intervals of several sturgeon species indicate that young sturgeon of all species undergo ontogenetic changes in behavior and migration (Richmond & Kynard 1995, Gisbert et al. 1999, Zhuang 1999, Kynard & Horgan 2002). Behavioral preferences of embryos and larvae for physical environmental factors and migratory behavior are innate and little affected by experimental environmental factors such as temperature and water velocity (Richmond & Kynard 1995, Kynard et al. 2002). Thus, the behavioral patterns observed in the laboratory correctly reflect young sturgeon behavior in the river. Ontogenetic behavior of the sturgeon species observed to date reflect adaptations to river conditions and not to phylogeny (Kynard et al. 2002). Studies of early-life behavior provide insight into the probable behaviors of fish in their natural habitat, are useful for modeling behavioral ecology (Noakes & Baylis 1990), and can be used to develop conservation strategies (Kynard & Horgan 2002). Understanding behavioral preferences of young fish may also assist artificial culture by improving rearing techniques (Richmond & Kynard 1995, Zhuang 1999).

Our objective was to document the ontogenetic behavior and migration of Chinese sturgeon from hatchling to 30-day-old late larvae in laboratory experiments and to use this information to make a conceptual model of the early-life behavior of wild Chinese sturgeon. We studied the daily habitat preference for water depth, illumination intensity, substrate color, and cover, and also documented diel activity and migration. This information was integrated with existing knowledge on young Chinese sturgeon in the natural environment to make the conceptual model.

Methods

Two female and three male pre-spawning Chinese sturgeon were captured just downstream of Gezhouba Dam in early October 1998. They were injected with the hormone LRH-A on 9 October, spawned at 9:00 h on 10 October, with each female's eggs inseminated with sperm from all males. We transported 3000 eggs (combined, both females) to the Yangtze River Fisheries Research Institute, Jingzhou, Hubei Province, and placed them into re-circulating incubation containers with water temperature of 18.6–21.2°C. After 115 h of incubation, hatching began at 4:00 h on 15 October and

lasted about 24 h. We used this date for the birth date of the group, i.e., day 0 was 15 October, day 1 was 16 October, and so on. This notation of age excludes the cleavage egg and embryonic development intervals (Balon 1999).

Sturgeon development was scaled to age and cumulative daily temperature. We recorded water temperature daily and used these data to calculated daily thermal units and cumulative temperature units (CTU) in degree-days after hatching. Cumulative degree-days were calculated to mid-day of each day when behavioral tests were carried out and reflected temperature during the first 12 h of the current day and the second 12 h of the previous day. For example, day 0 fish accumulated 0 degree-days and day 1 fish accumulated $0.5 \times$ temperature °C on day 0 plus $0.5 \times$ temperature °C of day 1.

After most embryos had hatched at 12:00 h on 15 October, we removed 2000 for experiments to a 1.8 m diameter round fiberglass tank with 0.35 m water depth. One-half of the tank's top was covered and a sheet of black nylon tissue and several rocks (diameter, 8 cm) were put on the bottom to provide concealment. When free embryos developed into larvae and began to feed, bottom cover was removed. Fish were fed live brine shrimp, *Artemia* spp., four times a day when they started feeding on day 12. After day 19, we fed fish mixed live brine shrimp and soft moist commercial diet six times per day, and gradually reduced the proportion of brine shrimp in the diet to zero by day 26. After day 26, fish were only fed moist commercial food six times a day.

Some testing procedures were the same for all habitat preference experiments. Prior to a test, all test fish were removed randomly from the rearing tank and placed together in a 2 l plastic holding jar. During tests, fish were tested singly, then returned to the rearing tank. Thus, there was no chance that an individual could be tested twice in any particular test replicate. There was a small chance that a fish could be collected and captured in other tests, but the chance of recapture was small in the rearing tank with 2000 fish.

Throughout the paper, we use the term embryo to refer to hatched free embryos, and larvae to refer to the initial feeding life-stage. We did not observe juveniles, which developed after our 30 day observation period.

Illumination choice

We tested 10 sturgeon daily for their preference of illumination intensity. The plastic test aquarium (50 cm long × 38 cm wide × 20 cm water depth) was a dark blue color, so external light could not penetrate through the four vertical sides. Light over the aquarium was supplied by three 40-watt fluorescent lamps. A black cover over one-half of the aquarium's top divided the water area into three almost equal portions of illuminated area (1200–1500 lx), a light transition area (250–300 lx), and a dark area (35–50 lx). The position of the top cover was reversed daily to prevent side bias of fish. We replaced aquarium water periodically during tests to keep water within 1°C of rearing tank water.

During testing, a single fish was removed from the holding jar and placed at the water surface in the center of the aquarium. Each fish was acclimated for 2 min, then we recorded movement for 5 min as a continuous time series relative to position in the tank (illuminated or dark area). After each fish was tested, we returned it to the rearing tank, and introduced another from the holding jar. The time spent in the illuminated area was converted to percent of total time and we used this percent in all data analyses.

Substrate color choice

We daily tested 10 sturgeon for preference of white and dark substrate. The test aquarium was the same dimension as the aquarium used for illumination tests. The bottom of the aquarium was covered with two pieces of white and black plastic that divided the bottom equally. Three 40-watt fluorescent lamps over the aquarium provided 850 lx across the top. We reversed the orientation of the white and dark sheets daily to control for position effect on fish choice and replaced water periodically to keep aquarium water within 1°C of rearing tank water.

During testing, a single fish was removed from the holding jar and placed at the water surface in the center of the aquarium. After 2 min of acclimation, we recorded fish movement over the two bottom habitats for 5 min as a continuous time series relative to time spent on white or black substrate. After each fish was tested, we returned it to the rearing tank. The time spent on white substrate was converted to percent and we used this percent in all data analyses.

