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ONTOGENY AND LIFE HISTORY OF SHORTNOSE STURGEON (*ACIPENSER BREVIROSTRUM* LESUEUR 1818): EFFECTS OF LATITUDINAL VARIATION AND WATER TEMPERATURE

A Dissertation Presented

by

ERIKA L. PARKER

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2007

Organismic and Evolutionary Biology

ONTOGENY AND LIFE HISTORY OF SHORTNOSE STURGEON (*ACIPENSER BREVIROSTRUM* LESUEUR 1818): EFFECTS OF LATITUDINAL VARIATION AND WATER TEMPERATURE

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Approved as to style and content by:

_____
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William Bemis, member

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Ethan Clotfelter, member

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Joseph Elkinton
Director, Graduate Program in Organismic and Evolutionary Biology

DEDICATION

To my son, Austin.

Your birth during the final stages of my preparation of this dissertation gave new meaning and inspiration to my life and my work.

ACKNOWLEDGEMENTS

I am grateful to Boyd Kynard for chairing my dissertation committee and providing guidance on every aspect of this project, and for being my mentor and friend for the past ten years. William Bemis, Ethan Clotfelter, and Cristina Cox Fernandes served as members of my dissertation committee, and I would like to thank them and also Jeffrey Podos for helpful comments on experimental design and dissertation preparation and for helping me to see my research as part of "the big picture" of evolutionary biology. Eric Hilton provided guidance with morphological examination of sturgeon larvae and allowed me access to his unpublished data. Timothy Parker constructed experimental tanks, viewed videotapes, entered data, and helped with fish care. Donald Pugh assisted with experimental tank construction and prepared Figure 2.1, and Brian Kynard assisted with viewing videotapes and entering data. Martin Horgan provided helpful suggestions for data analysis, and comments from Darren Lerner improved the tables and figures. This research was conducted at, and partially funded by, the S.O. Conte Anadromous Fish Research Center (USGS, BRD), and I would like to thank everyone there for their friendship and support. Additional funding was provided by the National Marine Fisheries Service (Charlestown, SC). Savannah River shortnose sturgeon eggs were provided by Kent Ware (USFWS, Bears Bluff National Fish Hatchery, Wadmalaw Island, SC), and sturgeon starter feed was supplied by Richard Barrows (USFWS, Bozeman Fish Technology Center, Bozeman, MT). I would like to thank my family for their patient and loving encouragement. I am especially grateful to my husband, Timothy Parker, whose support, both at the lab and at home, was essential to the success of this project.

ABSTRACT

ONTOGENY AND LIFE HISTORY OF SHORTNOSE STURGEON (*ACIPENSER BREVIROSTRUM* LESUEUR 1818): EFFECTS OF LATITUDINAL VARIATION AND WATER TEMPERATURE

MAY 2007

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Ontogenetic niche shifts usually occur concurrently with a change in developmental stage and likely evolved as a strategy to reduce mortality and optimize growth at each developmental stage. The optimal shift point may be flexible, however, and may be influenced by environmental cues. In this dissertation I address the following three objectives: (1.) Compare habitat preferences and dispersal duration and timing of early life stages of shortnose sturgeon from a northern (Connecticut River, MA, USA) and a southern (Savannah River, SC, USA) river, (2.) Determine the effect of three temperature regimes on the timing and pattern of downstream dispersal of shortnose sturgeon larvae, and (3.) Link changes in morphological development with ontogeny of behavior in shortnose sturgeon.

During the period of yolk-sac absorption, fish from the Connecticut and Savannah Rivers which were reared at the same temperature selected cover and dark habitat, sheltering under rocks and preferring darkness and black substrate. Once fish

began feeding exogenously, they switched rapidly to a preference for open, bright habitat, emerging from rocks and selecting illuminated areas and white substrate. Connecticut River fish moved downstream for 6 days (days 7–12 after hatching) beginning immediately after feeding began. However, Savannah River fish had a longer dispersal with multiple, prolonged peaks and fish continued a low level of downstream movement for the whole larval period and as early juveniles (at least until day 62). The differences in dispersal between Connecticut and Savannah River fish, however, were expressed under the same laboratory conditions, including temperature. Thus, genetic differences between the populations do exist and conservation strategies should consider this. In tests with Connecticut River fish to determine temperature effects on dispersal pattern, rearing fish at 10°C delayed the onset of dispersal, but increasing the temperature (15 and 20°C) produced a dispersal with multiple peaks, rather than simply shifting the peak to a younger fish age. Fish were morphologically similar when they began dispersing, regardless of river or temperature. Colder temperature caused development to slow and fish to delay beginning dispersal. These results show dispersal of shortnose sturgeon early life stages is influenced by river temperature.

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CHAPTER 1

OVERVIEW

During ontogeny, behaviors can develop gradually or undergo saltatory changes (Balon 1979). Many animals undergo changes in feeding, habitat use, morphology, physiology, competitors, and predators during their life history (Warkentin 1995, Jones et al. 2003). These ontogenetic niche shifts usually occur concurrently with a change in developmental stage and likely evolved as a strategy to reduce mortality and optimize growth at each developmental stage (Werner 1986, Werner and Hall 1988, Jones et al. 2003). An ontogenetic habitat change should occur when the expected ratio of growth to mortality in an alternate habitat exceeds the ratio in the current habitat, and an optimal size or developmental stage for the shift should exist. This optimal shift point may be flexible, however, if growth and mortality rates vary temporally or spatially, and may be influenced by environmental cues (Rowe and Ludwig 1991, Jones et al. 2003).

Differing environments can drive evolutionary changes in ontogeny of behaviors. For example, young threespine stickleback (*Gasterosteus aculeatus*) typically learn predator avoidance by evading their father's attempts to capture them in his mouth and return them to the nest (Huntingford et al. 1994) However threespine stickleback from a lake without predatory fishes displayed little antipredator behavior which the researchers attributed to a loss of the ability to learn the behavior from evading their father. Song learning in cowbirds can be influenced by social environment during ontogeny, resulting in geographic differences in song types, which lead to differences in mating systems and are passed from fathers to sons (West et al. 2003). The kea (*Nestor notabilis*), a New Zealand parrot, displays ontogenetic differences in vocalizations with juveniles producing

a “squeal” call that adults do not use (Bond and Diamond 2004). The researchers found that this juvenile vocalization varies between birds from different geographic areas, as does the adult “kee-ah” call.

Genetically-based geographic variation in behavior occurs in a wide range of animal taxa. Behaviors that vary geographically include migratory behavior, aggression or territorial behavior, structure or repertoire of calls or songs, courtship behavior, female preference for male calls, songs, or courtship displays, dietary preferences, antipredator behavior, and method of prey attack (Foster 1999). Animal ranges may span natural gradients in habitat, such as latitudinal or elevational gradients, so different traits are advantageous in different parts of the range (Ehrlich and Raven 1969). If geographic variation is genetically-based, it is usually maintained by selection (Ehrlich and Raven 1969). Local adaptation and geographic variation may also be due to phenotypic plasticity (Miner et al. 2005).

Intraspecific comparisons of behavior between populations tend to show loss of, or change in, ancestral patterns, rather than acquisition of novel behaviors (Foster 1999). For example, timing of migration or reproduction may change, or previously migratory populations may stop migrating. A subpopulation of the blackcap (*Sylvia atricapilla*) in Europe changed its migratory direction to travel to a new wintering area (Berthold 1995). Sockeye salmon (*Oncorhynchus nerka*) and American shad (*Alosa sapidissima*) in the Columbia River (WA, USA) changed the timing of their migrations as dam operations altered the spring temperature and flow regime of the river (Quinn and Adams 1996). Studies of introduced populations of house finches (*Carpodacus mexicanus*, Able and Belthoff 1998) and chinook salmon (*Oncorhynchus tshawytscha*, Quinn et al. 2000)

demonstrate that these species can change their migratory behavior in response to novel environmental conditions. All of these changes happened over a relatively small number of generations.

American shad on the east coast of North America return to their natal rivers to spawn, and northern populations have different life history characteristics than southern populations. In the north, where spawning conditions may vary widely from one year to another, a larger proportion of individuals are repeat spawners, and in the south, where springtime temperature and river discharge are more predictable, a larger proportion of fish spawn only once (Leggett and Carscadden 1978).

Intraspecific population comparisons can elucidate mechanisms of behavioral evolution. In some cases measurements of behavior under common conditions (common garden experiments) can reflect population differences and reveal selection pressures in the natal environments of each population (Foster 1999, Thorpe et al. 2005). Common garden experiments compare behavior or performance of animals from different locations under a particular set of environmental conditions. Sometimes the test is in the form of a challenge, such as exposure to temperature, salinity, or a predator. Each group is expected to perform better in its own environment. This type of experiment tests whether a particular environmental factor is an agent of selection. Choice experiments can also be used to study food, habitat, or mate preferences between populations in a common setting. For example, Ptacek and Travis (1997) found that female sailfin mollies (*Poecilia latipinna*) from different geographic areas preferred larger over smaller males and in some cases preferred males from their own population to foreign males. Females appear to have divergent preferences for size-specific values of traits in which males

differ; thus, the researchers concluded that sexual selection plays a role in maintenance of male variability, both within and among populations of this species. In other cases behavior is conditional (phenotypic plasticity) and measurement of reaction norms is more appropriate. In these cases population comparisons can be used to test predictions about the evolution of behavioral plasticity (Carroll and Corneli 1999, Thompson 1999).

Environment can shape behavior, and conspecific animals from different environments may express different behaviors in response to the same set of experimental conditions. Brown and Braithwaite (2004) found that tropical poeciliid fish (*Brachyraphis episcopi*) from low predation streams navigated more actively within an experimental maze, spent less time exploring the maze, and found and consumed a food reward more quickly than fish of the same species from high predation streams. The researchers attributed this difference to the fact that fish in the low predation sites experience more intraspecific competition and form rigid dominance hierarchies. Under these conditions quickly locating and defending a good foraging patch would be advantageous, whereas in the high predation streams fish likely benefit from spending more time exploring a new area to locate potential threats and potential refugia or escape routes (Brown and Braithwaite 2004).

Understanding geographic differences in behavior can be an important part of conservation. Pacific salmon *Oncorhynchus* spp. are one of the classic examples. These fishes have a great deal of variation in life history characteristics, including migration distance and timing, spawning time, age at spawning, age at outmigration, and body size (Beechie et al. 2006, Groot and Margolis 1991). Environmental factors such as seasonal stream flow regime affect the expression of these life history traits and salmon with

certain life histories are found more often in certain types of streams (Beechie et al. 2006). Thus, preserving the diversity of life history traits in Pacific salmon depends in part on preserving the diversity of environments where Pacific salmon are found (Beechie et al. 2006).

Another example is the work of Decker et al. (2003), who found that copepods (*Acartia tonsa*) from Chesapeake Bay, where areas of low dissolved oxygen occurred even before European colonization, will move to avoid hypoxic water, but copepods of the same species from Florida, where summertime hypoxia is a recent, anthropogenic problem, do not display behavioral avoidance of low oxygen water. Copepods are an important prey species for many fishes, and geographical differences in their behavioral responses to anthropogenic stressors may result in geographic variation in the severity of anthropogenic disturbance of aquatic food webs (Decker et al. 2003).

In this dissertation I address the following three objectives: (1.) Assess habitat preferences and dispersal patterns of early life stages of shortnose sturgeon from a northern and a southern river to determine if between-river differences exist in behavior of early life stages, (2.) Determine the effect of temperature regime on the onset and cessation of downstream dispersal of shortnose sturgeon larvae, and (3.) Link changes in morphological development with ontogeny of behavior in shortnose sturgeon.

CHAPTER 2

LATITUDINAL DIFFERENCES IN ONTOGENY OF BEHAVIOR BETWEEN TWO POPULATIONS OF SHORTNOSE STURGEON (*ACIPENSER BREVIROSTRUM* LESUEUR 1818): A LABORATORY STUDY

Introduction

Shortnose sturgeon (*Acipenser brevirostrum*) are migratory fish found in rivers along the east coast of North America from New Brunswick to Georgia, and they are protected throughout their range (COSEWIC 2005, USFWS 1967). Shortnose sturgeon life histories and adult behavior differ with latitude (Kynard 1997). Genetic variation exists among shortnose sturgeon populations in different rivers (Wirgin et al. 2005, Grunwald et al. 2002, Quattro et al. 2002), and one study identified morphological variation in shortnose sturgeon populations among several rivers in the northeast (Walsh et al. 2001). Grunwald et al. (2002) found 29 mitochondrial DNA nucleotide-substitution haplotypes among 275 shortnose sturgeon specimens from 11 rivers and estuaries throughout the species' range with significant genetic differentiation observed among all populations except the Delaware River and Chesapeake Bay. The purpose of this study is to examine geographic variation in behavior of young shortnose sturgeon shortly after hatching. This is likely a critical time when much mortality occurs and year class strength is established (Gross et al. 2002, Kynard et al. 2002).

The abundance of adult shortnose sturgeon is greater in the northern and north-central populations (New Brunswick to Maryland) than in the southern populations (North Carolina to Georgia). Even prior to anthropogenic disturbance, southern rivers may not have had adequate habitat or forage to support populations as large as those in

the north, but the differences in adult abundance likely have been accentuated by the greater anthropogenic impacts, such as harvest, dams, and pollution, on southern populations (Kynard 1997). Hatchery propagation and stocking has long been debated as a method to restore sturgeon populations (Quattro et al. 2002) and is currently used for conservation of some species (Ireland et al. 2002, Jackson et al. 2002). Understanding population differences in behavior during early life is important to ensuring that stocking is done appropriately and responsibly, and that young fish are placed into an environment for which they are suited.

