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Ontogenetic Behavior of Shortnose Sturgeon, *Acipenser brevirostrum*

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Ontogenetic behavioral changes of young shortnose sturgeon *Acipenser brevirostrum* of Connecticut River stock are described for three morphological stages (embryo-larva-juvenile). Hatchlings (< 1-day embryos) were positively rheotactic, photonegative, benthic, and vigorously sought cover. If denied cover, they exhibited vertical swim-up and drift behavior until cover was found. Older 1–8 day embryos exhibited the same behaviors as hatchlings; except when denied cover, they searched along the bottom until cover was found. The photonegative and cover seeking behaviors are adaptations that enable embryos to complete development while concealed under structure at a spawning site. Larvae 9–16 days old left cover and were positively rheotactic and photopositive. An estimated 75% of 9–14 day larvae left bottom cover and swam in the water column, suggesting that larvae, not embryos, initiate the downstream migration from a spawning site. Larvae were most active at night and preferred deep water and silt substrate. Most 43–66 day juveniles were benthic swimmers and, like larvae, positively rheotactic, photopositive, and nocturnally active. Behavior of embryos and larvae suggests shortnose sturgeon should be classified in the lithophil reproductive guild, not the litho-pelagophil guild.

THE shortnose sturgeon *Acipenser brevirostrum* is an open substrate spawner exhibiting no parental care (Balon, 1975a). In the Connecticut River, polyandrous mating occurs in late April or early May and may be synchronized by decreasing river discharge and rising water temperature (Taubert, 1980; Buckley, 1982; Buckley and Kynard, 1985a). Females scatter demersal, adhesive eggs (Meehan, 1910) over rubble and boulder substrate (Buckley and Kynard, 1985a; M. Kieffer and B. Kynard, unpubl. data). Development of eggs to hatching typically takes less than 10 days (Buckley and Kynard, 1981).

Behavior of the early life stages of shortnose sturgeon has received scant study. The accumulated behavioral information concerning the early life period is limited to a few observations of cultured fish (Meehan, 1910; Buckley and Kynard, 1981; Washburn and Gillis Associates, Larvae 17–27 days old were significantly less active in the day than at night. In the day, larvae crossed the grid system at a mean rate of 0.03 grids/sec, whereas movement at night increased more than 10-fold to 0.37 grids/sec (t-test, $P < 0.01$).

Discussion

During development from embryo to larva, morphological and behavioral changes were exhibited almost simultaneously by all shortnose sturgeon. The morphological changes we observed were similar to those described by Disler (1960) for sevryuga. When fish developed from larva to juvenile, not all fish completed development at the same time, and we observed no striking change in behavior that indicated when fish became juveniles. Morphological characters indicated most fish were juveniles by day 40. Our behavioral observations on embryos and young larvae (fish to 16 days old) also were more complete than our observations on older larvae or juveniles. These stages deserve more study. In the following discussion, we examine behavior in relation to general sensory and morphological development and use laboratory observations to discuss the behavioral ecology and migration of wild fish.

Hatchling embryo.—Hatchlings were photonegative and vigorously sought cover under any available structure. After finding cover, hatchlings lay on their sides and constantly wiggled their tails and fin folds. This behavior enhances respiration (Disler, 1960). Meehan (1910) also found cultured hatchlings initially remained on the bottom for several days. Our observations differed with Buckley and Kynard (1981), who observed that hatchlings were active swimmers and photopositive for the first two days. We believe the hatchlings observed by Buckley and Kynard were not provided sufficient cover, so they continually searched for concealment. Disler also observed that hatchling sevryuga were photopositive in a brightly illuminated aquarium, but like Buckley and Kynard, Disler provided no cover. We suspect Disler's observations to be an artifact resulting from absence of cover. In a natural spawning area, the swim-up and drift behavior would enable hatchlings to move short distances until appropriate cover was found. The behavior could also result in downstream dispersal from the spawning area if cover was not found quickly.

Many hatchling Acipenseridae show swim-up and drift behavior, e.g., the Siberian sturgeon *A. baeri* (Votinov and Kas'yanov, 1979), the sevryuga (Disler, 1960), and the white sturgeon (E. Brannon, S. Brewer, A. Setter, M. Miller, F. Utter, and W. Hershberger, Bonneville Power Administration, Corps of Engineers, 1985, unpubl.). The distinctive swimming movement is determined by the fish's body shape and the anterior location of the center of gravity (Disler, 1960). Typically, hatchling shortnose sturgeon alternated swimming-drifting with resting until they were exhausted or until cover was found.

Embryos 1–8 days old.—These fish actively sought cover and, after finding concealment, lay on their sides fanning the fin folds. Unlike hatchlings, movement of embryos was mostly horizontally along the bottom. Disler (1960) made similar observations on the swimming behavior of 3–4 day sevryuga.

Shortnose sturgeon and sevryuga embryos may differ from white sturgeon embryos, which swam in the water column for up to five days after hatching in laboratory tests (E. Brannon, S. Brewer, A. Setter, M. Miller, F. Utter, and W. Hershberger, Bonneville Power Administration, Corps of Engineers, 1985, unpubl.). When shortnose sturgeon embryos were denied cover in our tests, they also continued swimming but stayed mostly on the bottom. We wonder whether the white sturgeon embryos observed would have continued to swim in the water column for days if adequate benthic cover had been provided.