Cover choice

We daily tested 10 sturgeon for cover preference. We used an identical plastic aquarium as used for previous tests to evaluate cover preference. Similar to Richmond & Kynard (1995), we put 10 piles of rocks

(each rock, 5–6 cm diameter; each pile, 100 cm^2) on the bottom of the aquarium in checkerboard fashion to provide cover habitat. There were approximately equal areas of cover and open habitats on the bottom. We replaced aquarium water periodically during tests to keep water within 1°C of rearing tank water.

During testing, we removed a single fish from the holding jar and placed it at the water surface in the center of test aquarium. After a 2 min acclimation, we recorded fish movements for 5 min as a continuous time series relative to time spent in cover or open. After each fish was tested, we returned it to the rearing tank. The time spent in cover was converted to percent of total time, and we used this percent in all data analyses.

Water depth choice

We daily tested 8 sturgeon for water depth preference in an artificial stream tube that simulated a vertical section of river (see design in Kynard et al. 2002). The stream tube was a clear plexiglass cylinder (diameter 15 cm; height 160 cm; water depth 150 cm) with a two-blade paddlewheel (total width 5 cm) down the center of the tube. The paddlewheel blades extended from 10 cm beneath the water's surface to 8 cm above the bottom. This allowed fish at the bottom or top to remain there without disturbance from the turning of the paddlewheel blades. A variable speed motor connected to the paddlewheel clockwise rotated it creating a horizontal current around the tube at 3 cm s^{-1}. The outside of the tube was marked at 1 cm intervals bottom to top (0–155 cm) to record fish position. One-half of the bottom was covered by two layers of dark-colored, flat stones (each 5–6 cm diameter) and the other one-half, including the drain area, was left open. We added a 5 cm wide band of black plastic around the outside of the lower 5 cm of the tube to make the bottom dark. A tan curtain was placed around the entire outside of the tube to create an even background and to facilitate viewing fish. A small plastic tube to introduce fish was attached along the length of the paddlewheel. After exiting the introduction tube on the bottom, fish had a choice of remaining at the bottom or moving above the bottom into the water column, and if they chose the bottom, of remaining in cover (rocks) or open.

During tests, we introduced fish singly into the stream tube. Then we started the paddlewheel, waited 1 min for fish acclimation, and recorded up- and downward movements of fish. Fish depths were recorded continuously during two periods: 1–2 min and 9–10 min (based on the method of Kynard et al. 2002). We also recorded when fish swam into or with the current. After each fish was tested, we partially drained the water, removed the test fish, and refilled the stream tube to keep water temperature within 1°C of rearing tank.

Migration and diel activities

We observed sturgeon in a light blue colored oval endless channel (see the design in Kynard & Horgan 2001). The tank's channel had a circumference of 5 m, width of 15 cm, and water depth of 15 cm. A small pump in the tank created velocity in the channel of a mean of 4.6 cm s^{-1} (range 2.8–10.6 cm s^{-1}). The channel bottom was smooth, and 4 rocks (diameter 5–8 cm) were placed at each end of the oval tank to provide cover habitat and slow water velocity. Over the tank at one location, we installed an overhead video camera with infrared (IR) light to observe the migrants that passed. White reflective tape was attached to the channel bottom and sides in the video field of view to enhance seeing the small sturgeon at night. The video system recorded for 5 min each hour for 24 h. Photoperiod was natural and temperature was 17.8–20.3°C, a temperature regime similar to the river. Tank water was partially changed every day.

We observed 15 fish for 30 days in the oval channel. After fish started feeding on day 12, we fed them the same schedule as other sturgeon in the rearing tank. Only two fish died, one each on days 3–4. They were immediately replaced with new fish randomly selected from the rearing tank. From the videotapes, we visually determined the number of up- and downstream migrants for each hour of each day, then subtracted the number of upstream from the number of downstream migrants, to obtain the net number of downstream migrants. This number of fish was used in all analyses. We termed fish moving up- and downstream as migrants because we believe they would be migratory if in the river.

Data analyses

We converted the time fish used habitat areas (illumination, substrate color, and cover) into percent of total observation time. After arcsine transformation of these percentages (Zar 1999), we used STATISTIC 5.0 to examine the daily percent of fish preferring a habitat condition for significant trends with age. Paired t-tests of the median percent were used to determine

whether fish showed significant differences for habitat preference. We calculated binomial 95% confidence intervals for each day to see if they included 50% (no preference).

For water depth preference in stream tube tests, we only calculated the daily median value of height fish used above the bottom at 9–10 min. Kynard & Horgan (2002) showed this time interval was better than the earlier time periods.

Downstream migration timing was determined using the daily net downstream migrant numbers (substract the number of daily upstream migrants from the number of daily downstream migrants). Net downstream migrant numbers of day versus night were also compared with paired t-test to see if fish showed significant differences for diel activity.

Results

A summary of the size of Chinese sturgeon at each developmental interval and cumulative daily temperature is presented in Table 1 and a summary of ontogenetic behavior and migration is shown in Table 2. Because the specific behaviors observed were not the same for each day, a daily account of each behavior is shown.

Illumination preference

Days 0–20 Chinese sturgeon were photopositive except for a brief period on day 8 (Figure 1). Hatchlings (day-0 fish) were 100% photopositive and this behavior continued to day 4. Most 5–6 day old sturgeon were still photopositive. Sturgeon 7–10 days old also significantly preferred illumination, but the response was less strong (day 7, median = 81.8%, $p = 0.0213$). Day 7 sturgeon were significantly less photopositive than day 5–6 fish ($t = 2.82$, $p = 0.0015$). On day 8, the percent preferring illumination was the lowest observed, but there was no significant preference for illumination or dark because of the great variation in response (median = 62.5%, $p = 0.9080$).

Table 1. Summary of the size of Chinese sturgeon at each developmental interval and cumulative daily temperature from hatchling (day 0) to early juvenile (day 52).