Behavior of early life stages of sturgeons is mostly innate and thus studies in appropriate laboratory tanks can give insight into behavior of wild fish (Kynard and Horgan 2002). Behavior of early life stages follows several predictable saltatory changes, the expression and timing of which can easily be compared between species or between populations of the same species (Kynard et al. 2002). Behavior of sturgeon during early life stages varies by species and can also vary by population within a species (Kynard and Horgan 2002, Kynard and Parker 2004, Kynard and Parker unpublished data). Species or population comparisons can be done as common garden experiments with all fish reared and tested in the same controlled laboratory environment (Kynard and Horgan 2002).

The objective of this study was to assess habitat preferences and dispersal duration and timing of early life stages of shortnose sturgeon from a northern (Connecticut River, MA, USA) and a southern (Savannah River, SC, USA) river to determine if between-river differences exist in behavior of early life stages. I predicted that fish from both rivers should have similar preferences for habitat, choosing dark

habitat after hatching then switching to bright habitat upon beginning to feed. A previous study demonstrated this behavior in Connecticut River shortnose sturgeon (Kynard and Horgan 2002) and spawning and early rearing environments (i.e. before fish begin downstream dispersal) are likely similar between the two rivers (Kynard 1997). However, I expected Savannah River fish to move downstream more slowly and for a longer period of time, as did Gulf of Mexico sturgeon (*Acipenser oxyrinchus desotoi*) which live in rivers with habitat very similar to that of the Savannah River (Kynard and Parker 2004).

Methods

Eggs from each river were produced by the artificial spawning of one male and one female. Connecticut River fish were spawned at the S.O. Conte Anadromous Fish Research Center. Savannah River eggs were shipped from the Bears Bluff National Fish Hatchery (Wadmalaw Island, SC). All fish culture and experiments were done at the Conte Center. I reared eggs in a McDonald hatching jar and hatchling yolk-sac larvae swam naturally in over-flow water to 18-L circular rearing tanks. Larvae were fed a sturgeon starter diet (See Acknowledgments) twelve times daily using a timed feeder and also fed four times daily with live *Artemia* nauplii.

I used the number of days post-hatching to characterize age of fish, not the number of days post-fertilization, because I did not know how water temperature varied during shipping of Savannah River eggs. I used dechlorinated city water (Montague, MA) for rearing and all experiments. Temperature in rearing and test tanks was similar (± 1°C). I maintained the natural photoperiod for the Turners Falls, MA location. I

examined behavior during three life intervals: yolk-sac larva, larva, and juvenile. Terminology for stages follows that used by Bemis and Grande (1992).

In all experiments, I mixed the rearing tank water and randomly selected test fish from approximately 500 fish in the tank. I tested fish singly, then returned all to the rearing tank. No individual was tested twice in a daily replicate, but there was a small chance a fish could be captured and used in other tests.

Illumination and substrate color preference

Fish were tested daily for their response to illumination (phototaxis) and substrate color. These tests give some insight into whether fish prefer to be in open, bright areas such as up in the water column or dark areas of deep water or cover. For tests, I used two 20-L rectangular glass tanks with overhead light provided by two 20-W fluorescent lights and black plastic excluding other light. A black cover over one-half of the illumination aquarium's top divided the tank into equal areas of bottom illumination (8.2–3.0 lx) and dark (2.2–0 lx) over a uniform tan bottom. The bottom of the substrate tank was clear glass, and under the glass, the bottom area was divided equally into a black and a white square. Underwater light intensity on the bottom was: 4.3–2.6 lx (white) and 3.3–3.0 lx (black).

Each day I tested 10 fish. Each fish was tested individually and the covered side and the colors were reversed after each fish to prevent recording side bias. Test fish were placed at the water surface in the center of the aquarium. After 1-min acclimation, I visually recorded fish movement for 1 min as a continuous time series of presence on each half of the tank (illumination test – dark vs. illuminated, substrate test – white vs. black). I calculated the percent of time each fish spent on the illuminated or white side

and the daily mean percent of time all fish spent on the illuminated or white side, and plotted the percent as a daily time series. I transformed the daily percentages on the illuminated or white side to arcsine values and calculated binomial 95% confidence intervals to determine if fish spent a significant percent of time on one side of the tank. A mean and confidence interval below 50% of time on the illuminated or white side indicated significant preference for darkness or black substrate and above 50% indicated significant preference for illumination or white substrate; confidence intervals that included 50% indicated no significant preference.

Swimming height above bottom

I tested eight fish daily in an artificial stream tube that simulated a vertical section of water with horizontal water flow, like in a natural stream (Figure 2.1a). Illumination level in the tube was a gradient that varied from 50 lx at the bottom and 300 lx at the top to 5 lx at the bottom and 30 lx at the top depending on time of tests. Fish were generally tested at the same time each day.

During tests, a single fish and water were poured into the top of the introduction tube, which carried fish to the bottom. Only upward swimming and cover seeking were noted for 1 min (acclimation period); then at 5–6 min, I visually recorded swimming height of fish above the bottom each 10 s for 60 s (total measurements = 7) using a depth scale (1-cm marks with 0 = bottom) inscribed on the outside of the tube. I calculated the mean of the seven measurements for each fish and present the grand mean for eight fish as a daily time series.

One half of the tube's bottom was covered with two layers of gray rocks (5-cm diameter); the other half was open. During daily tests, I recorded the number of fish in

the rocks or in the water column. Fish in the rocks were considered to have a swimming height of 0 for average swimming height calculations.

Dispersal and diel activity

I observed up- and downstream movement of 15 fish (introduced as hatchlings) in an oval, endless stream tank colored light green-blue (Figure 2.1b). This tank creates a channel with a continuous flow of water that simulates a natural stream. Fish can move continuously up- or downstream and never encounter a wall or barrier. This type of tank is used in a laboratory setting to allow fishes to move up- or downstream volitionally so a researcher can examine the frequency and duration of movement. Downstream movement in such a tank has been correlated with downstream movement or migration of wild fishes for some species (Atlantic salmon, Zydlewski et al. 2005; shortnose sturgeon, Kynard and Horgan 2002). Underwater light intensity was 20 lx (maximum). Three rocks (each 10–15 cm diameter) in each turn of the channel provided cover habitat (structure, low light, and a slow velocity). The in- and outflow of water was 1-L min^{-1}. Water temperature during tests ranged from 16–23º C. Fish were observed until they had ceased or greatly decreased downstream movement; thus Connecticut River fish were observed until day 35 and Savannah River fish were observed until day 60. Fish were fed in this experimental tank as described above, with an automatic feeder that dispensed feed 12 times daily and with live *Artemia* nauplii four times daily.

I viewed fish movements with a video camera and infrared (IR) light over the tank to observe fish both during the day and night. Silver retro-reflective tape covered the walls and bottom of the tank only in the area seen in the video recording (Figure 2.1b). Under IR light this tape creates a light background upon which the small, dark fish are

easier to see, particularly at night. Fish were observed for avoidance of or attraction to the reflective surface, and neither was seen (E. Parker, personal observation). I viewed fish for 5 min per hour each 24 h and reviewed videotapes counting the number of up- and downstream fish passes for every other hour. If a fish died, it was replaced. However, fish were not replaced until live observations (see habitat preference section below) had been taken for the day, so on some days fewer than 15 fish were in the tank. The number of fish moving up- or downstream was scaled to the number of fish present.

The IR lights were not functioning properly during the first two weeks of the test with Savannah River fish, so this test was repeated using the same methods in March 2005. Fish were once again obtained as eggs from the Bears Bluff National Fish Hatchery (Wadmalaw Island, SC) and reared as described above.

Habitat use

In the oval stream during five observation periods per day, I counted the number of fish in four habitats: under rocks, on the bottom in the open, in the water column (> 3 cm above the bottom), and at the water surface. I calculated the grand total of fish in each habitat type each day, converted this number to percent of total fish in each habitat, and presented the percent in each habitat as a daily time series. If a fish had died I replaced it after the last observation period so it could acclimate overnight before I included it in my observations the following day.

Results

Connecticut River fish were spawned on 6 May 2003 and hatched on 12 May 2003. I received a shipment of eggs from the Savannah River on 16 March 2004 which hatched on 18 March 2004 and another shipment on 11 March 2005 which hatched on 17

March 2005. Connecticut River fish began feeding exogenously, and thus became larvae, on day 7 (125 CTU), and Savannah River fish became larvae on day 6 (102 CTU) in 2004 and on day 7 in 2005. We considered fish to be juveniles (i.e. to have the full adult complement of fin rays and ossification of bony parts) when they reached 57 mm total length based on a morphological study by Snyder (1988). This occurred on day 40 (787 CTU) for Connecticut River fish, day 41 (816 CTU) for Savannah River fish in 2004 and day 42 for Savannah River fish in 2005.

Illumination preference

Connecticut River days 0–5 yolk-sac larvae significantly avoided illumination (Figure 2.2a). Day-6 yolk-sac larvae slightly preferred illumination although the preference was not significant. Days 7–10 and day-12 larvae significantly preferred illumination. Larvae to day 30 continued to show a preference for illumination, although the preference was significant only on days 14, 19, 24, 25, and 27–30.

Savannah River days 0–5 yolk-sac larvae significantly avoided illumination except on day 4 when preference was not significant (Figure 2.2b). Day-6 larvae preferred illumination, although preference was not significant. Days 7–40 larvae significantly preferred illumination each time they were tested.

Substrate color preference

Connecticut River days 0–6 yolk-sac larvae had no significant preference for white or black substrate, except for day-1 yolk-sac larvae, which significantly preferred black substrate (Figure 2.3a). Days 7–30 larvae also had no significant preference for either substrate color, except days 9, 10, 12, 15, and 21 larvae which significantly

preferred white. There was a general trend for yolk-sac larvae to prefer black and larvae to prefer white substrate.

Savannah River days 0–4 yolk-sac larvae had a slight but not significant preference for black substrate (Figure 2.3b) and day-5 yolk-sac larvae slightly, but not significantly, preferred white substrate. Days 6–40 larvae had no preference for white or black substrate except days 10 and 15 larvae which significantly preferred white substrate.

Swimming height above bottom

Connecticut River yolk-sac larvae and days 7–9 larvae swam to a mean height of 40 cm or less (Figure 2.4a). Many yolk-sac larvae hid in the rocks and 60% or greater of the observations on yolk-sac larvae each day were in the rocks. Percentages of observations in rocks declined sharply over days 7–9 and from days 10–30 all fish were in the open except one fish tested on day 13. Fish in rocks were scored as 0 cm to determine mean swimming heights for each day. Day-10 larvae swam to a mean height of 105 cm and larvae continued to swim to heights between 40 and 105 until tests stopped on day 30 (Figure 2.4a). Larvae showed a slight trend toward lower swimming height with age.

Savannah River yolk-sac larvae swam to a mean height of 27 cm and 29 cm on days 0 and 1 respectively. Days 2–3 yolk-sac larvae swam to a mean height of 67–98 cm respectively, then days 4 and 5 yolk-sac larvae swam lower (Figure 2.4b). Some yolk-sac larvae did use rock cover, with 37–50% of observations in the rocks. Larvae did not use rock cover except for two fish on day 7 and one fish on day 10. Larvae swam to a mean height of 67–117 cm on all days (Figure 2.4b).

Dispersal and diel activity

I observed Connecticut River shortnose sturgeon dispersal for 35 days, and Savannah River shortnose sturgeon dispersal for 62 days. During daytime visual observations on 15 yolk-sac larvae, a low percentage of Connecticut River fish moved downstream on day 0 (13.3%) and days 3 (6.7%), 4 (6.7%), 5 (2.7%), and 6 (1.3%). On days 1 and 2, 100% of the fish sought cover in the rocks (Figure 2.8a). Savannah River fish showed somewhat greater downstream movement as yolk-sac larvae and less use of rock cover (Figure 2.8b). Days and percent moving downstream (in parenthesis) follow: day 0 (60%), day 1 (33.3%), day 2 (13.3%), day 3 (13.3%), day 4 (20%), day 5 (13.3%). In both groups, if yolk-sac larvae were not moving downstream they were hiding in the rocks.

Connecticut River yolk-sac larvae had a very low-intensity downstream movement of < 0.4 passes per fish per 5 min during both day and night (Figure 2.5a). Savannah River fish were not video taped at night until day 16 due to a malfunction of the lights in 2004, but yolk-sac larvae moved downstream at rates of <0.5 passes per fish per 5 min during the day (Figure 2.6a). In 2005 Savannah River yolk-sac larvae moved downstream during the day at rates of <0.6 passes per fish per 5 min and during the night at rates of <0.5 passes per fish per 5 min (Figure 2.7a). In both years Savannah River yolk-sac larvae exhibited higher rates of downstream movement during days 0-2 than did Connecticut River yolk-sac larvae.

Connecticut River larvae were not observed moving downstream during daily visual observations, but the video data revealed a slow rate of nocturnal net downstream movement. Downstream movement peaked on days 7–12 at about 0.6–0.8 net

downstream passes per fish per 5 minutes. Connecticut River larvae did not move upstream during day or night at a rate higher than 0.1 passes per fish per five minutes, nor did they move downstream during the day at a rate higher than 0.1 passes per fish per five minutes. Connecticut River fish appeared to have stopped moving downstream by day 35 (Figure 2.5a). Connecticut River fish did not show any linear trend in activity by age. Overall activity (total number of up- and downstream passes separated by day and night) was higher at night than during the day (Figure 2.5b).

