REPRODUCTIVE ECOLOGY AND SEASONAL MIGRATIONS OF ROBUST REDHORSE (*Moxostoma robustum*) IN THE SAVANNAH RIVER, GEORGIA AND SOUTH CAROLINA

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Doctor of Philosophy
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by
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ABSTRACT

The objectives of this dissertation were to (1) establish a reliable means of sampling robust redhorse and other catostomid fishes for the purpose of broodstock collection and research; (2) determine the patterns of seasonal migration, daily movement, and habitat use of robust redhorse; and (3) evaluate the degree of spatial and temporal segregation of spawning habitat occurring among catostomid species on main channel gravel bars in the Savannah River, South Carolina and Georgia. The use of prepositioned grid electrofishers was determined to be viable and in many ways superior method for both collecting robust redhorse broodstock and sampling catostomid spawning aggregations. This method proved particularly effective in collecting ripe females when used in conjunction with an observation tower. Robust redhorse were found to be a highly mobile species making long distance migrations between spawning and overwintering habitats. However, they tended to maintain small daily use areas less then one kilometer in length. Robust redhorse were found to inhabit deep water along the outside bends of the river in close association with gravel substrate and woody debris. This species was also shown to exhibit a high degree of fidelity to both spawning and overwintering habitats. Catostomids appear to have specific spawning microhabitat preferences. Although some temporal and spatial overlap was observed, these preferences allowed adult Savannah River catostomids to effectively partition available spawning habitat. Frequent temporal overlap between the early life history stages of one species and the spawning adults of another occurred. There is also evidence to suggest that intraspecific superimposition of nest sites occurs.

DEDICATION

In loving memory of my grandfather, Robert Grabowski (1923-2006), whose patient and quiet love of nature inspired more of my life than he knew.

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PREFACE

Robust redhorse *Moxostoma robustum* is a large riverine catostomid with native populations existing in only three Atlantic slope river systems in North Carolina, South Carolina, and Georgia. It is currently considered a candidate species for placement on the endangered species list. However, little is known of its basic biology. This dissertation reports the findings from studies of the seasonal migrations, daily movements, habitat use, reproductive ecology, and interactions with other catostomid species of robust redhorse in the Savannah River, Georgia and South Carolina. For presentation purposes, this body of work is separated into three chapters: Use of Prepositioned Grid Electrofishers for the Collection of Robust Redhorse Broodstock; Seasonal and Diel Movement and Habitat Use of Robust Redhorse in the Lower Savannah River, Georgia and South Carolina; and Spatial and Temporal Habitat Segregation by Spawning Catostomids in the Savannah River, Georgia and South Carolina.

USE OF PREPOSITIONED GRID ELECTROFISHERS FOR THE COLLECTION OF ROBUST REDHORSE BROODSTOCK

Introduction

For an increasing number of endangered and threatened fish species, captive propagation and release of individuals has become an integral part of conservation and recovery (Olney et al. 1994; Bowles 1995). Typically, this requires the capture and transport of adult broodstock to holding facilities where they are hormonally induced to spawn (Piper et al. 1982; Branchaud and Gendron 1993). Hormone injections are often necessary because of the difficulty in acquiring females that are ready to spawn at the time of capture (Piper 1982; Branchaud and Gendron 1993; Szabó 2003). This process, while effective, is relatively time consuming (Branchaud and Gendron 1993; Zohar and Mylonas 2001; Szabó 2003). Further, the removal of broodstock is a potentially disruptive process that may affect natural reproduction of that population by disturbing spawning aggregations or simply reducing the number of individuals spawning. There are also concerns that artificial selection starting with broodstock selection and continuing in the hatchery environment may produce progeny that are not equivalent to counterparts produced through natural reproduction (Doyle 1983; Bussack and Currens 1995; Ford 2002).

The robust redhorse *Moxostoma robustum* offers a good example of the difficulties associated with broodstock collection. Robust redhorse is a large riverine catostomid whose known distribution is currently restricted to the Altamaha, Savannah, and Pee Dee river systems in Georgia, South Carolina, and North Carolina (Bryant et al. 1996; Wirgin et al. 2001). The core conservation goal of establishing genetically distinct refugial populations (Nichols 2003) requires the collection of brood-stock from specific locations. Robust redhorse form spawning aggregations in shallow water over main channel gravel bars during the spring. Males establish territories on the bars, but females in spawning condition do not spend much time there. Like most redhorse species, robust redhorse spawn in triads consisting of a single female flanked by two males (Page and Johnston 1990; Jenkins and Burkhead 1993). Therefore, collections made using boat electrofishers over these gravel bars are composed of mostly male fish. Females are generally collected from near-by staging areas after considerable effort. The impact of these repeated passes on the behavior of spawning adults is unknown, but reduced egg viability due to exposure to electric fields has been noted in other species such as razorback sucker *Xyrauchen texanus* (Muth and Ruppert 1996), Atlantic salmon *Salmo salar* (Godfrey 1957), brook trout *Salvelinus fontinalis* (Godfrey 1957), cutthroat trout *Oncorhynchus clarkii* (Dwyer and Erdahl 1995), and pink salmon *O. gorbuscha* (Marriott 1973).

Prepositioned grid electrofishers may offer an alternative method of broodstock collection. Prepositioned grids are most frequently employed to sample discrete areas to determine microhabitat relationships of stream fishes (Bain et al. 1985; Bowen and Freeman 1998; Walsh et al. 2002). Their effectiveness is limited to shallow (<1m), clear-water habitat (Bain et al. 1985, Dewey 1992; Fisher and Brown 1993) utilized by many species of conservation concern, such as catostomids and salmonids, while spawning. I investigated the use of grid electrofishers in conjunction with visual observation to reduce effort and enable the capture of reproductively active females with selected males, for streamside spawning of broodstock.

Methods

I positioned six grid electrofishers in an area where active spawning of robust redhorse was observed two days previous. Grid electrofishers were similar to the design of Fisher and Brown (1993) and consisted of two 5-m lengths of copper mesh wire spaced 1.25-m apart using PVC pipe. I placed each unit perpendicular to the current at a depth of 0.5-1.5 m and anchored them in position using 1 m ×1.5 cm reinforcement bar stakes. I spaced the grid electrofishers 1-2 m apart, resulting in a coverage area of approximately 55 m^2. I deployed grid electrofishers between 09:30 - 10:00 hours and did not disturb them for approximately 60 minutes prior to sampling. When spawning activity was observed from shore, I activated specific grid electrofishers for 30-60 s and attempted to collect all fish. Grid electrofishers were operated at approximately 670 volts and < 4.0 amps using 60 Hz pulsed DC.

Upon capture, I weighed (0.05 kg), measured (mm TL), and determined sex for each individual. Milt was expressed from males into 75-ml sterile vials and held on ice in the dark. Eggs were expressed from females into 2-L plastic trays. After collection, eggs were divided into three aliquots and the milt from separate males was used to fertilize each. Milt was added to dry eggs and mixed using mild agitation. After 1 min., river water was added and the eggs were allowed to water harden. Eggs were then rinsed and placed in plastic bags filled with river water and oxygen. Bags were sealed and placed in insulated shipping boxes for transport to the hatchery. Eggs were incubated, and hatching success was determined.

I returned to the study area and collected robust redhorse as part of my routine sampling on three additional dates. I deployed the electrofishing grids as described above, but did not wait for spawning activity to be observed before activating them.

Results and Discussion

At least 10 robust redhorse were observed in the study area upon my arrival on 04 May 2004. Although deploying the grid electrofishers displaced these fish, they returned to locations within several meters of their previous locations within a few minutes. An additional 10 individuals entered the study area after I deployed the grid electrofishers and at least another 15 robust redhorse were observed outside the area of influence of the electrofishing grids. Spawning activity was observed almost continuously within the area covered by the grid electrofishers from 10:00 to 15:00 hours when the study was terminated. Three of the six grids were operated a total of five times, and a minimum of three fish were collected during each event (Table 1). Spawning activity was not observed in the remaining three grids. Individuals in other portions of the study area did not appear to be disturbed during the operation of a grid. All fish collected were in the running-ripe condition. Female robust redhorse were collected during four of the five events on that date. All fish recovered fully and were released alive after the procedure. Fry were successfully produced from each cross and are being reared at the Dennis Wildlife Center in Bonneau, SC. Additional female and male fish in breeding condition were collected during subsequent visits to the study area (Table 1) but no eggs or sperm were collected.