Age (day)	Developmental interval	Total length (mm)		Sample size (N)	Cumulative temperature (degree-days)	Events
		Mean	Range			
0	Hatchling	13.4	12.0–15.4	20	0	Hatching
1	Early embryo	16.2	15.1–16.7	20	19	Peak migration ceases
11	Late embryo	31.3	29.6–32.0	20	215	
12	Early larva	32.7	30.3–34.1	20	234	Feeding begins
30	Late larva	44.2	41.7–46.1	20	556	
40	Early juvenile	50.8	47.4–56.2	18	728	Teeth lost
52	Early juvenile	65.5	59.7–70.6	28	930	

Table 2. Summary of the ontogenetic behavior and migration of Chinese sturgeon from hatched embryo (day 0) to late larva (day 30).

Age (day)	Response to physical environment				Migrate downstream	Diel behavior
	Prefer illumination	Prefer white substrate	Prefer cover	Swim far above bottom		
0–1	Yes	Yes	No	Yes	Yes	D/N[1]
2–4	Yes	Yes	No	Yes	Yes	Diurnal
5	Yes	No	No	Yes	Yes	Diurnal
6–7	Yes	Yes	No	No	Yes	Diurnal
8	No	No	Yes	No	No	D/N
9–10	Yes	Yes	Yes	No	No	D/N
11–16	Yes	Yes	No	No	No	D/N
17–20	Yes	Yes	No	ND[2]	No	D/N
21–30	ND	ND	No	ND	No	D/N

[1]D/N – day and night active. [2]ND – no data.

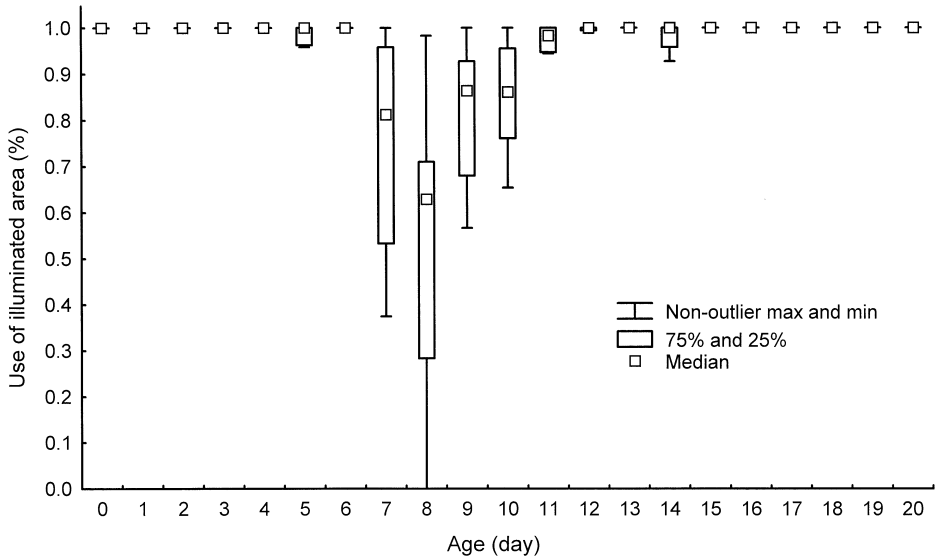

Figure 1. Preference of Chinese sturgeon for illumination intensity. Figure shows the percent of time (median ± range) in the illuminated area of the illumination preference test tank by age.

There was no significant difference between day 7 and day 8 sturgeon ($t = 1.45$, $p = 0.15$), but day 8 fish were significantly different from day 5 and day 6 fish ($t = 5.43$, $p = 0.0002$). From day 9 to day 10, the percent showing positive phototaxis increased again, and fish preferred illumination on day 9 (median = 85.2, $p = 0.0678$) and day 10 (median = 86.4, $p = 0.0501$). During days 11–14, fish were photopositive with over 98% (median) preferring illumination. From day 15 to 20, all sturgeon were photopositive.

Substrate preference

There were three periods when substrate preference changed (days 0–4; days 5–12; and days 13–20; Figure 2). One hundred percent of 0–4 day old sturgeon preferred white substrate. From days 5 to 12, except day 8, most sturgeon still preferred white substrate, but the range of preference was variable. Only day 8 fish showed no preference for substrate (median = 49.7%, $p = 0.9786$), and they were significantly different from days 5 to 7 ($t = 3.36$, $p = 0.0250$) and days 9–12 ($t = 3.0$, $p = 0.0050$). Fish again strongly preferred white substrate after day 11 (day 11 median = 100%, $p = 0.0010$; day 12 median = 100%, $p = 0.0347$; days 13–20, 100% preferred white substrate)

Cover preference

All days 0–6 sturgeon strongly preferred open habitat (Figure 3). A low percent (median = 15%) of day-7 fish chose cover ($p = 0.0019$), but this was the first indication of a behavioral change in preference. On day eight 88.3% chose cover and this similar preference continued to day 10 (day 8-median = 88.3%, $p = 0.0023$; day 9-median = 90.0%, $p = 0.0045$; and day 10-median = 78.6%, $p = 0.0005$). During days 11–17, preference for cover gradually decreased, i.e., no preference on day 11 (median = 50.0%, $p = 1.0000$), preference for open habitat on day 12 (median = 39.3%, $p = 0.0125$), and similar decreasing preference for cover on days 13–17. By day 18 all sturgeon preferred open habitat again. Preference for open habitat continued during subsequent tests to day 30. Day 30 fish were in the late-larva period, so both early and late-larvae preferred open habitat.