In the Connecticut River, shortnose sturgeon spawn on rubble and boulder substrate (Buckley and Kynard, 1985a; M. Kieffer and B. Kynard unpubl. data), and our laboratory observations indicate that hatchlings and embryos should remain concealed under rocks and in crevices at the spawning area. The strong photonegative reflex and cover preference of hatchlings and embryos are probably adaptations to conceal the poorly developed fish and prevent injury or death caused by reckless swimming and poor avoidance of predators. Although metamorphosing fish may mitigate their vulnerability by cryptic coloration and behavior (Galis, 1993), the vulnerability of shortnose sturgeon embryos probably remains high. The captures of embryos downstream from spawning areas in the Connecticut River (Taubert, 1980) and the Merrimack River (Kieffer and Kynard, 1993), probably represents fish that were unable to find cover and drifted downstream. When hatchlings and embryos could not find cover in our laboratory tests, they continued swimming. This behavior in the wild would carry young fish downstream where they may find cover but at great risk. Premature movement of hatchlings and embryos from a spawning site could be a major source of mortality for young shortnose sturgeon. A spawning substrate with abundate crevices for concealment of eggs and embryos would seem critical to the survival of these life stages.

Larva.—Larvae left bottom cover, swam in the water column facing the current, and began feeding. As with other species of sturgeon beginning to feed, the mouth is filled with teeth. The mouth does not become toothless and fully protrusible until the juvenile stage (Disler, 1960).

The swimming ability of young larvae was greatly improved compared to embryos. Larvae 9–14 days old maintained position in a maximum water flow of 5.4 cm/sec. Similar results were obtained by Washburn and Gillis Associates (unpubl. report), who found 11-day larvae (n = 4) routinely swam distances of 50 cm in water velocities of 5.2 cm/sec; but when the velocity increased to 6.8 cm/sec, fish swam only 5 cm.

The high frequency (75%) of swimming by larvae 9–14 days old (14–17 mm TL) in the rearing tank suggests that in the wild these fish would be leaving the spawning area and migrating downstream. Although we did not test larvae for downstream movement, field captures of a few fish support the prediction of a migration by larvae. Two larvae, 13.0 and 14.7 mm TL, captured in the Saint John River, New Brunswick, Canada, were aged at "about two weeks" (Taubert and Dadswell, 1980). All of the fish (n = 4) collected by Bath et al. (1981) in the Hudson River were within our larval size range. Also, peak migration of lake sturgeon *A. fulvescens* larvae (mean TL, 17.5 mm) from a spawning site were 8–13 days old (Kempinger, 1988). The lake sturgeon larvae had well-developed barbels, mouth, gills, and fins. Some species of European *Acipenser* may migrate during the larval stage and at a similar age as shortnose and lake sturgeons. Thirty-one percent of the young sevryuga and Russian sturgeon *A. guldenstadti* captured migrating in the River Terek were 10–15 days old (Amirkanhov, 1969).

The percentages of swimming larvae (75% on day 9, 35% on days 15 and 42, and 13% on day 60) suggest that fish may use swimming time to regulate downstream dispersal distance, e.g., the time spent swimming could determine the dispersal distance. In the Connecticut River, concentration areas containing juveniles and adults are located downstream both near and far from the spawning area (Buckley and Kynard, 1985b; T. Savoy, Connecticut Department of Environmental Protection, 1991, unpubl.). The short period of swimming suggests that most larvae may move only a short distance before ceasing migration. Fish that continue swimming for many days may move to concentration areas far downstream from the spawning site.

Although the depth experiments did not give fish a choice of water depths available in the river, the results suggest that larvae less than 21 days old prefer the deepest water available. Thus, we would predict that wild larval migrants this age should be found in river channels. Young larval shortnose sturgeon have been captured within 1 m of the bottom in river channels (Connecticut River—Taubert and Dadswell, 1980; Hudson River—Bath et al., 1981; and Saint John River, New Brunswick—R. Pottle and M. J. Dadswell, unpubl. report). The larvae of other sturgeon species have also been found in channels: Atlantic sturgeon *A. oxyrhynchus* (Bath et al., 1981), sevryuga and Russian sturgeon (Amirkanhov, 1969; Sbikin and Bibikov, 1989), and the sterlet *A. ruthenus* (Veshchev, 1981).

Larvae about 20–21 days old appeared to undergo a major change in habitat preference related to water depth and substrate type. Whether these behavioral changes indicate a switch from migrant to resident is not known.

The nocturnal activity pattern of larvae in the rearing tank indicated that wild larvae probably migrate mostly at night. Larval lake sturgeon migrated from a spawning area at night with a peak between 2300–2400 h, and with 6.5-fold more migrants captured at night than in the day (Kempinger, 1988).

The adaptive significance of the day and night color phases of shortnose sturgeon larvae may be related to providing crypsis during downstream migration or for living in water of different depths or on substrates of varying brightness, or both. Sbiken and Bibikov (1989) also noted changes in coloration of juvenile sturgeon, and they attributed the phenomenon to changes in background brightness. Perhaps, both background brightness and illumination intensity level can stimulate the same coloration response of larvae.

Juvenile.—Although 15–27 day larvae and juveniles about 60 days old were different morphologically, they were similar for some behaviors, e.g., positive rheotaxis, photopositive, and active at night. Fish > 40 days old spent most of the time feeding on the bottom; thus, the incidence of benthic swimming may characterize, in a general way, a behavioral change from larva to juvenile. Larvae developed at different rates; and because we observed a group of fish