Table 1. Date, grid number, and number of male (N_{male}) and female (N_{female}) robust redhorse captured per event by grid electrofishers on the Savannah River during May 2004.

Date	Grid	N_{male}	N_{female}
04 May	5	3	0
04 May	1	4	2
04 May	4	3	1
04 May	4	3	1
04 May	1	4	2
05 May	4	3	3
09 May	4	4	0
09 May	1	3	0
09 May	4	2	0
09 May	1	1	1
14 May	4	4	1
14 May	4	1	0
14 May	1	0	1

The use of prepositioned grid electrofishers was an effective method for the collection of robust redhorse in breeding condition. The use of these grids has several advantages over traditional boat electrofishing methods for broodfish collection. While a sufficient quantity of males in spawning condition generally can be captured regardless of collection method, females collected using other methods often require hormone injections (Branchaud and Gendron 1993; Barret 1997). I was able to harvest eggs from every female robust redhorse I collected without injecting hormones to induce spawning. Grid electrofishers also reduce the amount of artificial selection by allowing the female to select her mates. In many cases, I collected breeding triads and produced embryos that were at least initially genetically similar to those that would have been produced naturally. This does not alleviate concerns of domestication occurring during rearing within hatcheries (Doyle 1983; Busack and Currens 1995; Ford 2002). However, it can potentially address concerns of artificial selection occurring due to human broodstock selection.

I was able to capture my target number of females with less effort using grid electrofishers (approximately 5 min. of pedal time). I was also able to selectively choose areas of the spawning ground from which to collect broodfish and was able to leave the remainder undisturbed. This is consistent with the findings of Bain et al. (1985) and Fisher and Brown (1993), who documented minimal disturbance outside the area encompassed by an active grid electrofisher. However, using prepositioned grid electrofishers in areas of actively spawning fish raises the same concern as other electrofishing techniques. While the effects of electrofishing on fish embryos and larva are largely unknown (see Snyder 2003 for review), several studies suggest the potential for reduced viability as a result of exposure to electric fields (Godfrey 1957; Lamarque 1990; Muth and Ruppert 1997). Minimizing the affected area and duration of exposure should be top priorities if broodstock collection on active spawning grounds cannot be avoided. Therefore, use of grid electrofishers in conjunction with visual observation under some circumstances warrants further consideration as an effective tool for the collection of reproductively active broodstock for conservation purposes.

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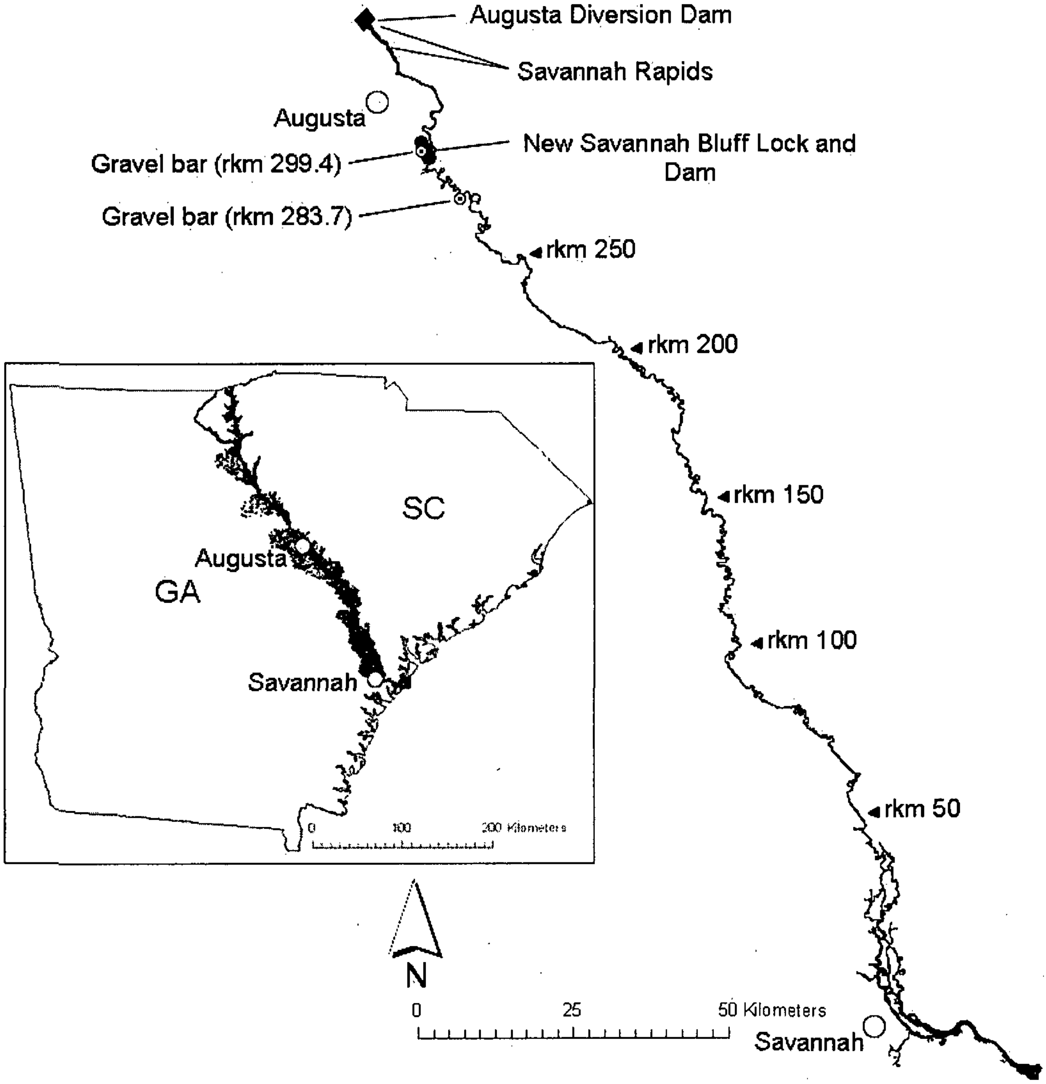

Figure 1. The study area consisting of the lower Savannah River below the Augusta Diversion Dam. River kilometers (rkm) below New Savannah Bluff Lock and Dam are indicated by solid triangles. Inset shows the Savannah River watershed with the cities of Augusta and Savannah indicated by open circles..

SEASONAL AND DIEL MOVEMENT AND HABITAT USE OF ROBUST REDHORSE IN THE LOWER SAVANNAH RIVER, GEORGIA AND SOUTH CAROLINA

Introduction

Robust redhorse *Moxostoma robustum* is a large-bodied, riverine catostomid whose known native distribution is currently restricted to three Atlantic slope drainages in the southeastern U.S. This species was originally described from the Pee Dee River Basin in North Carolina (Cope 1870) but subsequently was effectively lost to science for over a century (Bryant et al. 1996). Its rediscovery in the 1980s prompted conservation efforts to prevent further population decline and listing under the Endangered Species Act (Bryant et al. 1996; Cooke et al. 2005). Populations have been discovered in the lower piedmont and upper coastal plain regions of the Oconee and Ocmulgee Rivers in the Altamaha River system (Georgia); the Savannah River (Georgia and South Carolina); and Pee Dee River system (North Carolina and South Carolina). Robust redhorse probably occurred in the river systems between the Pee Dee and Altamaha Rivers, such as the Santee River Basin (Bryant et al. 1996). However, populations have yet to be identified from these other rivers and are presumed extirpated. The decline of robust redhorse, like that of other catostomid species, has been blamed on numerous factors including introduced predators (flathead catfish *Pylodictus olivaris*: Bart et al. 1994) and competitors (buffalo *Ictiobus* spp: Moyle 1976); habitat degradation and fragmentation (Jennings 1998; Weyers et al. 2003); and recruitment failure due to life history bottlenecks (Jennings 1998; Weyers et al 2003). However, the exact causes of decline and the current status of robust redhorse populations are currently uncertain.