Water depth preference

Hatchling and day-1 sturgeon immediately swam-up off the bottom and were 107 cm (median) above the bottom at 9–10 min (Figure 4). On days 2–3, fish swam higher, some even to the water's surface (median = 140.0 cm). From days 4 to 8, the distance fish moved

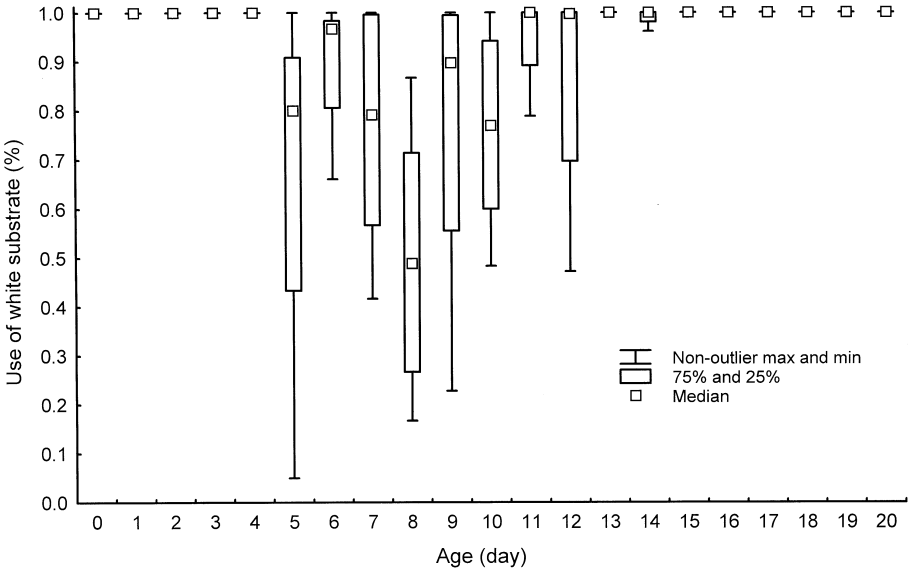

Figure 2. Preference of Chinese sturgeon for black and white substrate color. Figure shows the percentage of time (median ± range) on white substrate of the white vs. black test tank by age.

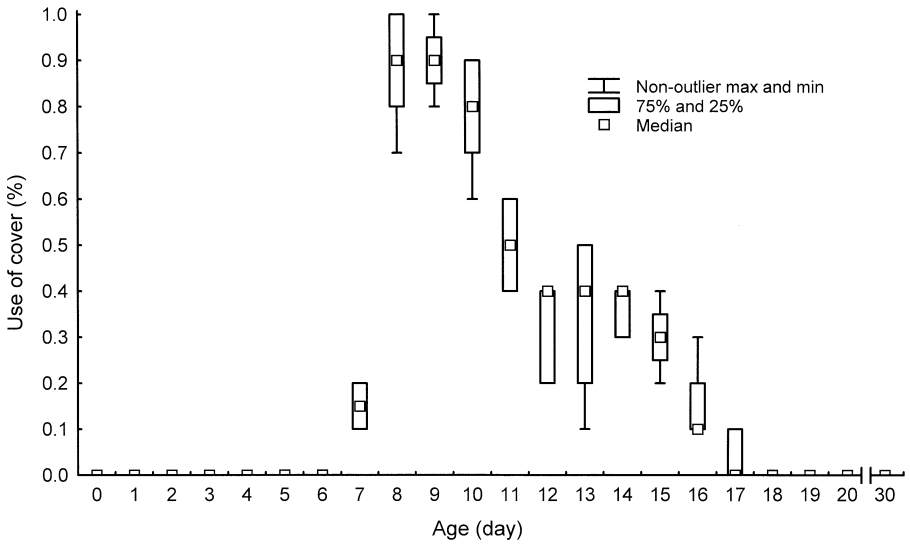

Figure 3. Preference of Chinese sturgeon for cover. Figure shows the percent of time (median ± range) in cover of the cover vs. open test tank by age.

above the bottom was greatly reduced, but the behavior was highly variable with some fish moving to the surface. By day 9 most fish remained near the bottom and by day 10, all fish used the bottom. A few fish moved above the bottom for a short distance on days 11–12. For the remainder of our observations, sturgeon were on or near the bottom.

Migration and diel behavior

Migration began at hatching on day 0 (Figure 5). There was a 2-day peak downstream migration period from day 0 (median of downstream migration number = 50) to day 1 (median = 46). During days 2–7, the number of migrants decreased to 50% or less of peak

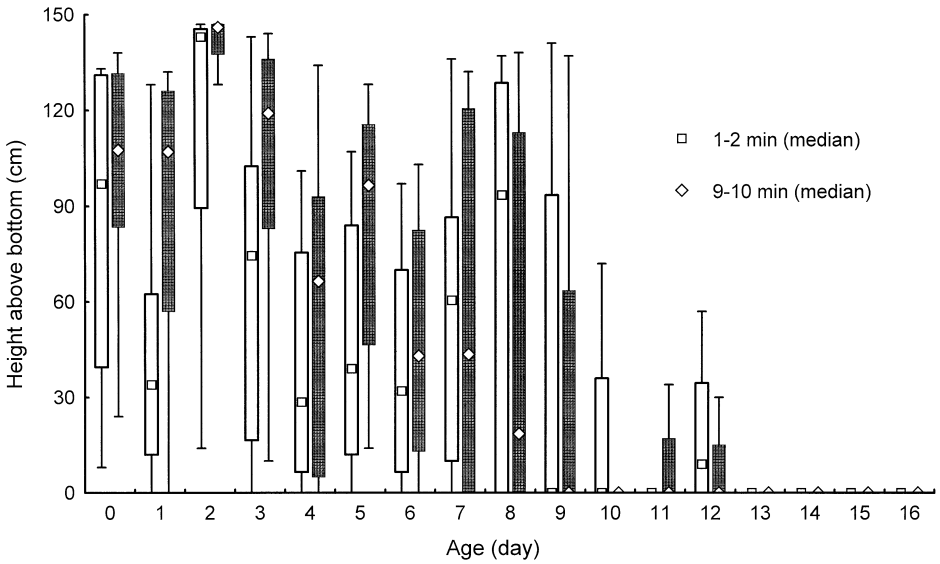

Figure 4. Preference of Chinese sturgeon for swimming height above the bottom. Figure shows distance above the bottom (median ± range) in 1–2 min and 9–10 min in the stream tube by age. Symbols are: open column = 1–2 min observation, solid column = 9–10 min observation.