During daytime visual observations in 2004, Savannah River larvae (day 6 fish and older) were not seen moving downstream until day 25. The video data showed a very slow downstream movement during the daytime at < 0.1 passes per fish per five minutes until day 22. However, when we began collecting nighttime video data on Savannah River fish on day 16, they showed net downstream movement of 0.4 passes per fish per five minutes. From days 16–30 fish moved downstream at night at 0.4–1.0 passes per fish per five minutes. Daytime downstream movement peaked from days 22-34. From days 30-35 nighttime net downstream movement decreased, until on day 35 there was no net movement up or downstream at night. Net downstream movement during the day decreased from days 33-35, and on day 35 fish showed a slight net upstream movement during the day. On days 60-62, fish had a slow net downstream movement of 0.1-0.3 passes per fish per five minutes during both day and night. During this major directed long-term movement, fish actively swam headfirst downstream and were not drifting.

A similar pattern occurred in 2005 (Figure 2.7a). Net downstream movement of larvae gradually increased with the peak of movement occurring from days 22-41.

Between days 41 and 60, when observations ended, net downstream movement continued but at a slower rate. Most downstream movement occurred at night with larvae moving only at a rate of <0.2 passes per fish per five minutes during the day. There was less daytime downstream movement in 2005 than in 2004, but in both years daytime movement peaked during the same time as nighttime movement.

Overall activity of fish increased with increasing age during both day and night in 2004 (Figure 2.6b). Fish moved both up- and downstream more as they grew, but upstream movement increased more, yielding an overall increase in activity but a decrease in net downstream movement. In 2005 nighttime activity increased much more with increasing age than did daytime activity (Figure 2.7b). As in 2004, upstream movement increased more than downstream as fish grew so that net downstream movement decreased with age, but overall activity increased.

Habitat use

Visual observations on non-dispersing Connecticut River fish during the day in the oval stream show there was a gradual ontogenetic trend, from yolk-sac larvae to larvae, for fish to occur with decreasing frequency in rock cover and increasingly on the open bottom (Figure 2.8a). There was no major ontogenetic shift in use of rock cover when yolk-sac larvae developed into larvae on day 7, but by day 14 all fish were foraging on the open bottom. Fish rarely swam up into the water column (Figure 2.8a).

Savannah River yolk-sac larvae increased their use of cover from 40% on day 0 to 86.6% on day 2, then use of cover stayed at 80–86.6% until day 5 (Figure 2.8b). Day-6 larvae were all in cover, then use of cover decreased with age until day 13, when all fish were foraging in the open. Fish generally stayed near the bottom (Figure 2.8b).

Discussion

Fish from both rivers preferred dark habitat and used rock cover as yolk-sac larvae. Upon becoming larvae both groups showed an ontogenic behavioral shift to preferring bright, open habitat. Both groups showed some downstream movement as yolk-sac larvae; this was more pronounced in Savannah River yolk-sac larvae, which used rock cover less in the first three days after hatching. Dispersal of Connecticut River fish peaked on days 7–12 after hatching, beginning when they became larvae. Savannah River fish had a longer dispersal with multiple, prolonged peaks; fish continued a low level of downstream movement for the whole larval period and as early juveniles, as I predicted.

A previous study on Connecticut River shortnose sturgeon in the same tank but at higher densities showed a similar dispersal pattern with a brief peak on days 18-20, beginning two days after fish became larvae (Kynard and Horgan 2002). Fish took more days to absorb their yolk and become larvae because the water temperature was lower than in the present study. A study of shortnose sturgeon spawned in a semi-natural enclosure also showed a brief dispersal beginning just after fish made the transition to the larval stage (Kynard et al. In press, b), as did netting in the Connecticut River (Kynard et al. In press, a).

A long larval and early juvenile dispersal like that of the Savannah River group was also present in Gulf of Mexico sturgeon (*Acipenser oxyrinchus desotoi*), a related species in similar rivers (Kynard and Parker 2004). This type of dispersal may be a widespread adaptation to habitat conditions in southern rivers, which could have serious implications for southern sturgeon in dammed rivers. Sturgeon tend to spawn 200-300

km upriver, likely to prevent larvae that are drifting downstream from reaching saltwater before they develop salinity tolerance (Kynard 1997). However, dams block adults from reaching historical spawning areas and can cause adults to spawn below the dam, at a location that is potentially far downstream of the historical spawning area (Kynard 1997). This behavior of adults, coupled with the long larval and juvenile dispersal, may cause juveniles to contact saltwater too early. Additionally, my data show that shortnose sturgeon from different rivers can have different migration styles, and if fish are stocked into a river with conditions that are not suited to their migration style, they likely will not survive.

The behavioral differences between the Savannah and Connecticut Rivers were likely related to habitat differences, particularly abundance of forage and possibly also predation risk. In the southern river, less abundant forage and higher predation risk might select for increased movement and dispersal (Kynard and Parker 2004). Rivers in southeastern (Mason 1991) and far northern (Chiasson et al. 1997) parts of North America have lower benthic invertebrate abundance than more central rivers. The longer dispersal may help fish increase their chances of encountering prey and distance them from each other, reducing competition. Costs of dispersal can also determine where and when dispersers settle, and increases in the risk of mortality during dispersal reduce habitat selectivity of dispersers (Ward 1987, Stamps et al. 2005). Rivers in southeastern North America have a higher diversity of benthic predators such as suckers (Family Catostomidae) and catfishes (Family Ictaluridae) than rivers in northeastern North America (Jenkins and Burkhead, 1993). Kynard and Horgan (2002) argue that low predation risk in the Connecticut River favors yolk-sac larvae staying in or near the

spawning area and waiting to disperse as larvae. Perhaps movement is also more costly in the Connecticut River than in the Savannah; possibly there are more benthic predators in the Savannah River and more predators in the water column in the Connecticut River.

The differences in dispersal may also reflect differences in patchiness or predictability of habitat in the two rivers (Stamps et al. 2005). In habitats with small suitable patches separated by large unsuitable patches dispersers are more likely to select a patch and stay there, as Connecticut River fish did, whereas in more uniform habitat dispersers are more likely to keep moving, as Savannah River fish did (Baker and Rao, 2004).

Early life stages of shortnose sturgeon are the life stages most vulnerable to predation and tend to suffer high mortality from a variety of causes; thus year-class strength is likely determined early (Gross et al. 2002, Kynard et al. 2002). Understanding habitat needs of early life classes and taking appropriate measures to protect those habitats is an effective way to protect sturgeon populations (Gross et al 2002, Kynard et al. 2002). Stocking is also a method of conservation that targets survival of early life stages (Gross et al. 2002) and is currently used for restoration of populations of several sturgeon species including lake sturgeon (*Acipenser fulvescens*, Jackson et al. 2002) white sturgeon (*Acipenser transmontanus*, Ireland et al. 2002). Stocking has also been considered for shortnose sturgeon conservation, and an experimental stocking study was conducted in which 97, 483 hatchery-reared shortnose sturgeon were stocked into the Savannah River from 1984-1992 (Smith et al. 2002). However, stocking must be carried out responsibly to ensure than young sturgeons are put into an environment suitable for

their survival and that their introduction will not negatively impact wild juvenile sturgeons already present.

In this study, I identify some habitat preferences of early life stages of shortnose sturgeon and a difference in dispersal strategy of early life stages between two populations. Other researchers have noted genetic differentiation between rivers (Grunwald et al. 2002) and the importance of protecting habitat appropriate to the needs of particular life stages in particular rivers (Collins et al. 2002). My data support the idea that shortnose sturgeon are locally adapted to particular rivers, and conservation efforts should focus on restoring habitat and reducing anthropogenic impacts in specific river reaches rather than stocking captively reared fish into wild populations.

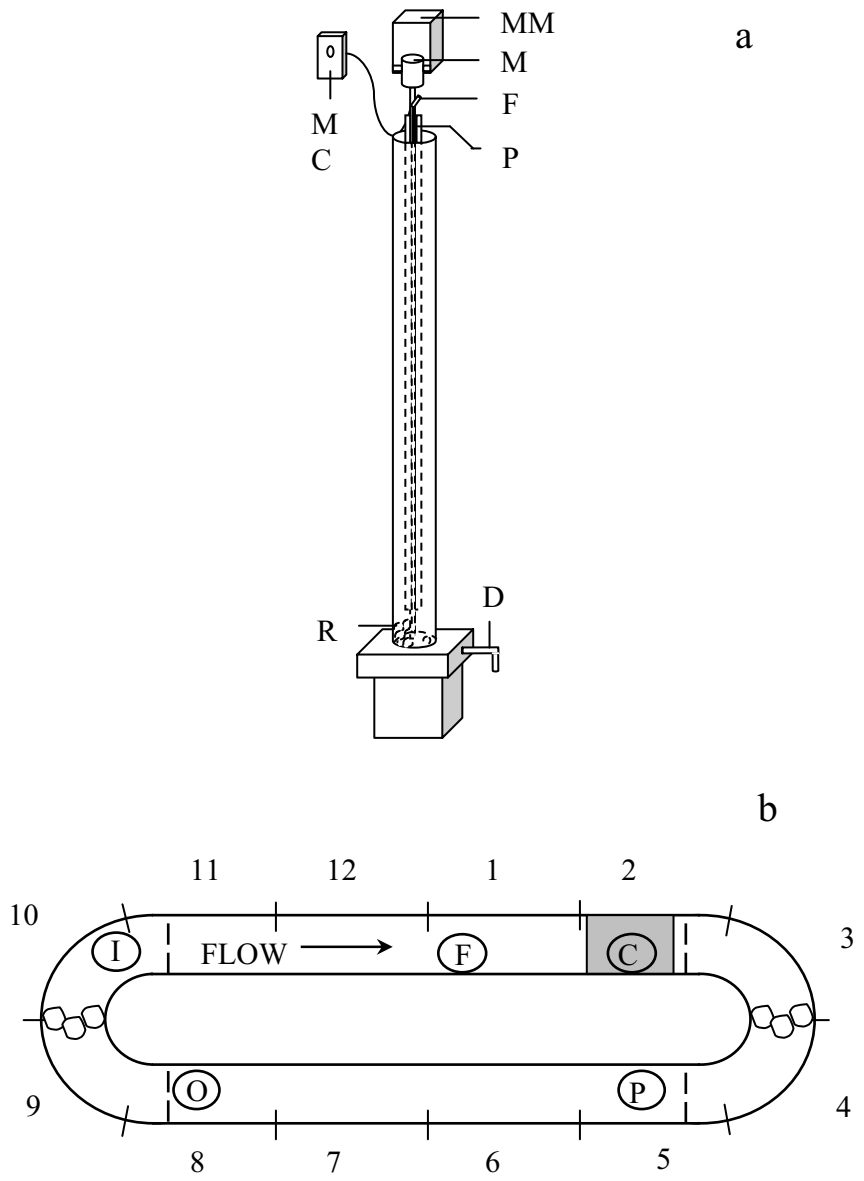

Figure. 2.1 Panel a shows the stream tube (water depth, 150 cm; diameter, 15 cm) used to determine swimming height and cover use of white sturgeon. Key to components: M = motor, MM = motor mount, MC = motor control, F = fish introduction tube, P = paddlewheel, R = rocks, and D = drain. The rotating paddlewheel created a clockwise horizontal water current with a velocity of 2 cm/s. Panel b shows the oval stream (32 cm wide, 7.3 m in circumference, with water 20 cm deep) used to observe migration and habitat use. Three rocks at each end provided cover. The stream was marked into 12 sections, each 62 cm long. Mean bottom velocity was 3.5 cm/s (range, 1–9 cm/s). The following notations show features: arrow = flow direction, I = water inflow, O = water outflow, P = submerged pump, F = feeder, C = video camera and infrared light, and shaded area = video field of view.

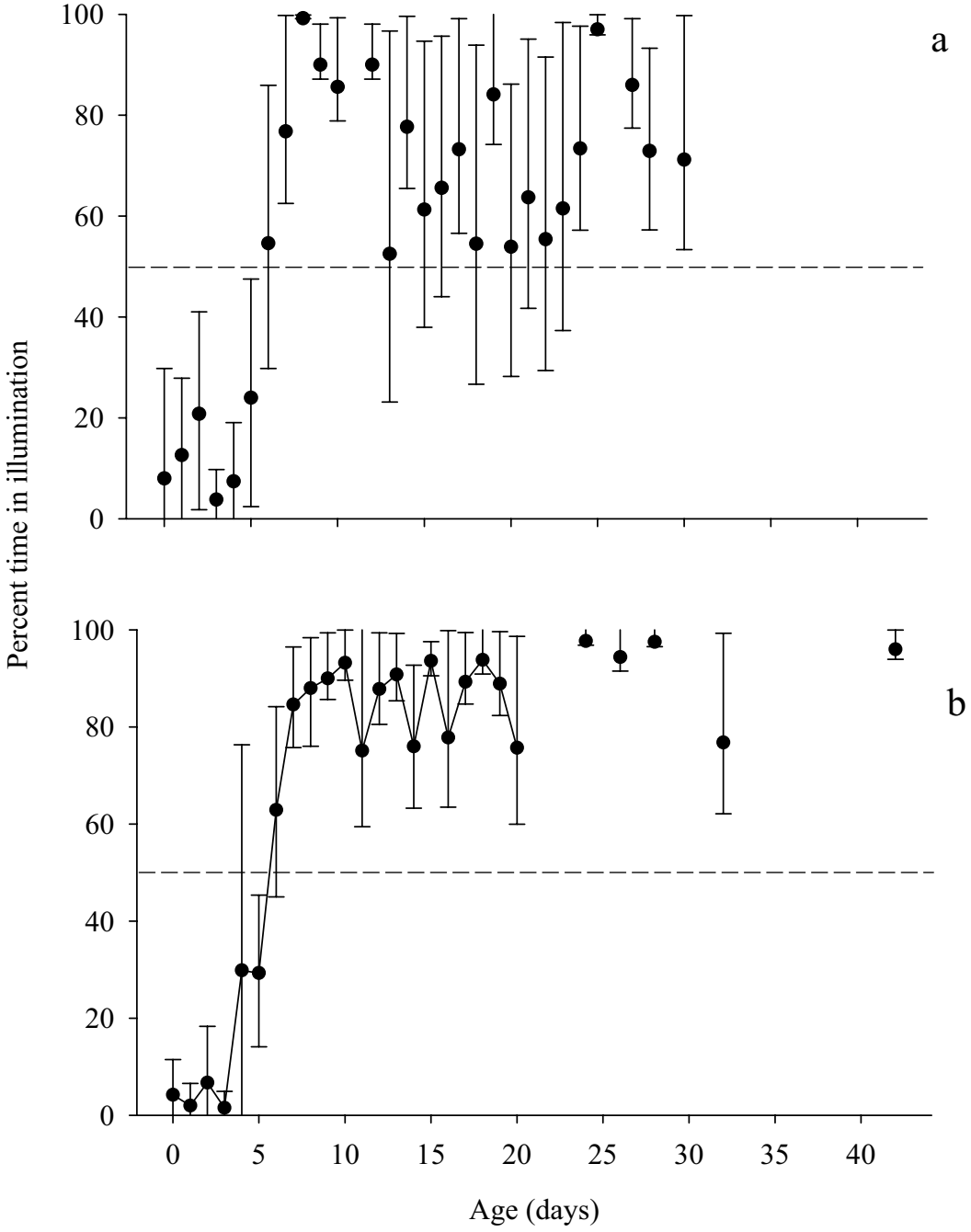

Figure 2.2. Means and 95% confidence intervals of percent time fish spent on illuminated side of illumination vs. darkness choice tank. If a confidence interval includes 50% (indicated by dashed line) preference is not significant. Panel a shows Connecticut River fish and panel b shows Savannah River fish.