Despite being the focus of conservation and restoration efforts, virtually nothing was known about the movement or habitat use of adult robust redhorse prior to this study. Adult fishes have been observed to form spawning aggregations on shallow main channel gravel bars in the Oconee and Savannah Rivers during May and June when water temperatures are 18-22°C (Freeman and Freeman 2001). Anecdotal reports suggest adults are generally collected in association with woody debris and swift current throughout much of the year. To date, there have been few comprehensive, long-term telemetry studies of the movement or habitat use of catostomids and none of adult robust redhorse.

My objectives for this study were to characterize seasonal migration, diel movement patterns, and essential habitat of robust redhorse in the Savannah River. I assessed the effects of temperature and flow as cues for seasonal upstream and downstream migrations. I also determined the degree of site fidelity in relation to spawning, staging, and overwintering habitats.

Methods

Study area

The Savannah River is one of the largest Atlantic Slope drainages, encompassing a watershed of approximately 25,000 km^2 (Marcy et al. 2005). It is 505 km in length; however, only the lower 300 km below New Savannah Bluff Lock and Dam (NSBL&D) in Augusta, Georgia is free flowing (Figure 1). The NSBL&D is the terminal dam on the

Savannah River and first barrier to upstream migration. It is passable only during lock operation and high water events when river discharge exceeds 20,000 cfs. Upstream of NSBL&D is a 26.7-rkm segment that encompasses Savannah Rapids (also commonly referred to as the Augusta Shoals) and ends at the impassable Augusta Diversion Dam. Native populations of robust redhorse in the Savannah River currently are known only from these two river segments.

Data collection

Robust redhorse were captured during June 2002 using standard electrofishing techniques. I sampled once immediately below Savannah Rapids and twice near a main channel gravel bar at rkm 283.7. I collected fish in May 2004 from the spawning aggregation at this gravel bar to replace individuals who had died or shed tags. The sex of each individual was determined based upon presence of nuptial tubercles and gamete expression. I also measured total length (mm TL) and weighed (g) each fish. Fish were anesthetized in a 100-mg/L buffered tricaine methanesulfonate (MS-222) solution and a PIT tag and two T-bar anchor tags were inserted into the musculature near the dorsal fin.

To ensure that the transmitter weight never exceeded 1.5% of the body weight of the fish, I used one of two sizes of pulse coded radio transmitters with trailing wire antennae (Lotek Wireless Inc., Newmarket, Ontario, Canada). A 10.0-g transmitter with a minimum battery life of 560 days was used for fish < 500 mm TL and a 26.0-g transmitter with a minimum battery life of 912 days for larger fish. Both transmitters were detectable at a range of approximately 500 m when submerged. I implanted a radio transmitter into the peritoneal cavity of all captured fish following the surgical procedures of Walsh et al. (2000). Briefly, a small (< 30 mm) incision was made off the ventral midline between the pelvic fins and vent after the fish was anesthetized. The transmitter was inserted and the incision was closed with three interrupted 3-0 coated absorbable sutures. The antenna was allowed to exit the body through the original incision. The procedure took approximately three minutes, and fish were allowed to recover for approximately 30 minutes in an aerated holding tank before release. Water temperatures in the Savannah River were < 20 °C during the surgeries.

I established the locations of radio-tagged robust redhorse using a Lotek SRX-400 telemetry receiver (Lotek Wireless Inc., Newmarket, Ontario, Canada) with a four-element yagi antenna. Fish were considered located when maximum signal strength was received for three consecutive pulses. Fish position was recorded ±8.0 m using a hand-held global positioning system receiver. Additionally, I plotted the location of each fish to within 100-m sections on National Oceanic and Atmospheric Administration nautical charts (11514 and 11515) after visual triangulation to river markers, terrestrial landmarks, and river features such as inlets, tributaries, and cut-offs. I recorded the position of the fish relative to the bank or center of the channel. Fish were located approximately every two weeks by boat from June 2002 to September 2003; however, tracking frequency was increased to once per week during the 2003 and 2004 spawning seasons. After September 2003, frequency was reduced to once a month until tagged fish began upstream migrations. The fish captured and released near the Savannah Rapids frequently moved into areas inaccessible by boat, necessitating that I track these fish from shore.

Additionally, I used the protocol described above to locate a subset of individuals once every two hours during a consecutive 48-hour period over a fixed transect.

Transects typically were 26 rkm in length (range, 16.0 - 27.7 rkm) and contained 5-10 radio-tagged robust redhorse. Diel tracking was conducted once per calendar season on 18-20 October 2002 (fall), 27 February-01 March 2003 (winter), 11-13 June 2003 (spring), 12-13, 20 September 2003 (summer). The summer diel tracking was interrupted due to mechanical problems with the boat.

Data analysis

I calculated absolute distance moved, range, displacement, and estimates of minimum daily movement for both seasonal and diel data sets. Absolute distance moved is the sum of the distance moved between relocations. Range is the distance between the most upstream and downstream locations within a season or day. Displacement is the net distance moved, with upstream movements positive and downstream movements negative. Estimates of minimum daily movement were calculated only for the seasonal data and is equal to the absolute distance moved between subsequent observations divided by the number of days elapsed. The hypothesis that these parameters differed among seasons (fixed effect) was tested using a mixed model analysis of variance while controlling for individuals, sex, and year (random effects) (Zar 1996). All means are reported ± SE. A significance level of $\alpha = 0.05$ was used for all tests.

Results

I captured a total of 19 adult robust redhorse ranging in size from 460 to 690 mm TL during June 2002 (Table 2). Two males were captured immediately below Savannah Rapids at rkm 324.2. Another 17 individuals (12 males; 5 females) were captured below

Table 2. Identification number, sex, total length (TL), weight (W), date of capture, release point, and number of relocations for radio-tagged robust redhorse in the Savannah River.

ID	Sex	TL (mm)	W (g)	Date of capture	Release point (rkm)	Number of relocations		
						Seasonal	Diel	Total
26	M	460	1400	21-Jun-02	283.7	40	85	125
41	M	585	2750	2-Jun-02	324.2	31	0	31
42	M	590	2800	11-Jun-02	283.7	52	59	111
43	M	540	1800	11-Jun-02	283.7	65	84	149
45	M	570	2600	11-Jun-02	283.7	50	42	92
46	F	590	3100	11-Jun-02	283.7	50	22	72
47	M	550	1800	11-Jun-02	283.7	50	21	71
48	M	625	3350	11-Jun-02	283.7	50	0	50
49	M	660	3400	11-Jun-02	283.7	31	21	52
50	M	550	2100	11-Jun-02	283.7	48	42	90
51	F	625	3400	11-Jun-02	283.7	41	41	82
56	M	620	3800	2-Jun-02	324.2	29	0	29
59	F	665	3950	21-Jun-02	283.7	53	55	108
61	F	690	3900	21-Jun-02	283.7	39	43	82
65	M	560	3100	2-May-04	283.7	14	0	14
67	M	680	4700	2-May-04	283.7	10	0	10
70	F	680	4300	2-May-04	283.7	14	0	14

NSBL&D from a main channel gravel bar at rkm 283.7. The individuals captured from this gravel bar were presumably part of a spawning aggregation. Captured fish exhibited characteristics consistent with those described for breeding *Moxostoma* spp. such as fully formed nuptial tubercles, a loss of mucus, and cornified scales (Jenkins and Burkhead 1993). In addition, most of these individuals expressed gametes with mild abdominal pressure. Four robust redhorse died or shed their transmitters within the first two weeks after release, and one died or shed her transmitter after 21 months. An additional five individuals (4 males; 1 female) were captured at the same gravel bar in May 2004 (Table 2). Two of these fish died or shed transmitters within two weeks of release.