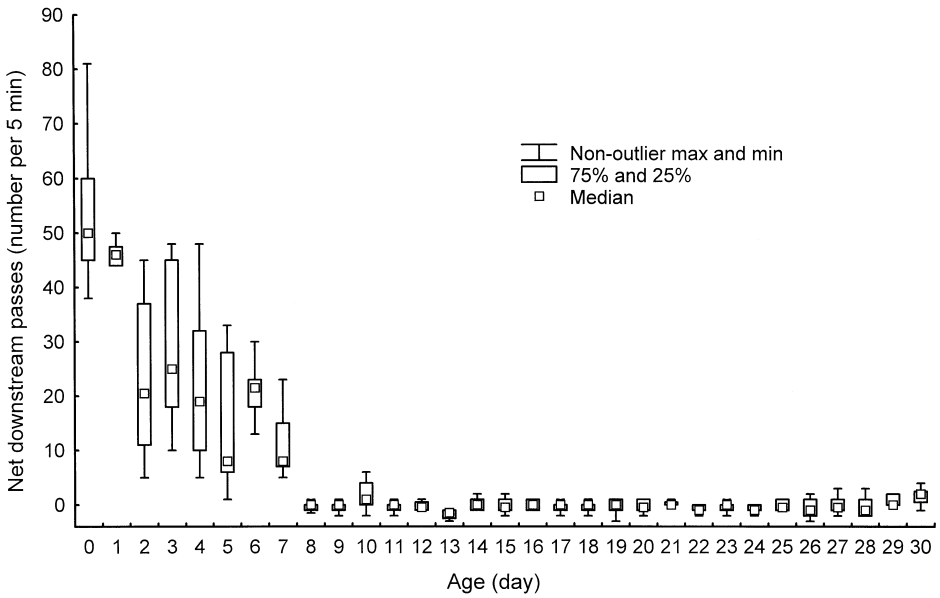

Figure 5. Migration of Chinese sturgeon. Figure shows the number of net downstream migrants (median ± range) of 5 min per hour in the oval endless channel from hatchling to late-larvae developmental stages.

migrant days (day 2-median = 20, day 3-median = 25, days 5 and 7-median = 8). On day 8, the number of migrants was zero. Zero or a low number of migrants were observed daily until day 30. The CTU from day 0 to day 1 (2 day peak migration) was 19 degree-days and 157 degree-days to day 8 (migration end).

The diel activity of young sturgeon is shown in Figure 6. The net number of embryos moving

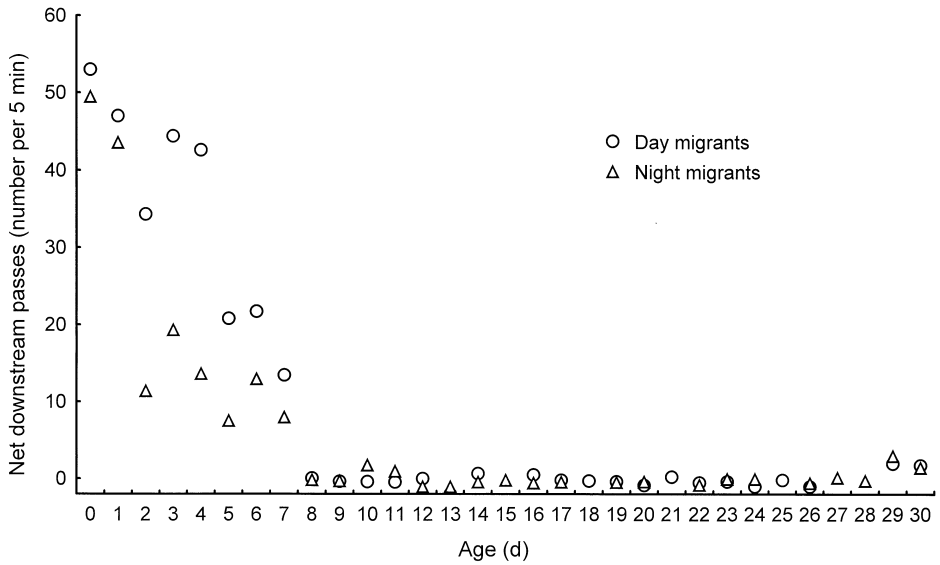

Figure 6. Diel downstream movement of Chinese sturgeon. Figure shows the number of net downstream migrants (median) observed for 5 min per hour in the day and at night. Fish were observed by video in the oval endless channel from hatchling to late-larvae developmental stages.

downstream per hour was higher in the day than at night during days 0–1, but the difference was not significant (day-0 fish, $p = 0.5635$; day-1 fish, $p = 0.5848$). However, days 2–7 fish moved more during the day, particularly on day 2 ($p = 0.00005$), day 3 ($p = 0.0001$), and day 4 ($p = 0.0000$). There was no daily significant difference for diel activity after day 8 (day 8, $p = 0.8245$). Late embryos (day 8) and late larvae (day 30) behaved similarly, with no difference in downstream activity during the day or night. Based on morphological observations (disappearance of teeth in mouth), larvae developed into juveniles around day 40 at a mean TL of 50.8 mm (Table 1).

Discussion

Hatched embryos (age day 0)

Hatchlings were a mean of 13.4 mm long (Table 1), photopositive, and after hatching, immediately swam to near the water surface of the artificial stream tube (Table 2, Figure 4). Their swimming motion, a strong back and forth movement of the tail, was almost continuous and fish only rested briefly (drift phase) before resuming upward swimming. Hatchlings did not return to the bottom after 10 min of swimming and likely would not after a much longer time, but data are lacking. Although we did not collect swimming duration information, anytime that we observed hatchlings in the rearing tank or in the migration tank, they were swimming off the bottom. Hatchlings can continue this strong swimming behavior 24 h a day (Figure 6).