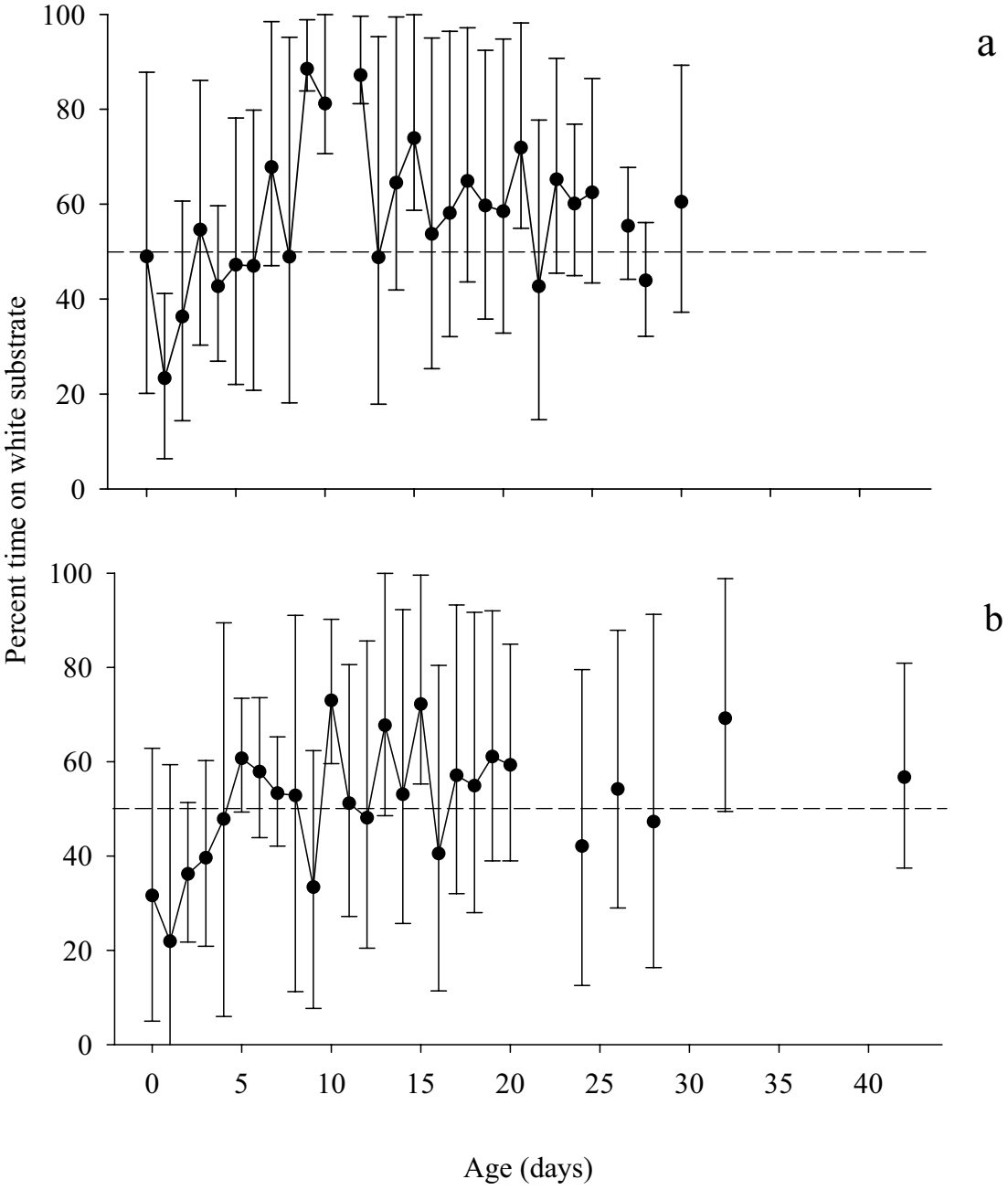

Figure 2.3. Means and 95% confidence intervals of percent time fish spent on white side of black vs. white substrate choice tank. If a confidence interval includes 50% (indicated by dashed line) preference is not significant. Panel a shows Connecticut River fish and panel b shows Savannah River fish.

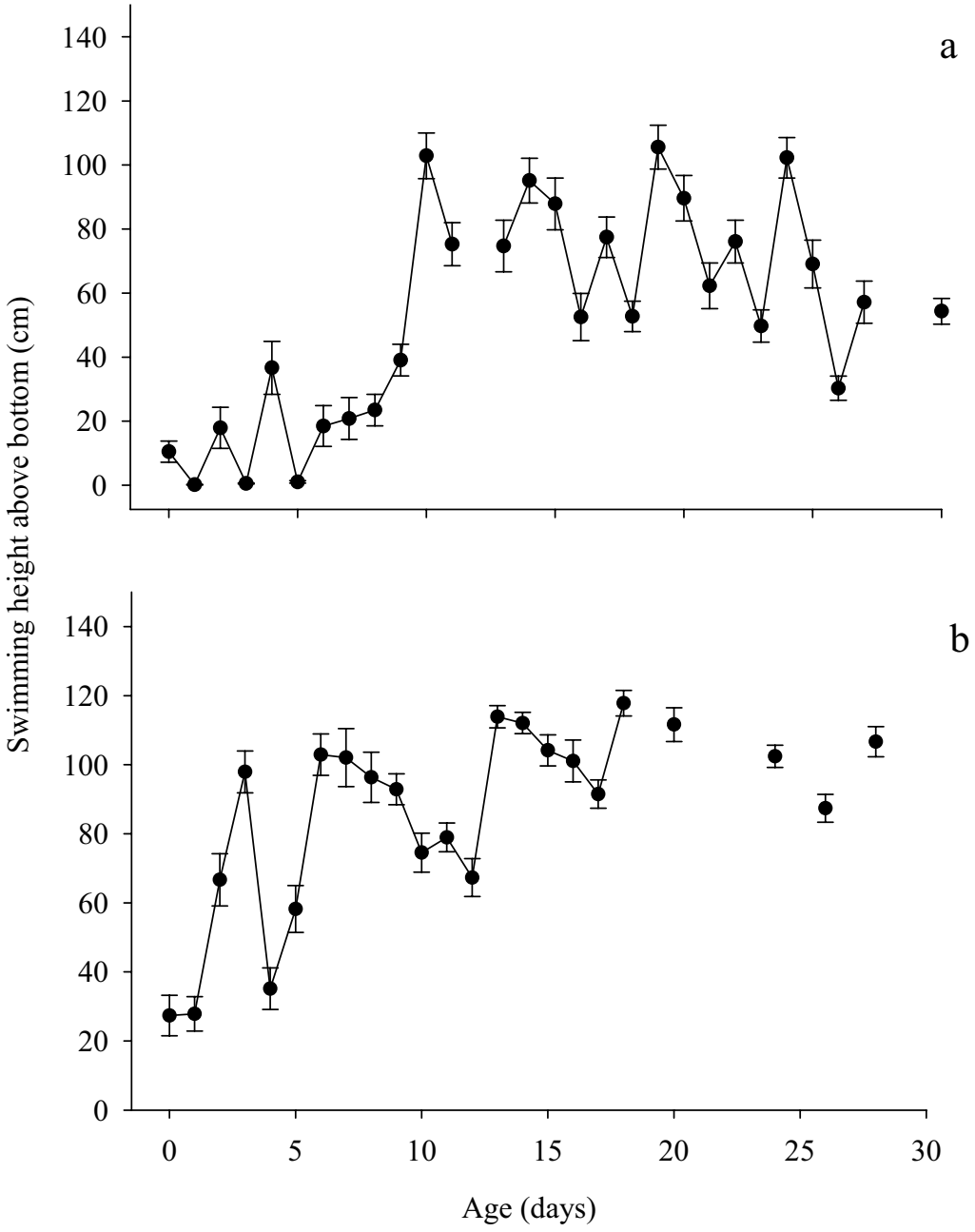

Figure 2.4. Mean (± SE) swimming height above the bottom in the stream tube. Panel a shows Connecticut River fish and panel b shows Savannah River fish.

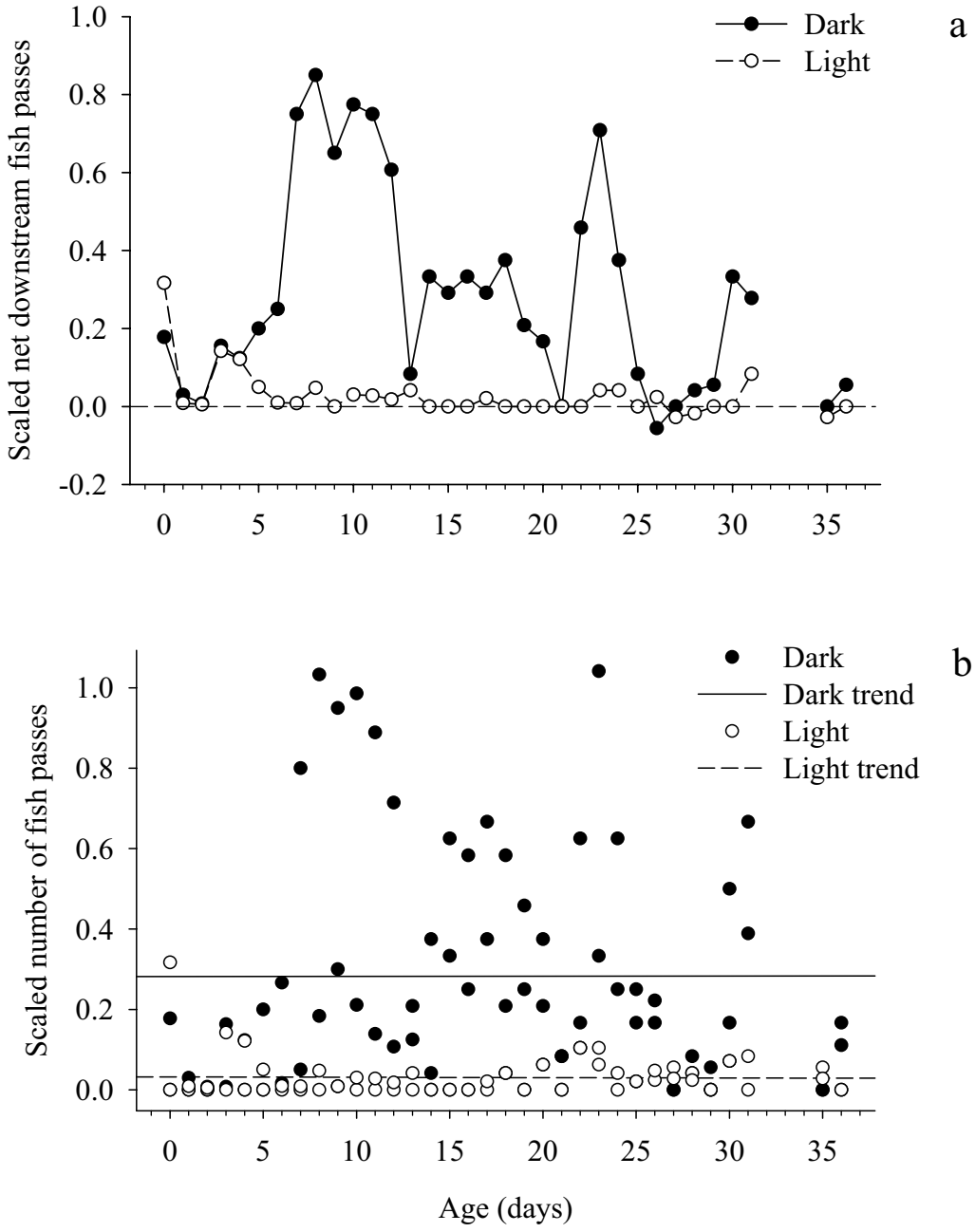

Figure 2.5. Graph of dispersal intensity and general activity in the oval stream tank over time for Connecticut River fish in 2003. Panel a shows the scaled mean net number of downstream fish passes separated by day and night. Positive numbers of passes indicate downstream movement, whereas negative numbers indicate upstream movement. Panel b shows the scaled mean number of both up- and downstream fish passes (as a measure of activity) separated by day and night. Linear regression was used to plot trend lines for daytime and nighttime activity.