Between June 2002 and April 2005 I relocated radio-tagged robust redhorse 1,182 times. Diel tracking accounted for 515 of these observations. Individuals were relocated from 10 to 165 times (Table 2). Individual females were relocated an average of 71.6± 15.59 times and males were relocated an average of 73.1± 14.93 times. The two individuals captured above NSBL&D were relocated a combined 60 times. These two fish along with fish captured in 2004 and fish 48, were not incorporated in at least one of the diel tracking transects (Table 2).

The majority of the robust redhorse remained near their release site (±6.5 rkm) throughout summer 2002 (Figure 2). However, one individual moved 172.8 rkm downstream within one week of release and remained there throughout the fall and winter before moving upstream in spring 2003. The remaining fish below NSBL&D began downstream migrations to overwintering areas in early to mid fall 2002 (Figure 2). Overwintering fish dispersed along the length of the river down to rkm 90 (Figure 2). The majority of radio-tagged robust redhorse showed a high degree of overwintering-site fidelity (Figure 2), returning to the same 100 to 200-m lengths of shoreline each year. These overwintering areas were distributed along the outside edge of river bends in water 3.0 to 5.0 m in depth. Observations using an underwater camera system showed coarse gravel substrate and structurally complex habitats consisting of large woody debris. Fish began to make upstream migrations in early to mid March of 2003, 2004, and 2005

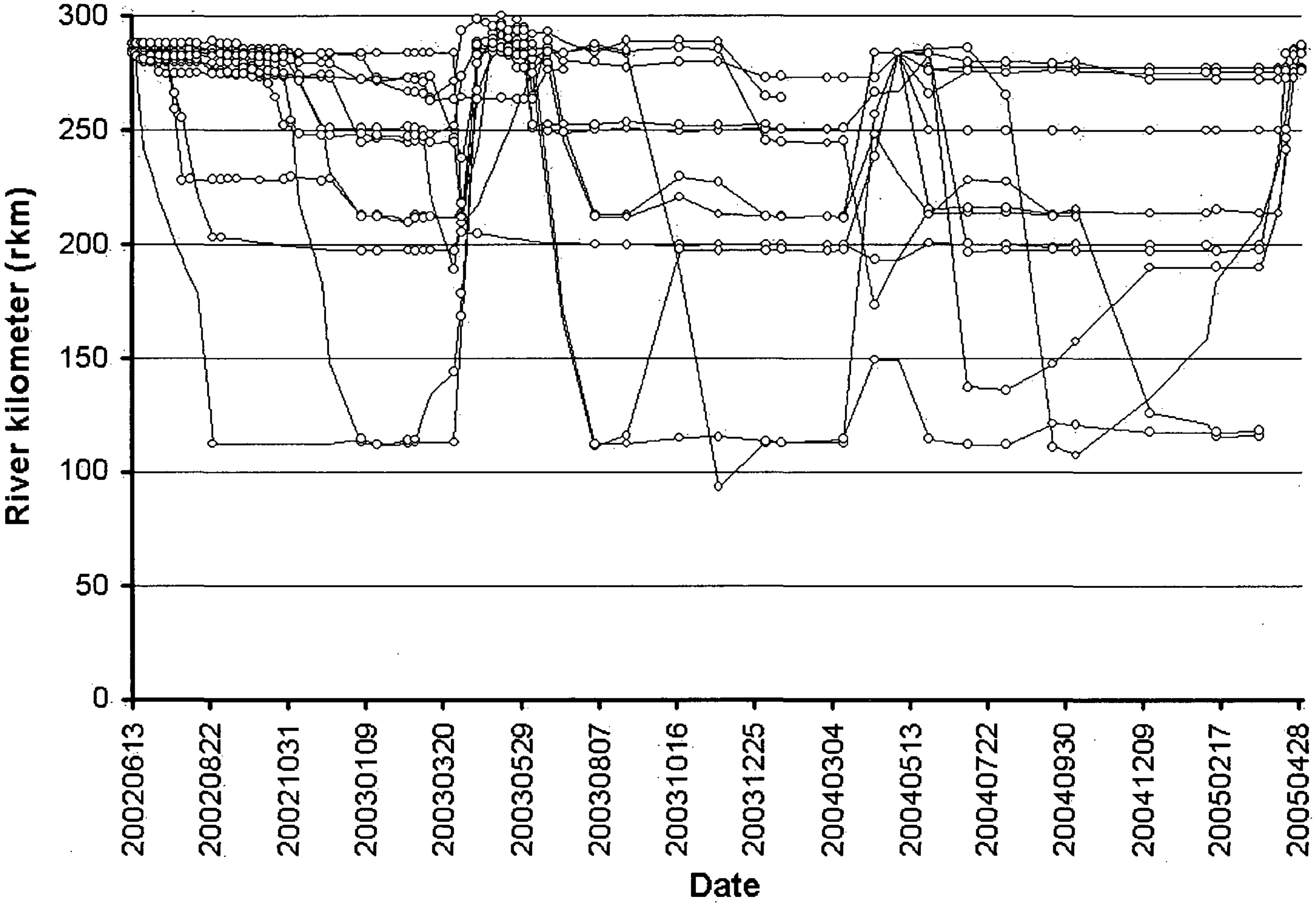

Figure 2. River kilometer (rkm) positions of individual radio-tagged robust redhorse in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to May 2005.

(Figure 2) when water temperatures were approximately 10-12°C. Most individuals made upstream migrations each year. Radio-tagged robust redhorse also demonstrated a high degree of spawning-site fidelity. Fish returned to either the gravel bar at rkm 283.7 or to staging and holding areas immediately upstream or downstream of it (Figure 2). Fish spent the remainder of spring and early summer in the vicinity of their spawning grounds before dispersing downstream in late June and early July to their overwintering areas (Figure 2).

This general pattern of behavior was somewhat different during the high water year of 2003. High flows occurred in winter and spring and continued into late summer. In contrast, 2002 and 2004 were drought years, with flows rarely exceeding the median daily streamflow. During high water, radio-tagged robust redhorse accessed the floodplain occupying flooded forest habitats. This was the only time during the study when I observed robust redhorse out of the main river channel. My fish did not use any of the smaller order streams that flow into the Savannah, regardless of flow conditions. Spawning habitat fidelity also appeared to decrease during high water. Radio-tagged robust redhorse spent time at both main channel gravel bars during spring 2003 (Figure 2). One radio-tagged robust redhorse was able to pass NSBL&D during high flow periods in 2003. Fish 51 was last observed below the dam at rkm 276.2 on 28 June 2003 and not again until it was relocated above NSBL&D on 9 August 2004 at rkm 326.6 in the Savannah Rapids.

Radio-tagged robust redhorse above NSBL&D did not exhibit any seasonal movement patterns (Figure 3). These individuals remained in the shoal and pool habitat of the Savannah Rapids. Gaps in the data are presumed to occur when fish moved out of