The behavioral drive to remain above the bottom (95 cm or higher for hatchlings and day 1 fish) seemed to dominate all other behaviors and should move embryos far downstream. In the Yangtze River, hatchlings should swim above the bottom and leave the spawning site immediately after hatching, drifting rapidly downstream with river flow. Bottom river velocity in the channel of the Gezhouba reach is fast (about 100 cm s^{-1} at 100 cm above the bottom, Kynard unpublished data). If embryos remained in a velocity of 100 cm s^{-1} (similar to conditions at Gezhouba), they should move downstream about 86 km in 24 h. However, the river widens about 25 km downstream from Gezhouba and velocity slows, making the downstream progress of embryos much slower. This would be the case even if they remain in the channel like other migrant acipenserid early-life intervals (Kynard 1997). Considering all factors, it seems probable that during a 2 day peak migration all embryos could potentially move about 100 km downstream. The embryos that continue to migrate to day 7 could be distributed much farther downstream.

The rapid downstream movement of hatched embryos is supported by capture of wild sturgeons. Thirty hatchlings (14.4–16.0 mm long) were captured 20 km downstream of the Gezhouba spawning site on 6 November 1982 by Yu et al. (1986). Additionally, 7 hatchlings were captured just downstream of the historical Sankuaishi spawning site, 27 km upstream of Yibin City on 3 November 1971 (Ke & Tian 1988). The water velocity in the Sankuaishi site was 14 cm s^{-1} (river bottom), 58 cm s^{-1} (river column), and 115 cm s^{-1} (river surface) when sturgeon spawned on 24 October 1975. Thus, for embryos in the water column moving about 50 km per day, peak migrants could move about 100 km in 2 days.

The behaviors of Chinese sturgeon hatchlings we observed were similar to other sturgeon species that migrate as embryos. These species are Amur sturgeon, *A. schrenckii,* Russian sturgeon, *A. gueldenstaedti* (Zhuang 1999), pallid sturgeon, *Scaphirhynchus albus*, shovelnose sturgeon, *S. platorynchus* (Kynard et al. 2002), and Siberian sturgeon, *A. baerii* (Votinov & Kas'yanov 1979). This behavior differs with species that migrate as larvae, such as shortnose sturgeon, *A. brevirostrum* (Richmond & Kynard 1995, Kynard & Horgan 2002) and Atlantic sturgeon, *A. oxyrinchus oxyrinchus* (Kynard & Horgan 2002).

Embryos (age days 1–11)

The body size of Chinese sturgeon free embryos was larger than most Acipenseridae species. Day 1 embryos were a mean of 16.2 mm long, and day 11 embryos were a mean of 31.3 mm long (Table 1). Day 1–2 embryos continued to swim above the bottom from 100 cm to the water's surface at 150 cm (Figure 4). Because the water depth in the stream tube was only 150 cm, we do not know how far above the bottom the day 2 fish would have gone if water had been deeper, but they showed the desire to go farther than 150 cm. Days 0–1 embryos were the peak downstream migrants, so all fish migrated for about 48 h. On days 2–7, some fish continued to migrate (about 50% or less of peak migration; Figure 5). Because the sample of days 2–7 fish used in preference tests included both migrants and nonmigrants, we likely tested fish that preferred to swim far above the bottom and others that did not; thus, the wide variation in response of fish in the stream tube. By day 8, all embryos in the oval tank had stopped downstream migration, were becoming photonegative, and most remained near stream tube's bottom. When embryos remained on the bottom, most also sought cover. This behavior was different from pallid and shovelnose sturgeon (Kynard et al. 2002), whose embryos migrate, but they never seek cover. Late embryos of Chinese sturgeon were photopositive, preferred white substrate, and had a decreasing preference for cover habitat. This suggests a habitat switch from a migratory mode to a foraging mode in preparation for feeding. In the river, an illuminated, light-colored bottom open habitat would likely be in sandy shallows, not in the channel, so late nonmigrant embryos may switch from channel to shoal habitat.

Generally, sturgeon should not exhibit preference for cover and illumination on the same day. While embryos were only significantly photonegative on day 8, many fish avoided illumination on days 7–10, the same period they had the highest preference for cover (days 8–10). Many fish seeking cover did not show a high preference for the dark habitat. This result may be due to using an illumination level on the dark side that was too high to evoke a strong preference for the dark side. For example, the dark area had 35–50 lx of illumination and this level may not be low enough to evoke a strong preference for darkness. Kynard et al. (2002) used a dark habitat with an illumination level of 0.1–0.7 lx in the test tank for tests with pallid and shovelnose sturgeon. This may be a better level to use.

The occurrence of a positive phototaxis of early embryonic Chinese sturgeon was initially difficult to understand because spawning occurs on the river bottom in total darkness at Gezhouba. Illumination level at just 1-m below the water surface in the Gezhouba spawning site was zero and the river depth was 15–20 m during the 1995 spawning period (Kynard unpublished data). It seems likely that generation discharge from Gezhouba Dam disturbs bottom deposits of silt in the reservoir and greatly increases the turbidity level below the dam. However, the bottom darkness is not likely the historical spawning situation. Observations from 1971 to 1975 in the Sankuaishi historical spawning site showed that spawning occurred from mid-October to mid-November after the last flood of the year. Spawning occurred when water depth decreased to a mean of 5.6 m from a mean depth of 12.3 m during floods, and silt level decreased to a mean of 0.5 kg m^{-3} from 3.0 kg m^{-3} during floods (Ke & Tian 1988). These hydrological changes suggest that illumination would penetrate deep into the water column during the sturgeon spawning period. Thus, free embryos would likely be exposed to illumination on the bottom. Because free embryos are encountering an environment (darkness)

that they did not evolve adaptations for, they could have reduced survival compared to the natural situation.