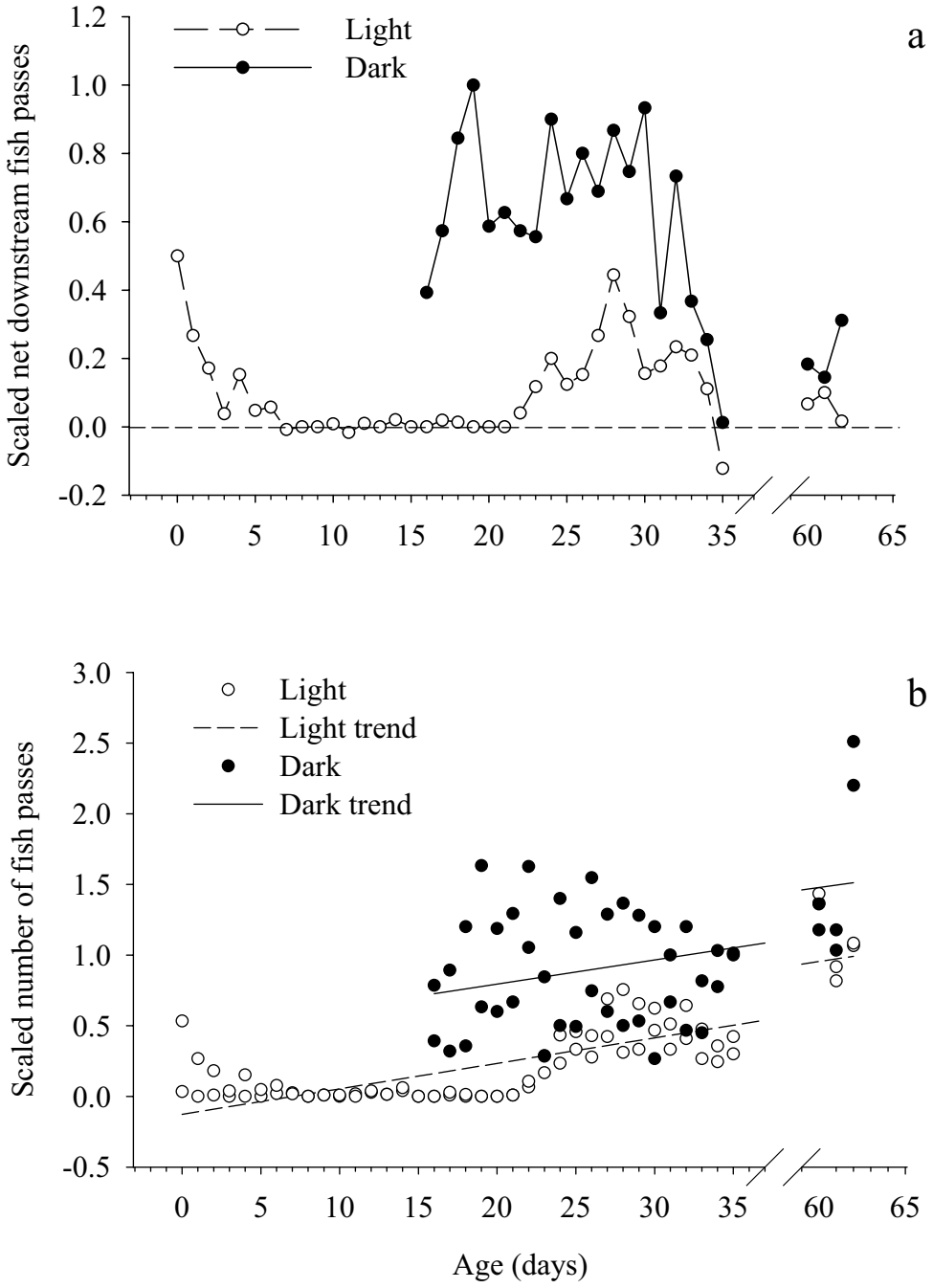

Figure 2.6. Graph of dispersal intensity (panel a) and general activity (panel b) in the oval stream tank over time for Savannah River fish in 2004. Fish were not video taped at night until day 16 due to a malfunction of the infrared lights which provided illumination at night.

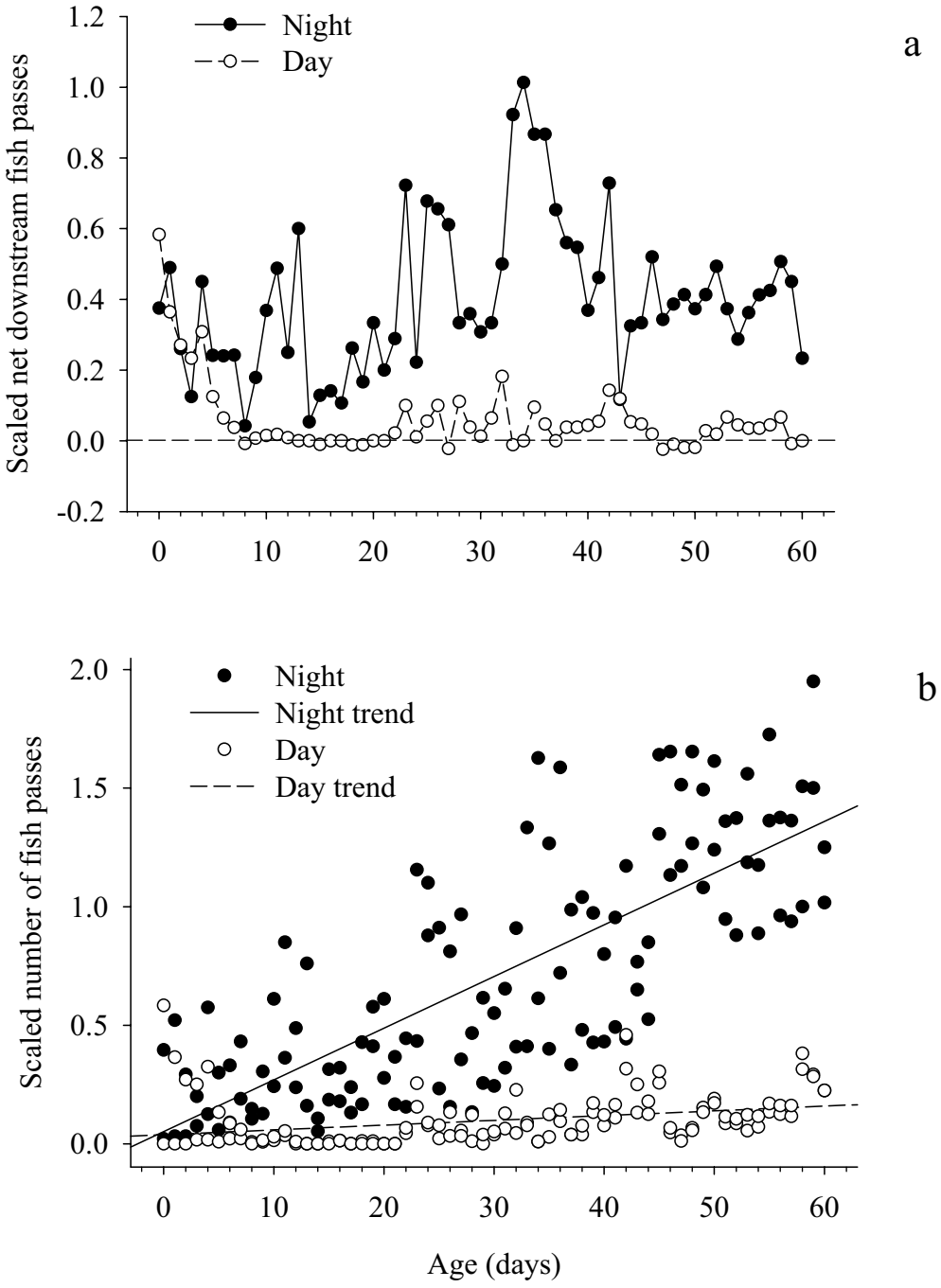

Figure 2.7. Graph of dispersal intensity (panel a) and general activity (panel b) in the oval stream tank over time for Savannah River fish in 2005.

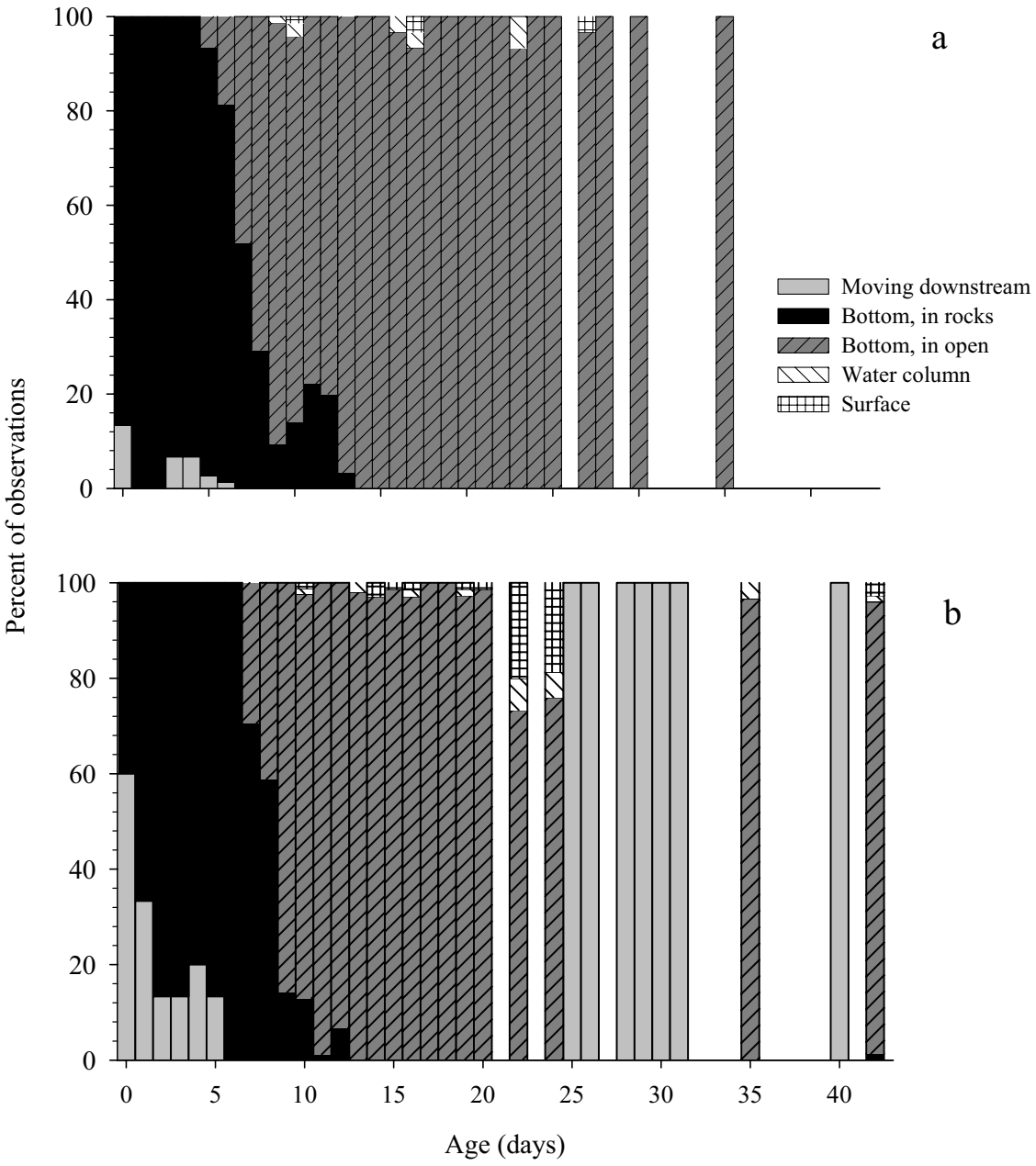

Figure 2.8. Percent of fish using four habitats (surface, water column, open bottom, and on the bottom under rocks) or moving downstream in the oval stream by age. Panel a shows Connecticut River fish and panel b shows Savannah River fish.

CHAPTER 3

EFFECT OF REARING TEMPERATURE ON THE ONSET AND DURATION OF DISPERSAL OF EARLY LIFE STAGES OF SHORTNOSE STURGEON (*ACIPENSER BREVIROSTRUM* LESUEUR 1818)

Introduction

Many animals undergo changes in feeding, habitat use, morphology, physiology, competitors, and predators during their life history (Warkentin 1995, Jones et al. 2003). These ontogenetic niche shifts usually occur concurrently with a change in developmental stage and likely evolved as a strategy to reduce mortality and optimize growth at each developmental stage (Werner 1986, Werner and Hall 1988, Jones et al. 2003).

Temperature may affect the timing of ontogenetic niche shifts in ectothermic animals both by acting as a cue of environmental variation and by direct effects on the developmental rate of the animals. The effect of temperature on development of ectothermic animals has been studied extensively. Within an animal's thermal limits, developmental rate increases with increasing temperature. The relationship is not necessarily linear however, and a number of models have been used to describe the relationship between developmental rate and temperature for different species (Ojanguren and Braña 2003, Kamler 2002, Cossins and Bowler 1987). The simplest way to describe development in terms of temperature is by expressing developmental time in degree-days (i.e., sum of daily mean temperatures across days). By altering developmental rate, temperature can change the amount of time an animal takes to reach the optimal size or

developmental stage for a niche shift, and environmental temperature may explain a large part of the variation in timing of niche shifts within a species (Elliott and Hurley 1998). Studying behaviors that change predictably with ontogeny, such as dispersal of early life stages of shortnose sturgeon, can elucidate the relationship between temperature, development, and behavior.