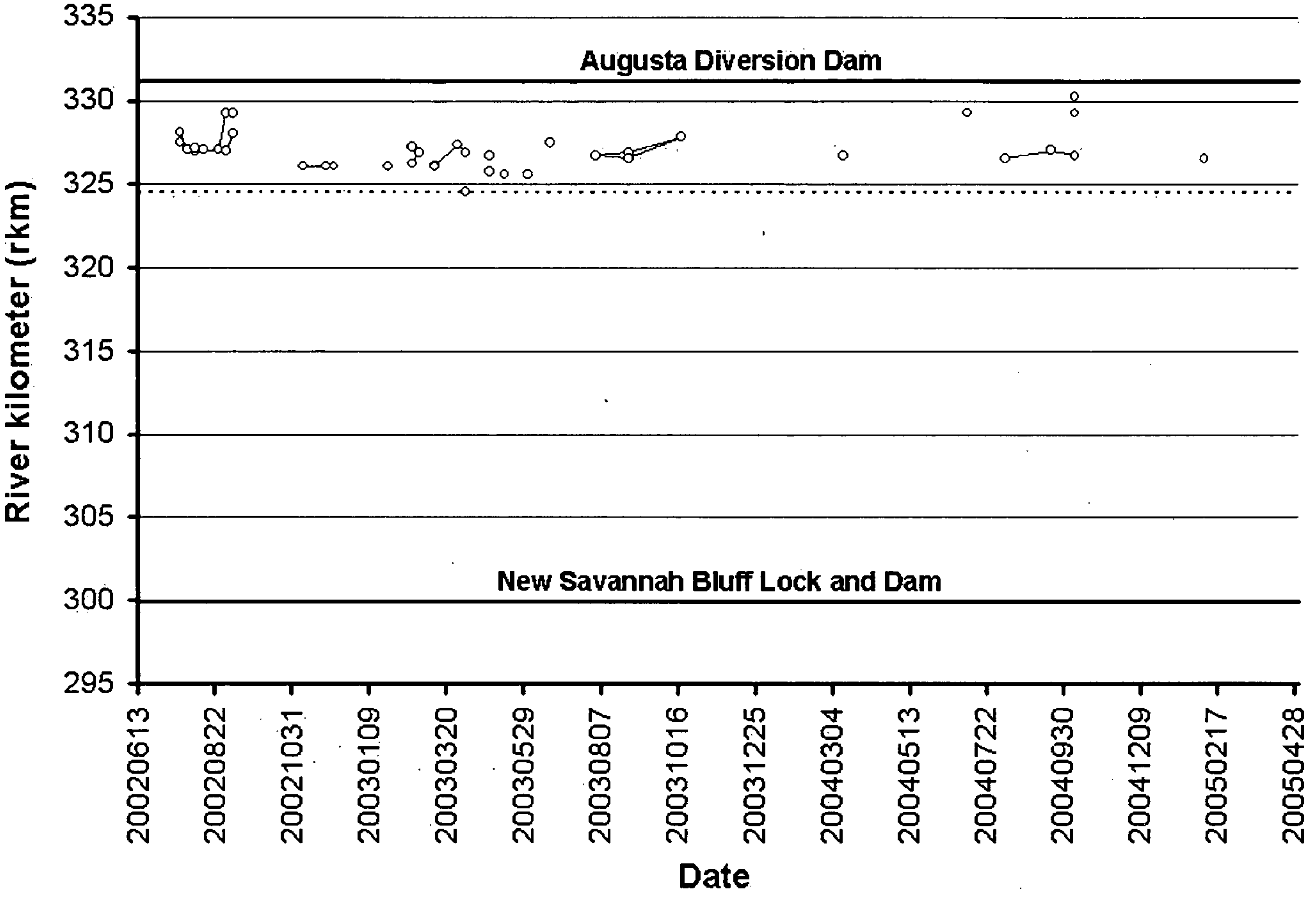

Figure 3. River kilometer (rkm) positions of individual radio-tagged robust redhorse in the Savannah River between the Augusta Diversion Dam and New Savannah Bluff Lock and Dam from June 2002 to May 2005. Dashed line represents the downstream limit of the Savannah Rapids.

range of the receiver within the shoals as they were never located in the navigable portion of the river below the shoals between rkm 323.0 and NSBL&D.

Season was the most important correlate to robust redhorse activity and movement over the course of a year. No differences between sexes in absolute movement ($F_{1,\,132}$=3.40, p=0.0676), displacement ($F_{1,\,132}$=0.03, p=0.8552), seasonal range ($F_{1,\,132}$=0.23, p=0.6354), or minimum estimates of daily movement rates ($F_{1,\,132}$=0.02, p=0.8954) were observed. Spring and summer were the only seasons in which any of these parameters statistically differed from zero ($t_{155} \geq 2.14, p \leq 0.0336$). Radio-tagged robust redhorse were most active in spring ($F_{3,\,155}$=7.27, p=0.0001) moving on average a total of 52.7±8.9 km (Figure 4). In terms of directed movement or displacement, movement patterns were different in spring and summer ($F_{3,\,155}$=7.76, p<0.0001). Fish migrated a mean distance of 23.4±8.4 km upstream in spring and returned 24.6±9.0 km downstream in summer (Figure 4). Minimum estimates of daily movement rates were highest in spring ($F_{3,\,155}$=14.02, p<0.0001) and ranged from 0.8±0.1 km/d in spring to 0.1±0.02 km/d in winter (Figure 4). Radio-tagged robust redhorse also exhibited the greatest seasonal range in spring ($F_{3,\,155}$=9.23, p<0.0001), with a mean distance of 31.3±6.0 km between the furthest upstream and downstream locations (Figure 4).

There were interannual differences in absolute movement ($F_{3,\,132}$=5.92, p=0.0008), seasonal range ($F_{3,\,132}$=2.76, p=0.0446), and minimum estimates of daily movement rates ($F_{3,\,132}$=4.45, p=0.0052). However, 2003 and 2004 were the only complete calendar years of data. Absolute movement was the only parameter that differed between 2003 and 2004 ($t_{132} \leq 1.70, p \geq 0.0912$). Fish were more active in 2003 than 2004 (t_{132}=2.30, p=0.0229) moving on average 22.6±9.5 km more in 2003.

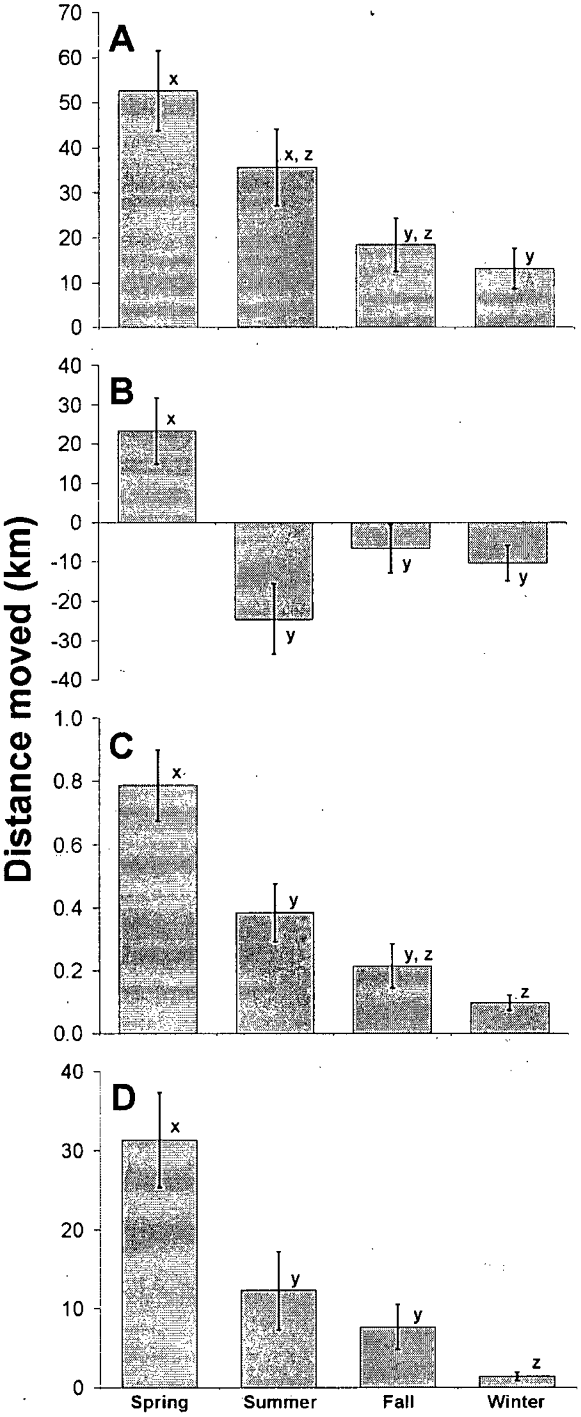

Figure 4. Mean seasonal absolute movement (A), displacement (B), minimum estimate of daily movement (C) and range (D) of radio-tagged robust redhorse in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to May 2005. Error bars represent standard error.