Diel activity changed during ontogeny from an initial 2 day period (days 0–1) of activity during the day and night to a 6 day period (days 2–7) of diurnal activity (day active), then a third period from the late-embryo to the late-larva intervals (days 8–30) when fish returned to day and night activity but at a very low level of activity. Shortnose sturgeon larva migrants (Richmond & Kynard 1995) and pallid sturgeon embryo migrants (Kynard et al. 2002) were strongly diurnal. However, larva migrant Atlantic sturgeon (Kynard & Horgan 2002) and embryo migrant Amur sturgeon (Zhuang 1999), were nocturnal and Russian sturgeon embryo migrants were active both day and night (Zhuang 1999). Thus, diel activity patterns of sturgeon migrants are highly variable. We do not understand the adaptive significance of this variation in diel behavior.

Larvae (days 12–30)

Embryos develop into larvae and begin to feed in the laboratory on day 12 (Zhuang et al. 1999). Day 12 larvae were a mean of 32.7 mm long, and day 30 late larvae were a mean of 44.2 mm long (Table 1). Our observation on the size of first feeding larvae is supported by Huang (1988), who noted that larvae started feeding when they were 30.0–31.5 mm long. A few early larvae (days 13–17) used cover, but use of cover declined to zero by day 18. Day 18 and older larvae used open habitat, were benthic, preferred light-colored substrate, and were photopostive. These behaviors of larvae were different from that of shortnose and Atlantic sturgeon (Richmond & Kynard 1995, Kynard & Horgan 2002), whose larvae were migratory. However, the behavior of Chinese sturgeon larvae was similar to other species that migrate as embryos, i.e., Amur sturgeon and Russian sturgeon (Zhuang 1999), and pallid sturgeon and shovelnose sturgeon (Kynard et al. 2002).

The Shashi reach 100 km downstream from the Gezhouba spawning site is likely the rearing area for Chinese sturgeon. Yu et al. (1986) collected 10 Chinese sturgeon juveniles (78–94 mm TL) from the Shashi reach on 27 March 1982 about 5 months after spawning. The Yangtze River below the Shashi reach is wide (1–2 km), braided, and sinuous with many islands and sandy shoals. Water velocity is reduced and several tributaries join the main channel. The information from Yu et al. (1986) and the present laboratory results indicate that the Shashi reach is likely the most upstream part of the rearing area of larvae and juveniles. The river is similar downstream to Wuhan, a distance of about 500 km, and the long distance migrants (some migrated 7 days) may stop in this reach.

The historical rearing ground of most Chinese sturgeon larvae and early juveniles in the upper Yangtze River was probably in the 700 km long Luzhou reach (from 100 km downstream of the Yibin spawning area to Fengjie). This reach is similar to the Shashi reach with abraded channel, sandy shallows, moderate water velocity, and several tributaries joining the main channel (Zen 1990). Dabry's sturgeon larvae and juveniles have also been found between Luzhou and Mudong (about 400 km downstream from Yibin), but not at the upper part of the Luzhou reach (Fu 1988b, Zhuang et al. 1997). Young Dabry's sturgeon feed on worms (Oligochaeta), shrimps (Crustacea), and small fish (Gobiidae; Zhuang et al. 1997), the same as young Chinese sturgeon (Huang 1988, Huang et al. 1991). It may be that historically, Chinese and Dabry's sturgeon used the same rearing area. The river below Fengjie enters the 207 km long Three Gorges reach. The river becomes narrow (smallest width 140 m) and deep (largest depth during flood 110 m), with few sandy shoals, and very swift water velocity (maximum surface velocity 7 $m\,s^{-1}$, Hubei Institute of Hydrobiology 1976). This reach may not be suitable for rearing young sturgeon and neither young Chinese sturgeon nor young Dabry's sturgeon has ever been found in the Three Gorges reach.

Initial feeding is a key step for any fish's survival. While no data are available on the food items eaten by wild Chinese sturgeon larvae, cultured larvae are reared on zooplankton, worms and mosquito larvae (Huang 1988). Chinese sturgeon initiate feeding at the age of 12 days, and the point-of-no-return is 24 days (12 days after larvae initiate feeding; Zhuang et al. 1999). Larvae are large, i.e., 12-day-old larvae have a mean TL of 32.5 mm (Table 1) and can feed on larger prey than most sturgeon larvae. We speculate that Chinese sturgeon larva habitats are the sandy shallow highly productive littoral zone. Larvae are photopositive and prefer white substrate, behaviors that may be related to enhancing visual predation of rapidly moving prey (Kynard & Horgan 2002).

Adaptations

Chinese sturgeon eggs and embryos encounter high predation pressure at the spawning site. In both

historical sites and the Gezhouba site, there are many benthic fishes that eat sturgeon eggs and embryos, e.g. *Coreius guichenoti*, *Coreius. heterodor*, *Rhinogobio typus*, *Pseudobagrus vachelli*, *Leiocassis longirostris* and several species of catfish, family Siluridae (Yu et al. 1986, Wu et al. 1988, Deng et al. 1991, Hu et al. 1992). At the Jinduizi spawning area (3 km downstream of Loudong Town) on the Jinsha River, spawning occurred on 26 October in 1963 (Ke & Tian 1988) and within 3–4 days, fishermen caught 800 predatory fish at the spawning site. Many sturgeon eggs were found in the predator's stomachs, i.e., over 1000 sturgeon eggs were found in the intestine of a 600 g *Coreius guichenoti*. However, fishermen could not catch any of the predatory species in the reach downstream. Then, after Chinese sturgeon embryos hatched, the predatory fish were caught again in the downstream reach. This anecdotal information suggests that predators concentrated at the sturgeon spawning site during spawning to feed on eggs, then moved downstream as embryos hatched and the embryos moved downstream. Except for the Chinese sturgeon spawning periods, fishermen rarely caught predatory fishes such as *Coreius guichenoti* and *Pseudobagrus vachelli* at the Jintuizi reach (Ke & Tian 1988). A similar situation may have occurred at the Gezhouba spawning site in the 1980s (Hu et al. 1985, Deng et al. 1991, Wu et al. 1992) and 1990s (Chang & Cao1999).