Shortnose sturgeon in the Connecticut River (MA, USA) undergo a downstream dispersal during the larval life stage. Fish initiate dispersal upon absorption of the yolk sac and stop after several days to begin a benthic lifestyle. Pallid sturgeon (*Scaphirhynchus albus*) also undergo downstream dispersal, beginning immediately after hatching and ending as fish absorb their yolk sacs and begin to feed. Studies with pallid sturgeon at different velocities but constant temperature showed that they continue dispersal for the same length of time regardless of current velocity (Kynard et al., In press, c). This suggests that fish are not basing their dispersal duration on traveling a particular distance or finding a particular river reach, but rather are moving until they reach a certain developmental stage. In that experiment, fish in all velocity treatments reached the same developmental stage at the same time because all fish were reared at the same temperature.

The objective of this study is to determine the effect of temperature regime on the onset and duration of downstream dispersal of shortnose sturgeon larvae and whether the number of degree-days fish require to reach particular developmental and behavioral stages depends on the temperature regime. This will enable me to more accurately describe and model the ontogeny of behavior of sturgeons in relation to water temperature, which can be important in answering questions related to sturgeon

conservation such as the effect of releasing cold water from a hydroelectric dam in a rearing area for larval sturgeons. I expect that colder temperatures will delay both onset and cessation of dispersal, and extend the entire dispersal period. Dispersal timing and duration are both likely controlled by developmental stage and colder temperatures slow development (Van Eenennaam et al. 2005, Hardy and Litvak 2004). I expect that the number of degree-days needed to reach particular stages will vary, with colder temperatures causing fish to require more degree-days to express particular behaviors.

Methods

I reared Connecticut River shortnose sturgeon yolk-sac larvae and larvae in replicate tanks to assess the effect of water temperature on the timing of initiation of dispersal and the duration of dispersal. I spawned Connecticut River shortnose sturgeon on 15 May 2005 and the eggs hatched on 23 May 2005. Eggs were hatched in McDonald hatching jars and reared as described in Chapter 2. Eggs were incubated at ambient Connecticut River temperature (about 15°C) to standardize hatching date. After eggs hatched I divided the yolk-sac larvae into three groups and introduced each group into a rearing tank at either 10°, 15°, or 20°C.

Also immediately after hatching, I introduced 10 individuals into each of nine test tanks. The test tanks were 1.8-m diameter circular tanks with a circular insert offset from the center of the tank to create two habitats, a channel flow around the tank wall and an eddy with reverse flow (Figure 3.1). The nine tanks were arranged into three replicate tanks at each of three temperatures, 10°, 15°, and 20°C. A recirculating water system linked each group of three tanks with a head tank, a sump tank, and a combination heater/chiller unit which kept the water temperature constant. Individual submersible

pumps in each of the tanks created circular flow. Ten 10-cm diameter rocks in the eddy provided cover. Water depth in all tanks was 30 cm, except in the video viewing area where a ramp reduced depth to 13.5 cm to bring fish closer to the camera. Each tank was covered with a fine-mesh netting to exclude insects and aerial debris. The entire system was built outdoors on a platform and protected from weather by a tent roof with open sides.

I mounted color video cameras above each tank to observe fish. To see fish at night, a 60-W red light was mounted on either side of the camera and the ramp was painted white. The video system recorded fish for 5 min per h each 24 h. I replaced fish that died with new fish from a rearing tank kept at the same temperature so that test tanks always contained 10 fish. The videotapes were reviewed to count the number of up- and downstream fish passes per 5 min. I used the daily number of fish passing around the tank per 5 min to compare fish among temperature treatments. The replicated design allowed me to address the question of whether the variation between temperature treatments is greater than the variation between tanks within a temperature treatment.

I linked daily development of fish to water temperature using the degree-days to which fish had been exposed. Day-0 yolk-sac larvae accumulated 0 degree-days, day-1 fish accumulated the mean °C of day 0, and day-2 fish accumulated the mean °C of day 0 + the mean °C of day 1. I compared the number of degree-days fish required to reach particular behavioral stages.

Results

Connecticut River shortnose sturgeon for these experiments hatched on 23 May 2005 and I introduced approximately 300 into rearing tanks at each of the three

temperatures. Fish in the 20°C treatment became larvae on day 7 after 140 degree-days, fish in the 15°C treatment became larvae on day 9 after 135 degree-days, and fish in the 10°C treatment became larvae on day 21 after 210 degree-days. Tests continued until day 35 for the 15 and 20°C treatments and until day 38 for the 10°C treatment.

Fish in the 15 and 20°C treatments required a similar number of degree-days to become larvae, but fish in the 15°C group took more degree-days to begin dispersal than fish in the 20°C group (150 and 100, respectively). Fish in the 10°C group took many more degree-days both to become larvae (210 degree-days) and to initiate dispersal (220 degree-days) than fish in the other two groups. An exponential curve provides a good fit for the relationship of incubation temperature to both days to initiate dispersal and degree-days to initiate dispersal (Figure 3.2).

The three temperature regimes produced three differing dispersal patterns. Fish reared at 10°C did not begin moving at a rate of more than 0.1 passes per fish per five minutes until day 15 when fish were still yolk-sac larvae (Figure 3.3a). Movement peaked on days 22-25 (220-250 degree-days), beginning a day after fish became larvae, then declined to < 3 passes per fish per five minutes and remained low. Fish reared at 15°C moved downstream slowly as yolk-sac larvae (Figure 3.3b). Dispersal first peaked on days 10-17 (150-255 degree-days), beginning one day after fish became larvae as in the 10°C treatment. Dispersal then peaked again on days 19-20 and 30-33. Fish reared at 20°C had five peaks of dispersal between hatching and day 35 (Figure 3.3c). The first peak was on days 5-8 (100-160 degree-days), beginning when fish were still yolk-sac larvae and ending one day after the transition to the larval stage. The other peaks

occurred on days 12-15, 19-21, 24-26, and 30-32. On day 35, when tests ended, the number moving downstream was increasing again.

Fish in all three temperature regimes moved downstream both day and night, with daytime and nighttime movement tracking each other and peaking at about the same time. Occasionally a fish moved upstream, but the rate was never greater than 0.1 passes per fish per five minutes, and I never recorded any net upstream movement (i.e. downstream movement was always much greater than upstream movement).

Discussion

During previous experiments comparing behavior of different species of sturgeons (e.g., Kynard and Parker 2004), we have assumed that sturgeons reach the same developmental stage after a particular number of degree-days, regardless of the water temperatures during those days. For example, a fish held at 18°C for 6 days and a fish held at 12°C for 9 days will both accumulate 108 degree-days and should both be at the same developmental stage after those 108 degree-days. However, comparing my data from Chapter 2 to some collected previously, I noticed that shortnose sturgeon reared at lower temperatures required more degree-days to reach the same ontogenetic switch in behavior (initiation of dispersal) than did fish reared at a higher temperature.

As I predicted, the data collected in this study also show that at colder temperatures fish required more degree-days to reach the same developmental stage. This phenomenon can be explained by the fact that growth and development in fish tend to have a non-linear, often exponential relationship to temperature (Dettlaff et al. 1993, Cossins and Bowler 1987). At optimal temperatures, growth and development proceed more rapidly, while at sub-optimal high or low temperatures growth and development are

slowed. Both 15° and 20°C are likely close to the optimum temperature for shortnose sturgeon growth; thus, similar numbers of degree-days were required for fish to reach the same developmental point at these temperatures.

The three temperature regimes produced different dispersal patterns, suggesting that dispersal of shortnose sturgeon early life stages is influenced by environmental conditions. Colder temperature delayed the onset of dispersal as I predicted, but increasing the temperature produced a dispersal pattern with multiple peaks, rather than simply shifting the peak to a younger fish age. Few studies of dispersal behavior of early life stages of riverine fishes have been done and this relationship between dispersal behavior and temperature has not been described in sturgeons or other riverine fishes before. Most studies of dispersal of early life stages of fish examine coral reef fishes (Leis 2006).

Onset of dispersal appears to be a function of development. Fish must reach a particular stage before they are ready to leave cover and begin moving downstream. Dispersers need to have some fin development and have absorbed their yolk, which likely also affects their swimming ability. Fish in all three temperature treatments initiated dispersal close to the same time they initiated exogenous feeding. Cooler temperatures delayed development and thus delayed the onset of dispersal. An exponential curve fit the relationship between both the number of days and the number of degree-days to initiate dispersal and temperature (Figure 3.2). Van Eenennaam et al. (2005) found a similar relationship of hours to hatch and temperature for green sturgeon (*Acipenser medirostris*). Thus, the behavior of initiating dispersal is affected by temperature in the same way that a developmental event (hatching) is.

Duration of dispersal, however, has a more complex relationship to temperature. Increasing temperature caused fish to disperse for a prolonged period of time with several peaks of movement. All fish tested were full siblings, and the experimental tanks differed only in temperature regime. Thus, dispersal behavior may be a plastic phenotype whose expression depends on water temperature and possibly other environmental conditions.

Studies with pallid sturgeon at different velocities but constant temperature showed that they continue dispersal for the same length of time regardless of current velocity, suggesting that fish are not basing their dispersal duration on traveling a particular distance or finding a particular river reach, but rather are moving until they reach a certain developmental stage (Kynard et al., In press, c). Dispersing sturgeon larvae may use water temperature as a cue to choose an appropriate rearing reach. In colder temperatures, the shortened dispersal peak will result in fish traveling a shorter distance and remaining more concentrated in a shorter river reach. In colder temperatures fish do not need as much food and may be able to tolerate being closer together, and the shorter dispersal may reduce the amount of time they are in the water column and are vulnerable to predation. In warmer temperatures fish move farther and may also spread themselves out more, resulting in less competition for food resources.

Emergence of young Atlantic salmon (*Salmo salar*) from their nest is one example of plasticity in ontogenetic niche shifts. Typically Atlantic salmon emerge when they have nearly absorbed their yolk and are ready to begin exogenous feeding. In a laboratory experiment, Jones et al. (2003) found that chemical cues from a diurnal predator caused young Atlantic salmon to emerge earlier and at a smaller size with more

yolk remaining, while chemical cues from a nocturnal predator caused fish to delay emergence. Atlantic salmon establish feeding territories and begin diurnal feeding upon emergence, and the best strategy against a diurnal predator may be to drift downstream and leave the immediate area of the nest before beginning to feed, whereas being larger at emergence may be adequate protection against a nocturnal predator (Jones et al. 2003).

As water temperature increased, shortnose sturgeon increased both the duration of their dispersal and the number of dispersal peaks. Dispersal duration is related to finding an appropriate rearing reach while the number of peaks is likely related to survival during dispersal. At higher temperatures fish had multiple periods of activity with less active periods between. This could be an adaptation to avoid predators. At warmer temperatures fish may be subjected to increased predation pressure as metabolic rates of predators such as other fishes and crayfish increase. Varying movement rate of the population, and variation between individuals within the population, may cause the dispersal to be less predictable to predators.

The multiple-peak dispersal pattern may also be an adaptation to increase foraging efficiency of young sturgeon. Warmer water also increases sturgeons' metabolic rate and may cause them to increase their foraging range and to disperse farther to spread themselves out and avoid competition for food resources. Perhaps at warmer temperatures fish need to eat more food than they can find while dispersing and so alternate between periods of dispersing and periods of foraging to feed most efficiently. This appeared to be the case for Amur sturgeon (*Acipenser schrenckii*) which had a similar multiple-peak dispersal pattern when tested in a similar stream tank at water

temperatures of 23-29°C (Zhuang et al. 2003). Warmer water and elevated metabolic rate may also simply cause fish to swim more.

The Connecticut River shortnose sturgeon examined in Chapter 2 were reared at 18°C, and their dispersal pattern is intermediate between the 15 and 20°C treatments. The onset of dispersal is similar to the 20°C treatment, and the number and spacing of dispersal peaks is similar to the 15°C treatment. The major difference between the pattern of dispersal described here and in Chapter 1 is that in these experiments the fish were moving both day and night. The elevated flow in the experimental tanks used in these tests likely caused the increased daytime movement.

The difference in duration and peaks of dispersal between the Connecticut and Savannah Rivers described in Chapter 1 is similar to the difference between the 15 and 20°C treatments. However, in my common garden experiment, the two populations were compared at the same temperature. Thus, there are likely genetically based population differences; the dispersal pattern is different under the same environmental conditions.

Shortnose sturgeon in the Savannah and Connecticut Rivers are reared under very similar temperature regimes. Adults spawn between about 9 and 12°C, eggs hatch between about 12 and 14° C, and yolk-sac larvae and larvae experience temperatures that gradually increase from about 14 to about 20°C during their first month of life (B. Kynard, pers.comm). However, Savannah River fish may be more sensitive to temperature effects, such that a smaller deviation from normal rearing temperatures causes them to express the multiple peak dispersal than Connecticut River fish.

This study compared three constant temperature regimes, rather than slowly increasing temperatures as fish would experience naturally. Thus, the dispersal patterns

described here may not be exactly as dispersal behavior would be expressed in a river. The knowledge that dispersal behavior is altered by temperature regime should be considered both in future experiments of this type and in conservation strategies for sturgeons.

The natural water temperature regime in rivers may be altered by hydropower dam operations or heated or cooled industrial effluents. Depending on the duration of temperature alteration, the other environmental factors related to higher or lower temperature may not be present, so the response of the fish may not be advantageous. The potential exists for a mismatch between the adaptation of the fish and the environment. Raising the temperature will cause fish to prolong their dispersal and perhaps move into areas without enough food or shelter. Lowering the temperature will cause fish to delay dispersal, perhaps remaining too long in an area of high predation or high anthropogenic impact, such as just below a hydropower dam. River temperatures may also be raised slowly over many years by global climate change. This could mean a different natural pattern of dispersal may emerge over time.