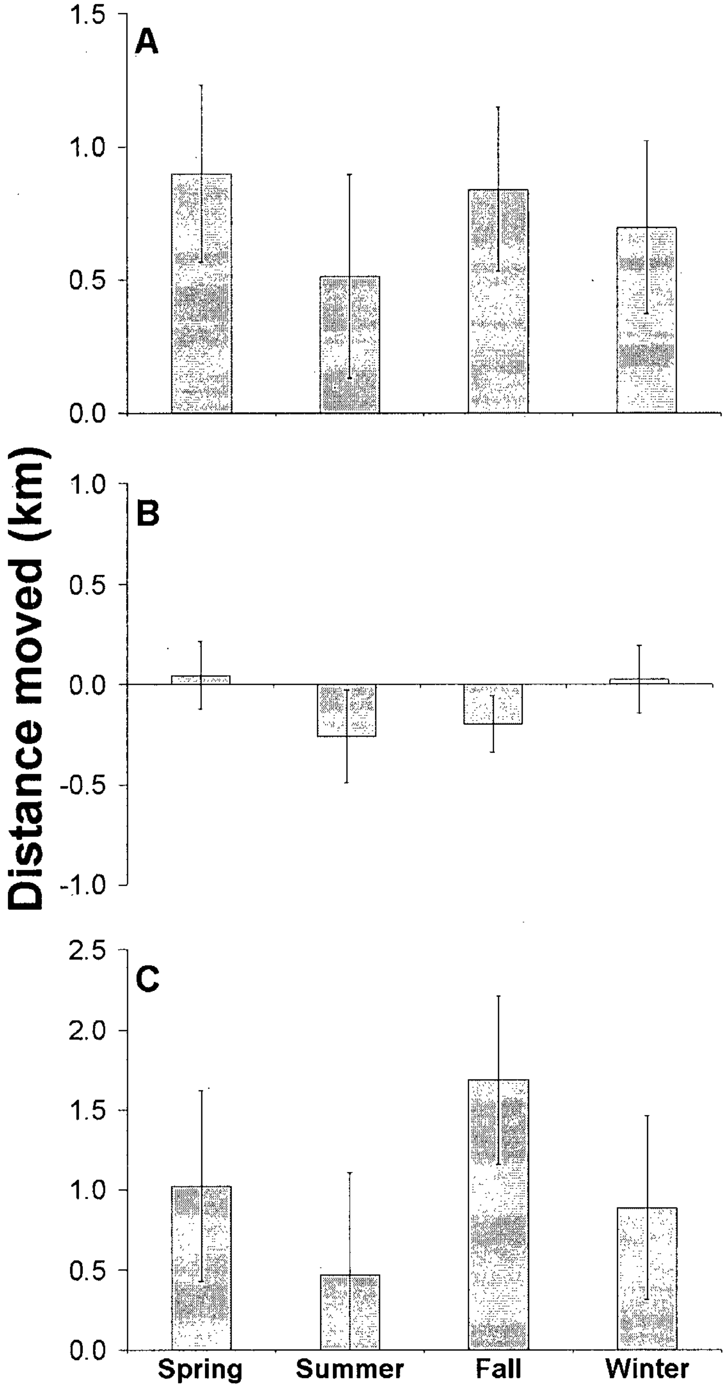

Figure 5. Mean diel absolute movement (A), displacement (B), and use area (C) by season of radio-tagged robust redhorse in the lower Savannah River below New Savannah Bluff Lock and Dam. Error bars represent standard error.

On average, radio-tagged robust redhorse moved between 0.5 and 1.0 km over a 24-hr period (Figure 5). There were no seasonal differences in the total activity of individuals ($F_{3,17}$=0.59, p=0.6236). There was no evidence of directed movement (Figure 5), as mean diel displacement did not differ from zero ($t_{141} \leq 0.28$, $p \geq 0.1638$). Daily use areas were approximately 1.0 km in length (Figure 5) and did not differ among season ($F_{3,17}$=1.13, p=0.3464). Absolute time of day did not have any effect on robust redhorse activity ($F_{11,551}$=1.46, p=0.1434). However, activity was influenced by photoperiod ($F_{3,17}$=6.96, p=0.0013), with significantly more movement occurring during daylight hours than at night (t_{141}=2.32, p=0.0219) or during twilight hours (t_{141}=3.65, p=0.0004) (Figure 6).

Discussion

Robust redhorse used almost the entire length of the Savannah River below NSBL&D, making extensive upstream migrations to spawning habitat and downstream migrations to overwintering areas. Like other catostomid species such as razorback sucker *Xyrauchen texanus* (Tyus 1987; Tyus and Karp 1990; Modde and Irving 1998), white sucker *Catostomus commersoni* (Olson and Scidmore 1963), and southeastern blue sucker *Cycleptus meridionalis* (Mettee et al. 1996), robust redhorse below NSBL&D appear to be potamodromous. Potamodromy is a migratory strategy involving movements entirely within freshwater employed by numerous riverine fishes including many species of sturgeons (Bemis et al. 1997), paddlefish *Polyodon spathula* (Bemis et al. 1997; Stancill et al. 2002; Zigler et al. 2003), large catfishes (Barthem et al. 1991; Barthem and Goulding 1997; Vokoun and Rabeni 2005), large cyprinids (Tyus 1990;

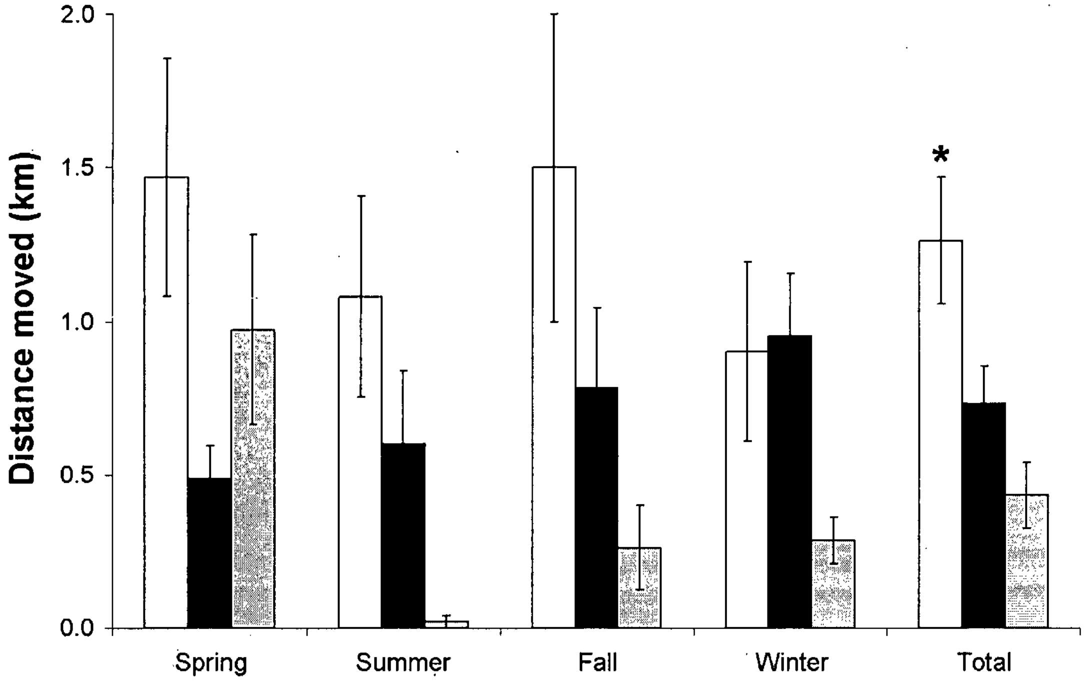

Figure 6. Mean absolute movement between 2-hour tracking periods of robust redhorse in the lower Savannah River below New Savannah Bluff Lock and Dam. White, black, and grey bars represent daylight, nighttime, and twilight respectively. Error bars represent standard error.