Estimates of the number of Chinese sturgeon eggs lost to predatory fishes are high at the Gezhouba spawning site. Chang (1999) analyzed adult abundance and egg consumption by predatory fishes at Gezhouba from 1988 to 1998 and found that the number of eggs spawned annually was 8.570–41.485 million (mean = 24.411 million) and that over 90% were consumed by predatory fishes. This suggests that predation on eggs and embryos at the spawning site by predatory fishes may be the major factor affecting survival of these life intervals.

The available evidence indicates there is a high level of predation on Chinese sturgeon eggs and embryos by native fishes, suggesting this selective factor has been occurring for many generations. Given the severe risk to these early-life intervals, natural selection should favor females spawning eggs in areas that favor egg survival and also, of hatchling embryos with behaviors that increase survival by avoiding predation. For Chinese sturgeon, survival of eggs is likely increased by females that spawn eggs over a bottom of rocks and boulders where eggs can sink into crevices and be concealed from predators. This situation has been found in North American sturgeons, the shortnose sturgeon (Kieffer & Kynard 1996, Kynard 1997) and the white sturgeon, *A. transmontanus* (Parsley & Beckman 1994). Where heavy losses of eggs and embryos from predation at a spawning site exists, selection should also favor phenotypes that immediately depart upon hatching. Furthermore, since the predatory fishes are all benthic, selection should also favor migrant embryos that swim far above the bottom. Hatchling embryos of Chinese sturgeon exhibited both immediate migration and high vertical movement, behaviors that move young sturgeon quickly downstream and away from the concentration of predators.

Migration of Chinese sturgeon should result in a wide distribution of embryos downstream of the spawning area. Almost 100% migrated for 2 days (days 0–1), then about 50% or less migrated for an additional 6 days. This migration pattern may reflect a behavior to disperse embryos over a wide area and reduce density of individuals in any one area, thus reducing predation and competition for resources, or both. When embryos stopped migration, they were still undeveloped with poor swimming ability and sought cover to complete development. Cover seeking is likely related to avoiding predation.

The CTU data on Chinese sturgeon suggests that sturgeon species with large-bodied embryos may allocate less energy contained in their yolksacs to migration and more to growth than species with small-bodied embryos. Peak migration of the large Chinese sturgeon embryos lasted only 2 days or 19 degree-days CTU, while the peak migration of the small embryos of pallid sturgeon lasted 3–4 days or about 60 degree-days (Kynard et al. 2002). Thus, Chinese sturgeon embryos completed their peak migration at about one-third the CTU used by pallid and shovelnose sturgeon. Moreover, the CTU for development to first feeding larvae of Chinese sturgeon (mean TL, 32.7 mm, day 12 fish) was 234 degree-days, while the CTU to feeding larvae of pallid and shovelnose sturgeon was only one-third of this value (79 degree-days for pallid sturgeon and 72–78 for shovelnose sturgeon, mean TL, 15 mm; days 4 or 5 fish; Kynard et al. 2002). Selection for large body size of Chinese sturgeon embryos, which likely expend a high level of energy swimming during migration, may have resulted in energetic factors related to body size being most important in determining migration duration and the eventual distribution of embryos. Examination of other sturgeon species with large embryos and an embryo migration should provide a test of the idea that large-bodied embryos have a

shorter peak migration and use less CTU for migration than small-bodied embryos.

Conservation implications

Our results give guidance for protection measures of early-life intervals of Chinese sturgeon. At the spawning site, eggs and embryos only need protection for about 1 week after spawning (5 days incubation, first 2 days after hatching). During downstream migration, embryos need protection from entrainment into water intakes and from discharge of effluents containing pollutants. In the rearing area, embryos, larvae, and juveniles need protection during these critical rearing intervals. They should be protected from capture or habitat disturbance, particularly from sand dredging, which can entrain and kill fish and also destroy feeding habitat. The present evidence suggests the rearing area is likely 100–200 km downstream of Gezhouba and includes the Shashi reach. However, additional field study is needed to verify this prediction.

Our results give guidance for the restocking program. Currently, 2-month old to yearling juveniles are annually released at the spawning site below Gezhouba Dam for the purpose of population restoration (Xiao et al. 1999). However, our results show the spawning site is not the appropriate place for releasing 2-month-old sturgeon because juveniles do not inhabit the spawning site. These fish should be released in the rearing area. Because stocked juveniles are not migratory (present data and unpublished data), they should not be released in the fast current of the main river channel, but in the slower flows in shoals. Also, because juveniles may compete for feeding space (Kynard & Horgan 2002), they should be dispersed over a wide area. Hydro-generation flows from Gezhouba Dam could have several deleterious effects on spawning of Chinese sturgeon. We have noted earlier that hydrogeneration causes high turbidity levels which create darkness on the bottom of the spawning area. Also, the high flows may affect timing of spawning by females, as occurs in shortnose sturgeon (M. Kieffer & B. Kynard unpublished data). The impact of hydrogeneration flows on Chinese sturgeon spawning should be evaluated to prevent potential loss of spawning success.

Efficient rearing of Chinese sturgeon contributes to population restoration or enhancement programs and to commercial aquaculture. Our results show that weak lighting should be provided over the rearing tank during all rearing and some directional water current should be provided to reduce stress in fish seeking current. Also to reduce stress, as fish develop, cover could be added to the tank bottom during the late-embryo period when they are seeking cover. After fish start feeding at 12 days, bottom cover should be removed and the rearing tank's bottom should be light-colored to help fish visually find moving food items.

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