Additional study is needed to elucidate the relationship of temperature change and dispersal pattern. I investigated the effects of constant temperature, but temperature in a river is increasing (spring-spawning species) or decreasing (fall-spawning species) during the time young sturgeons are developing and dispersing. Does the rate of temperature change effect behavior? Do years when spring comes early or late produce different dispersal patterns? Both climate change and industry such as hydropower dams can significantly and permanently alter river temperature regimes. For example, the Three Gorges dam on China's Yangtze River is now complete and actively generating power,

and Chinese sturgeon (*Acipenser sinensis*) are now forced to spawn directly below the dam. The release of cold water from the bottom of the reservoir during generation has caused the river to remain much colder during the time that the sturgeon are spawning (B. Kynard, pers. comm). Chinese sturgeon yolk-sac larvae typically disperse immediately after hatching, likely to avoid the significant number of predators present at the spawning sites (Zhuang et al. 2002). The decreased rearing temperature may cause yolk-sac larvae to delay their dispersal, thus remaining in an area of high predation pressure and possibly suffering significant mortality.

Hydropower dams and other industries may also operate intermittently and cause shorter-term fluctuations in river temperature. Future studies should also focus on the effect of the timing of temperature changes on dispersal. If fish have begun to disperse and temperature suddenly drops, does dispersal cease? If temperature is raised or lowered during the first few days of life, then returns to a natural regime, will the dispersal pattern be affected? Sturgeons are migratory fishes that tend to inhabit large rivers which often contain multiple hydropower dams. A more thorough understanding of the effects of temperature change on dispersal during early life history would be very useful in efforts to protect these vulnerable and important life stages.

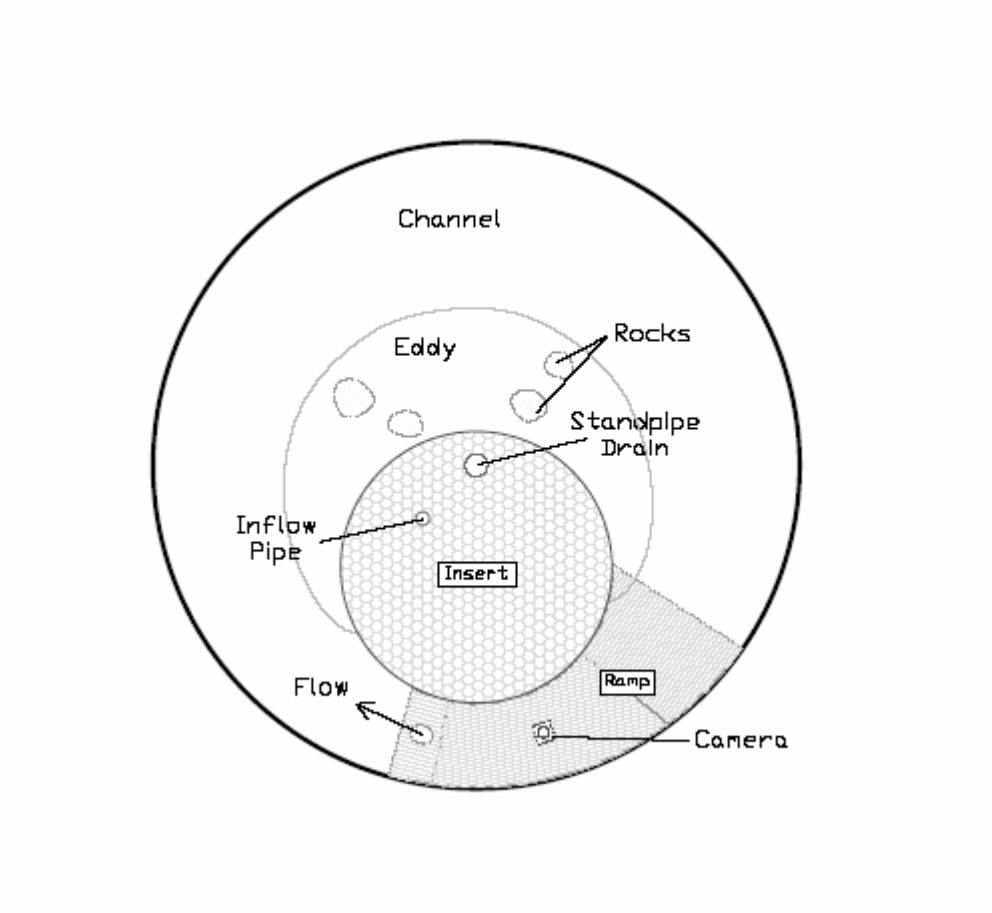

Figure 3.1. Diagram of experimental tank used to study effect of temperature on dispersal behavior.

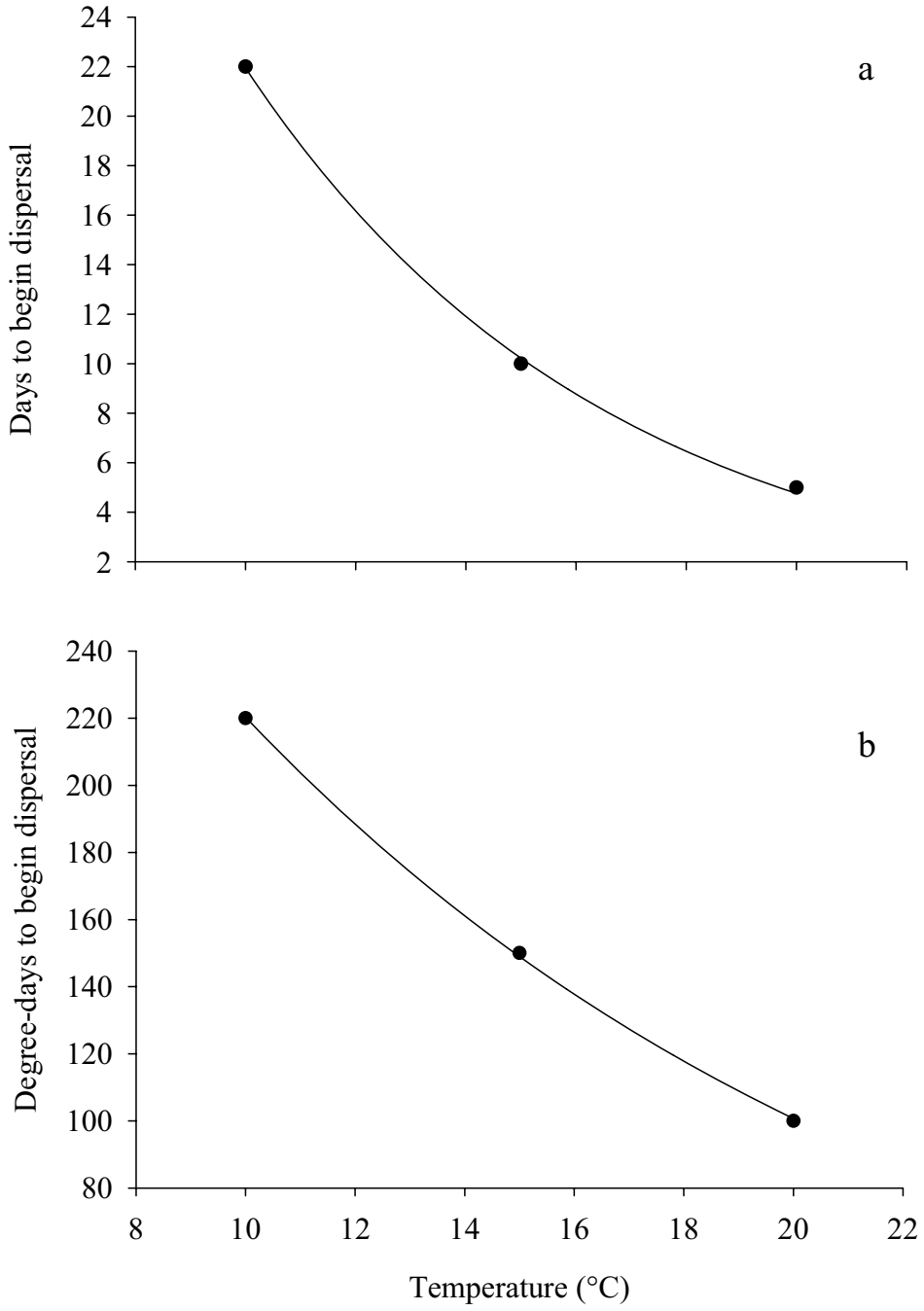

Figure 3.2. Graphs of relationship of number of days (panel a) and number of degree days (panel b) to begin dispersal with temperature.

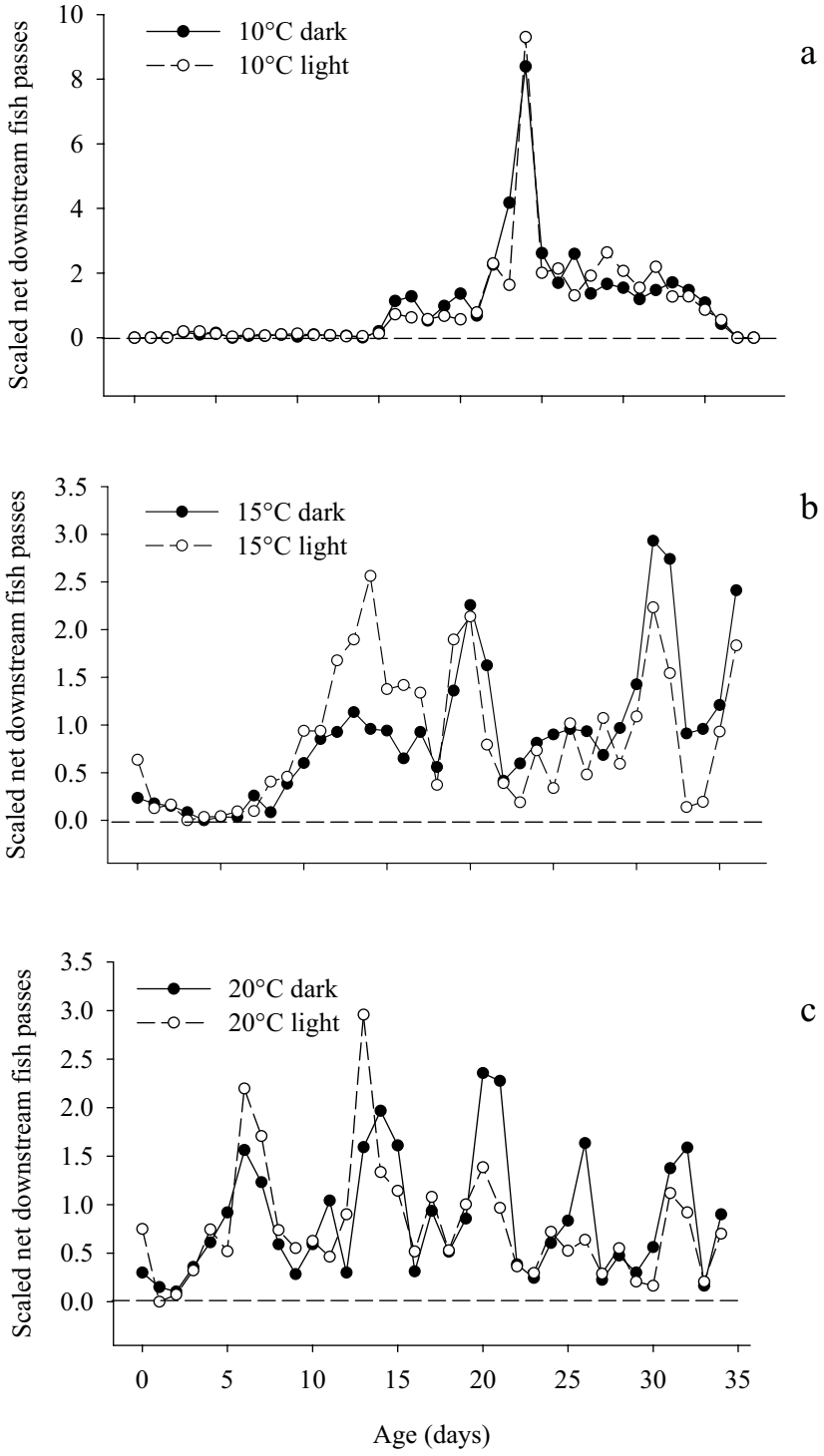

Figure 3.3. Graph of net number of downstream fish passes scaled to number of fish present at each of three temperatures. Each graph represents the mean of three replicate tanks at either 10°C (panel a), 15°C (panel b) or 20°C (panel c).

CHAPTER 4

MORPHOLOGICAL DEVELOPMENT OF SHORTNOSE STURGEON AS RELATED TO OBSERVED ONTOGENETIC BEHAVIORAL CHANGES

Introduction

Ontogenetic niche shifts are often accompanied by a change in morphology that allows the animal to better utilize the new niche. For example, many fishes feed first on zooplankton, then switch to feeding on benthic invertebrates, and finally become piscivores preying on other fishes. These ontogenetic dietary changes are accompanied by changes in mouth morphology, gape width, and body size and shape. The timing of the ontogenetic diet shifts can vary depending on prey availability, abundance of predators and competitors, and the rate at which fish grow and undergo the necessary morphological changes (Graeb et al. 2004, Hjelm et al. 2002). Another example of the correlation of morphology through ontogeny and life history is locomotion of salmonid fishes. Young salmonids use fast-start locomotor behavior to escape from predators and capture prey. A fish's performance of the fast-start changes during ontogeny and peaks when the fish absorbs its yolk sac and starts to feed, just the period of time when fast-start ability is likely very important for survival (Hale 1999).