Lucas and Batley 1996; Allouche et al. 1999; Winter and Fredrich 2003), and some characoids (Bayley 1973; Duque et al. 1998). Specific information regarding the migratory behavior of other *Moxostoma* species is very limited, but it appears Savannah River robust redhorse undertake much longer upstream migrations to spawning habitats than those reported for other redhorse species such as greater redhorse *Moxostoma valenciennesi* (Bunt and Cooke 2001) or river redhorse *Moxostoma carinatum* (Hackney et al. 1968). It also is likely robust redhorse migrated even further upstream to the extensive gravel bars in Savannah Rapids and beyond before the construction of dams on the Savannah River. Historical records indicate American shad *Alosa sapidissima*, and other anadromous fishes migrating over 614 rkm to the Savannah headwaters in the Tugaloo and Tallulah Rivers before the construction of dams on the system (Mills 1826; Eudaly 1999; Welch and Eversole 2000). Also, the capture locality of the holotype indicates robust redhorse penetrated well into the piedmont region of the Pee Dee River Basin (Cope 1870). The possibility that dams have limited availability or access to suitable spawning habitats for robust redhorse populations in the Savannah River needs to be assessed. The wide-ranging nature of these fish means that conservation efforts focused only upon key habitats without providing for passage between them are unlikely to be successful and that a whole system management approach should be encouraged (Cooke et al. 2005).

In addition to making long distance migrations, robust redhorse display a high degree of site fidelity, returning to the same areas used in previous seasons for staging, spawning and overwintering. Fidelity to spawning habitat has been demonstrated in many riverine fishes other than salmonids including white sucker (Olson and Scidmore

1963; Werner 1979), river carpsucker *Carpiodes carpio* and common carp *Cyprinus carpio* (Bonneau and Scarnecchia 2002), Colorado pikeminnow *Ptychocheilus lucius* (Tyus 1990), razorback sucker (Mueller et al. 2000), and paddlefish (Stancill et al. 2002). However unlike most of the abovementioned species and the majority of catostomid species (Curry and Spacie 1984; Page and Johnson 1990), my radio-tagged robust redhorse did not ascend tributaries to spawn. Instead they used main channel gravel bars similar to other large riverine redhorses, such as river redhorse (Hackney et al. 1968), greater redhorse (Jenkins and Jenkins 1980; Cooke and Bunt 1999) and copper redhorse *Moxostoma hubbsi* (R. Dumas, Société de la Faune et des Parcs du Québec, personal communication). Therefore fidelity to spawning habitat in the lower Savannah River may be overestimated as there are only two main channel gravel bars to choose from. For example, individuals exhibited a high degree of site fidelity when conditions were suitable for spawning in 2004 and 2005. However, individuals visited both gravel bars in May and June 2003 when high water rendered both bars unsuitable. This pattern of wandering among a few sites within a relatively small area during the spawning season has been observed in razorback suckers (Tyus and Karp 1990; Modde and Irving 1998; Mueller et al. 2000) and paddlefish (Paukert and Fisher 2001; Stancill et al. 2002) and suggests some assessment of habitat quality and suitability occurs before committing to a spawning site regardless of past use.

The degree of fidelity displayed for staging and overwintering areas by radio-tagged robust redhorse was unexpected. Radio-tagged robust redhorse often migrated >100 km to spawning habitats and then returned a few weeks later to the same fallen tree where they spent much of the previous winter. In many cases, this site specificity was on the order of 0.1 rkm for overwintering areas. Other telemetry studies of riverine fishes have not noted this level of specificity to overwintering and staging areas. However, fidelity to overwintering areas has been identified on coarser scales in reservoir populations of striped bass *Morone saxatilis* (Jackson and Hightower 2001; Young and Isely 2002) and razorback suckers (Mueller et al. 2000). It is not clear why robust redhorse would display such a high degree of fidelity to overwintering and staging habitats. Reports on the behavior of other catostomids offer no clear patterns. Some studies suggest these fishes are generally more active and wide ranging (Dauble 1986; Chart and Bergersen 1992), while others hint at similar behavior pattern (Matheney and Rabeni 1995; Bunt and Cooke 2001). It is important to note that these studies were either conducted on populations in smaller streams, were short duration telemetry studies, or relied upon mark-recapture, making direct comparisons to this study difficult.

A possible reason for the high degree of site fidelity to overwintering areas exhibited by robust redhorse is that they are able to fulfill all of their requirements except for spawning in a relatively small area. Robust redhorse appear to use their entire home range during the course of a day. In so doing, it appears their behavior and activity is consistent with that detailed in the restricted movement paradigm. The restricted movement paradigm holds that resident stream fishes spend the majority of their lives within short reaches (Gerking 1953, 1959; Rodriguez 2002). This theory has come under criticism (see Gowan et al. 1994; Rodriguez 2002) and has recently been revised to account for both potamodromy and infrequent home range shifts (Crook 2004). My results suggest this species is mostly sedentary and occupies relatively small linear home ranges for extended periods of time interspersed with long distance seasonal migrations.

While it was not common, I did observe some individuals shifting to new home ranges usually during their downstream migrations but only infrequently did they do so at other times of the year. Razorback sucker (Mueller et al. 2000) was the only catostomid species for which I could find a similar pattern reported in the literature; however, this behavior pattern has been described in other large riverine fishes such as golden perch *Macquaria ambigua* and common carp (Crook 2004).

Robust redhorse moved into previously unused habitats during winter and spring floods on the Savannah River in 2003. High water events were the only times I observed radio-tagged robust redhorse outside of the main river channel. In some cases, fish entered flooded tributaries, oxbows, and other backwater areas, but most fish were located on the floodplain immediately adjacent to the river channel. Riverine fishes movement into these habitats during flood events has been attributed to avoidance of displacement by high current velocities (Matheney and Rabeni 1998; Allouche et al. 1999; David and Closs 2002), to foraging on the floodplain (Ross and Baker 1983; Turner et al. 1994; Snedden et al. 1999), or to spawning in floodplain habitats (Welcomme 1979; Snedden et al. 1999). I was not able to ascertain the reason that robust redhorse left the main river channel during high water events, but hypothesize that robust redhorse may be using the floodplain habitats for feeding in preparation of spawning. This species spawns from May to mid June and may improve condition or fecundity by foraging on the floodplain in March and April.

The behavior of the two individuals captured above NSBL&D was markedly different from their downstream counterparts. These individuals did not undertake long migrations and instead preferred to remain in the Savannah Rapids and did not use the river below the shoals. This section of the river flows through downtown Augusta and is highly channelized. After flowing through the city, the river becomes more lentic in nature as it approaches the dam. These fish also did not appear to have the same affinity for large woody debris, even though this habitat was available to them. It is also notable that the one fish that was able to pass NSBL&D during the course of my study adopted a pattern of behavior similar to the two individuals that were originally captured in the Savannah Rapids. I hypothesize that the robust redhorse population above NSBL&D may be confined to a relatively small stretch of river (approx. 8.0 rkm) based on the inability or unwillingness of the radio-tagged fish to move out of Savannah Rapids. This requires further investigation due to the small sample size and difficulty in locating these fish during my study.

My observations of the behavior of radio-tagged robust redhorse in the Savannah River help to explain how this species was able to remain “lost to science” for over 100 years after its initial discovery. While historical overfishing (Cope 1870) and general apathy toward suckers (Cooke et al. 2005) likely contributed to its “disappearance,” robust redhorse demonstrate behaviors and habitat preferences that render them cryptic. This species spends the majority of its time in habitats that are inaccessible or difficult to sample effectively with common gear types such as boat electrofishers or gill nets. Individuals are easy to capture on their spawning habitat but their late spawning season puts them out of reach of the spring monitoring programs of state resource management agencies. Knowledge of the movement patterns and habitat use of this species should help with continuing investigations of the basic biology and ecology of robust redhorse in the Savannah River and throughout its range.

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SPATIAL AND TEMPORAL HABITAT SEGREGATION BY
SPAWNING CATOSTOMIDS IN THE SAVANNAH
RIVER, GEORGIA AND SOUTH CAROLINA

Introduction

The deposition of eggs on or in gravel substrate during spawning is a reproductive strategy commonly employed by riverine fishes. Species employing this strategy share similar spawning habitat requirements that include clean gravel substrate of a particular size range and well-oxygenated, flowing water (Balon 1975). Availability of suitable spawning habitat may be a limiting factor affecting both population and community structure of fishes utilizing this strategy (Benson 1953; Ming and Noakes 1984; Essington et al. 2000). In salmonids, redd site superimposition has been identified as a significant source of mortality and reduced reproductive success (Fukushima et al. 1998; Essington et al. 2000). Redd site superimposition is commonly observed within a species due to the behavioral preferences of females to deposit eggs on existing nest sites even when suitable habitat is abundant (Essington et al. 1998). However, interference between sympatric salmonid species is rarely observed unless they are closely related (Ming and Noakes 1984; Essington 1998; Fukushima and Smoker 1998). The underlying reasons for this have not been adequately investigated. It is likely in most systems, there is enough suitable habitat available to accommodate the number of spawning individuals of each species. It is also possible that sympatric species have microhabitat preferences different enough to segregate them spatially (Curry and Spacie 1984; Kwak and Skelly

1992; Essington et al. 2000) or use the same habitats at intervals sufficient to allow for the completion of incubation and larval swim-up and thus reduce interference.