As described in Chapter 2, shortnose sturgeon undergo a series of ontogenetic changes in behavior. These changes are likely related to morphological changes that occur during development. When shortnose sturgeon hatch, their sensory systems and fins are mostly undifferentiated; these systems become differentiated during the yolk-sac larval period, and fins, in particular, continue development throughout the larval period (Richmond and Kynard 1995, Bemis and Grande 1992, Dettlaff et al. 1993). Shortnose

sturgeon seek cover under rocks until they have absorbed their yolk sacs and begun to feed; then they initiate downstream dispersal, swimming above the bottom of the river. The ability to orient in river currents, move downstream, and feed requires development of fins and sensory systems; thus, the timeline of appearance of behaviors and structures should be correlated.

The objective of this study was to link changes in development of sensory and locomotor systems with ontogeny of behavior, and to compare developmental stages when particular behaviors occur between fish reared at different temperatures and between Connecticut River and Savannah River fish. I expect that behaviors such as the onset and cessation of dispersal occur at particular developmental stages. Because developmental rate of sturgeons is determined by temperature (Hardy and Litvak 2004, Dettlaff and Goncharov 2002, Dettlaff et al. 1993, Wang et al. 1985), I expect that fish reared at different temperatures will begin and end dispersal at different ages but at the same developmental stage. Development in sturgeons has the same temperature dependence at all stages of development; thus temperature effects are predictable and have been described for several species (Dettlaff et al. 1993). Murray cod in the Broken River, Australia, leave the parental nest and begin drifting downstream at a younger age in warmer water but at a particular developmental stage regardless of temperature (Humphries 2005).

Methods

During data collection for Chapters 2 and 3, I collected a developmental series of fish from each river (Chapter 2) and periodic developmental samples from each temperature (Chapter 3). I characterized the developmental stage of these fish with

respect to ontogenetic shifts in behavior and comparisons between rivers and between temperature treatments (for Connecticut River fish). For yolk-sac larvae, I used a published staging scheme for sturgeon (Dettlaff et al. 1993) This staging scheme is well described and Bemis and Grande (1992, 1999) correlate their descriptions of sensory system and fin development in paddlefish (*Polyodon spathula*) to this scheme. I also used their findings to assess the development of my samples of yolk-sac larvae because, as they note, sensory system and fin development in paddlefish and sturgeons is very similar. For larvae and juveniles, I also used a scheme based on observations of appearance of characters related to fish length in shortnose sturgeon (E. Hilton, unpublished data).

Connecticut and Savannah River shortnose sturgeon were reared from eggs and tested every day for their preference for dark or bright habitat and their swimming height above the bottom; the onset and duration of downstream dispersal was also examined (Chapter 2). During these behavioral tests with Connecticut and Savannah River shortnose sturgeon, I collected and preserved four fish from each river at the following times: each day until day 10 after hatching, every other day from day 10 to day 30, and on day 40. In separate tests to evaluate the effect of temperature regime on ontogeny of behavior (Chapter 3), a separate group of Connecticut River shortnose sturgeon was reared from eggs, placed into one of three constant temperatures (10, 15, or 20°C) after hatching, and observed for the effect of temperature on the timing and characteristics of downstream dispersal. During these behavioral tests, I collected and preserved five fish from each rearing temperature on days 3, 7, 11, 15, and 24 after hatching. All fish were fixed without anesthesia in 10% formaldehyde. I used a dissecting microscope to

examine my preserved specimens for possible correlations between development of fins, mouth, and chemosensory barbels, and the ontogenetic changes in behavior I have seen.

Using the Connecticut and Savannah River specimens, I compared length and developmental stage of fish at the following four developmental events: day 1 after hatching, the transition to the larval stage (and to preferring illumination), the first day fish swam to 100 cm in the swimming height test, and the peak of dispersal (Table 4.1). Each of these events occurred on one particular day. For length comparisons I measured four fish from each river on the day each developmental event occurred and used a t-test to determine if the mean lengths were significantly different. I also compared length and developmental stage of specimens from the three temperature treatments at the peak of dispersal and at the same number of degree-days (Table 4.2), and I compared growth of the three groups between day 3 and day 7 after hatching (Table 4.3). I measured five fish from each of the three temperature treatments and compared the mean lengths using one-way ANOVA and the Tukey test for multiple comparisons.

Results

Connecticut River fish in 2003 and Savannah River fish in 2005 had very similar growth and development (Table 4.1). I found no significant difference in mean length between the two groups ($p=0.23$) and both were at the same developmental stage (stage 36) at 24 hours after hatching (day 1). Fish from both rivers became larvae on day 7 after about 126 degree-days, and still were not significantly different in mean length ($p=0.23$). Both were at the same developmental stage (stage 43), had developed pectoral and pelvic fins, had a pre-anal fin fold, and had a well-developed mouth and sensory barbels. The

caudal and anal fins were beginning to differentiate but had not yet separated. Fish from both rivers began to prefer illumination and were dispersing on day 7.

Connecticut River fish first swam to a height greater than 100 cm above the bottom in the stream tube on day 10. Savannah River fish in 2005 first swam to a height greater than 100 cm on day 4. At this point fish from the two rivers were at different developmental stages and were significantly different in length ($p<0.001$; Table 4.1). Connecticut River fish were at stage 45 with the pre-anal fold still present but very small, the pelvic and pectoral fins relatively large, and the anal and caudal fins separated. Savannah River fish were at stage 40 with the pre-anal fold large relative to the pelvic fins, pectoral fins smaller than those of Connecticut River fish, and the anal and caudal fins still part of the same continuous fin fold.

A major difference in behavior between the Connecticut and Savannah River fish was the duration of dispersal and the timing of the peak (Table 4.1). Connecticut River fish on day 7 were beginning their highest peak of dispersal activity and were at stage 43 as described above. Savannah River fish on day 32 were beginning their highest peak of dispersal activity and were many days into the larval interval, beyond the developmental stages of Dettlaff et al. (1993), which only cover the period until the larval interval begins (i.e., up to stage 45). Connecticut River fish on day 7 had a pre-anal fold and the anal and caudal fins were still joined in one fin fold. Savannah River fish on day 32 had all fins separate and well differentiated, no pre-anal fold, and scutes beginning to develop. The two groups were also significantly different in mean length (Table 4.1; $p<0.001$).

Fish in the three temperature treatments showed effects of temperature on development (Table 4.2). I found a significant difference in mean total length of fish

($p<0.001$) among fish reared for a similar number of degree-days (220 degree-days in the 20°C treatment, 225 degree-days in the 15°C treatment, and 240 degree-days in the 10°C treatment). Fish from the 20°C treatment were significantly longer than fish in either the 15° or 10°C treatments ($p<0.05$); however, fish in those two treatments were not significantly different in length. Fish in the 20°C treatment were also at a more advanced developmental stage after 220 degree-days (stage 45) than were fish in the 15°C treatment after 225 degree-days (stage 44) or fish in the 10°C treatment after 240 degree-days (stage 43).

Fish in the three temperature treatments had no significant difference in length at the peak of dispersal (Table 4.2; first peak was used for groups with multiple peaks). Both the 20° and 15°C groups were at stage 44 at the first peak of dispersal and the 10°C group was at stage 43. In all three groups the pectoral and pelvic fins were developed and the pre-anal fold was present. The major difference in fin morphology between stages 44 and 43 is a minor difference, i.e., whether or not the pelvic fin extends beyond the edge of the pre-anal fold. Also, the 20 and 15°C groups had the caudal and anal fins beginning to separate, whereas the 10°C group still had no separation.

Fish grew significantly longer between day 3 and day 7 in the 20°C treatment than in the 10°C treatment (Table 4.3; $p<0.05$). Between days 3 and 7, fish in the 20°C treatment grew an average of 3 mm, fish in the 15°C treatment grew an average of 1.8 mm, and fish in the 10°C treatment grew an average of 1.6 mm. There was no significant difference between the growth of the 15°C group and either of the other two groups. Fish in all three groups advanced three developmental stages over the five day period.

Discussion

Shortnose sturgeon require certain morphological characteristics to be able to initiate dispersal, and the development of these is dependent on temperature. Fish that are dispersing are feeding; thus, the mouth and barbels must be developed. Electroreceptors on the rostrum also develop during the yolk-sac larval period (Bemis and Grande 1992) and are likely important for prey detection and capture. Larval shortnose sturgeon have teeth in their mouths and are active predators on zooplankton (Richmond and Kynard, 1995). To stabilize themselves in the river flow, fish need to have some fin development before dispersing. By dispersing while the pre-anal fin fold is still present and the anal and caudal fin folds are still joined, the tiny fish may be able to maintain a more stable position in the flow (E. Hilton, pers. comm). Recent research on behavior of fishes that disperse as larvae has shown that many species, including sturgeons, are active swimmers during their larval phase and do not disperse simply as passive particles in the current (Leis 2006, Kynard et al. 2005). The lateral line system of sturgeons becomes differentiated during the yolk-sac larval period as well (Bemis and Grande 1992, Dettlaff et al. 1993) and presumably also helps fish orient in river currents. During the first few days of life, shortnose sturgeon yolk-sac larvae tend mostly to lie on their sides in rock cover, fanning their tails (Richmond and Kynard 1995, E. Parker personal observation). The development of the lateral line or ear likely coincides with their swimming in an upright orientation and beginning to disperse (W. Bemis, pers. comm.).

Some plasticity exists in the link between the timing of behaviors and the development of morphological characters. Savannah River shortnose sturgeon have higher levels of dispersal at earlier ages than Connecticut River shortnose sturgeon and

also swim up into the water column at an earlier developmental stage (see Chapter 2). Selection pressure such as increased predation risk in the southern river may cause fish to leave cover and begin swimming and dispersing with less developed fins and more yolk remaining than in the northern river. Diversity of benthic predators such as catfishes (Family Ictaluridae) and suckers (Family Catostomidae) is higher in rivers in southeast North America than in rivers in northeast North America (Jenkins and Burkhead, 1993). In bluegill sunfish (*Lepomis macrochirus*) in different lakes the size at which ontogenetic habitat shifts occur is directly correlated with the density of largemouth bass (*Micropterus salmoides*), the major predator of young bluegill, in each lake (Werner and Hall 1988). Also, the presence of particular predators causes young Atlantic salmon to emerge from their nest earlier with more yolk remaining (Jones et al. 2003) and red-eyed tree frogs (*Agalychnis callidryas*) to hatch earlier (Warkentin 1995) than control groups with no predators.

Growth and developmental rate did not vary between rivers over the first seven days of life (yolk-sac larval period). Thus fish likely have a similar amount of yolk and utilize it in the same way. However, shortnose sturgeon may have latitudinal variation in growth later in development, after the maternal yolk stores have been depleted. Some species, such as striped bass (*Morone saxatilis*) and Atlantic salmon, exhibit countergradient genetic variation in growth with fish from more northern rivers having higher growth rates than those in the south due to shorter growing seasons and increased overwinter mortality of small fish in the north (Conover et al. 1997).

Shortnose sturgeon showed an effect of temperature on development. Fish in the 20°C group required fewer degree-days to reach stage 45 (i.e. the beginning of the larval

interval) than did fish in either of the other two temperature treatments. Also, fish in the 20°C group grew faster over both a similar number of degree-days and over the same number of days after hatching than either of the other two groups. However, the 10°C group was usually closer in size to the 15°C group than the 15°C group was to the 20°C group. This suggests that the 10°C group may be able to compensate for the effect of colder temperature on growth. Ojanguran and Braña (2003) found that brown trout yolk-sac larvae incubated at lower temperatures were larger at hatching, and the size difference persisted until the start of exogenous feeding. Behaviorally, however, the shortnose sturgeon reared at 15° and 20° C were more similar to each other than either was to the group reared at 10°C.

These results agree with the behavioral results in supporting the idea that colder temperatures delay the initiation of dispersal by delaying development. Understanding the effect of temperature on morphological as well as behavioral development aids in our understanding of the effect that anthropogenically altered river temperature regimes can have on early life stages of sturgeons.

Table 4.1. Mean length, number of days and degree-days, and developmental stage of Connecticut and Savannah River fish at key developmental or behavioral events. An asterisk (*) indicates lengths that are significantly different between the two rivers at the time of occurrence of a given developmental event.

Developmental Event	Group	Mean length (mm)	Day	Degree-days	Stage
24-h post-hatch	Connecticut	10.8	1	18	36
	Savannah	11.1	1	18	36
Prefer illumination	Connecticut	15.4	7	126	43
	Savannah	15.8	7	126	43
Swim to 100 cm	Connecticut	17.3 *	10	180	45
	Savannah	13.8 *	4	72	40
Dispersal peak	Connecticut	15.4 *	7	126	43
(highest peak)	Savannah	25.5 *	32	576	n/a

Table 4.2. Mean length, number of days and degree-days, and developmental stage of fish in the three temperature treatments at key developmental or behavioral events. An asterisk (*) indicates a significant difference in length.

Developmental Event	Group	Mean length (mm)	Day	Degree-days	Stage
Similar number of degree-days	20°	17.6 *	11	220	45
	15°	15.4	15	225	44
	10°	14.4	24	240	43
Dispersal peak (first peak)	20°	15.4 *	7	70	44
	15°	14.6	11	165	44
	10°	14.4	24	240	43

Table 4.3. Growth and development of fish in the three temperature treatments between days 3 and 7. Mean change in length was not significantly different between the three temperature treatments.

Group	Mean change in length (mm)	Stage day 3/day 7
20°	3.0	41/44
15°	1.8	39/42
10°	1.6	38/41

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