As many as seven species of catostomids regularly inhabit main channel habitats within the Savannah River, including the imperiled robust redhorse *Moxostoma robustum*, the recently recognized notchlip redhorse *Moxostoma collapsum*, the currently undescribed brassy jumprock *Moxostoma* sp., quillback *Carpiodes cyprinus*, highfin carpsucker *Carpiodes velifer*, spotted sucker *Minytrema melanops*, and northern hogsucker *Hypentelium nigricans* (Marcy et al. 2005). The members of this assemblage all have been reported to require clean gravel deposits in shallow flowing water for successful spawning (Balon 1975; Page and Johnston 1990; Marcy et al. 2005). This habitat type is extremely rare in the main channel of the lower Savannah River and dams impede access upstream where it is more abundant. The hypolimnetic discharge of these dams has altered temperature regime of the lower Savannah (Paller and Saul 1996). Changes in temperature regimes due to dams have been shown to delay reproduction and increase the length of the spawning season in gizzard shad *Dorosoma cepedianum* (Paller and Saul 1996). While some of the catostomid species present in the Savannah are known to ascend tributaries during spawning migrations in other drainages (Curry and Spacie 1984; Page and Johnston 1990; Jenkins and Burkhead 1993), available information regarding the life histories and preferences of these fishes suggests that many riverine populations complete this portion of their life cycle within the confines of the main channel (Jenkins and Burkhead 1993; Marcy et al. 2005; Grabowski and Isely *in review*). Catostomids that make spawning migrations into smaller tributaries have been observed to partition spawning habitat spatially and demonstrate distinct microhabitat preferences (Curry and Spacie 1984; Kwak and Skelly 1992; Dion and Whoriskey 1993). I predict that catostomids in the main channel of the Savannah River will demonstrate a greater degree of superimposition because of the limited availability of spawning habitat.

The objectives of my study were to document the specific spawning habitat requirements and determine the degree of spatial and temporal segregation of this habitat occurring among catostomid species in the lower Savannah River. I also assessed the degree of intraspecific overlap in nest sites on each of the two gravel bars.

Methods

Study area

The Savannah River is one of the largest of the Atlantic Slope drainages and encompasses a watershed of over 25,000 km^2. It is approximately 500 km in length, but only the lower 300 km below the New Savannah Bluff Lock and Dam (NSBLD) at Augusta, Georgia are free flowing. The Savannah River is a highly modified and regulated system with seven main stem dams, five of which have hydroelectric generation capabilities.

My study area consisted of the two mid-channel gravel bars in the lower Savannah (Figure 7). The upper bar is located at rkm 299.4 just below the tailrace of NSBLD. It is approximately 170 m long and 150 m wide, and is composed of a relatively thin layer of gravel over packed sand. This bar rises almost 3 m from the bottom on the Georgia side of the river channel at base flows and has a teardrop shape

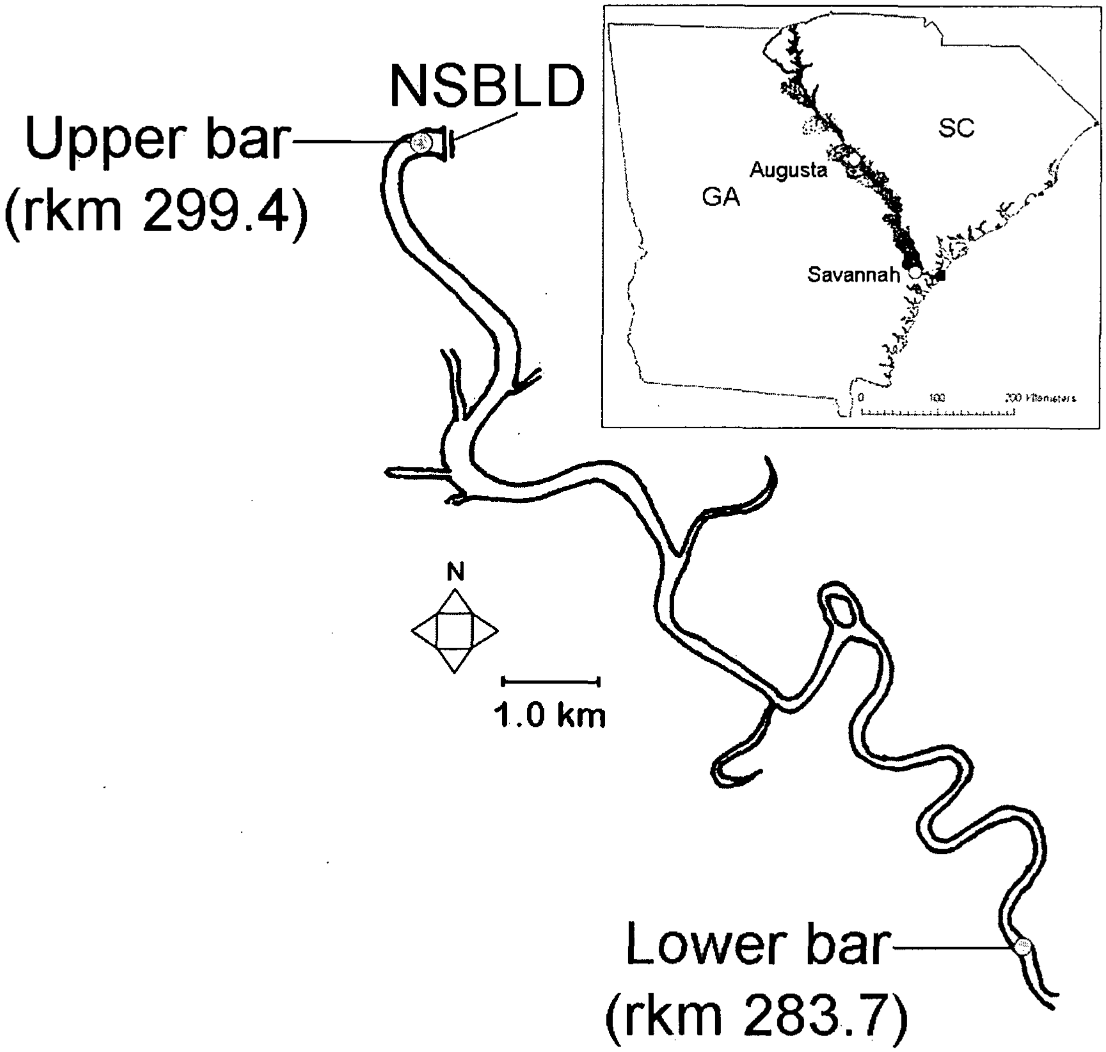

Figure 7. Map of the 16 river kilometer reach of the lower Savannah River below New Savannah Bluff Lock and Dam (NSBLD) showing the location of the upper and lower gravel bars. Inset shows location of the Savannah River. Enlarged reach begins just below Augusta, Georgia.

(Figure 8). A smaller, secondary gravel bar is associated with the upper bar and is located immediately downstream. This secondary bar is located along the South Carolina bank and is separated from the upper bar by a narrow channel. Observations were made every other day at the upper bar during spring in both 2004 and 2005. The lower gravel bar is both smaller than the upper one, approximately 60 m by 70 m, and lower relief, rising less than 2 m from the river bottom at base flows. Located at rkm 283.7, the lower bar is composed primarily of gravel over a layer of loosely packed sand and is shaped like the letter Y (Figure 9). The lower bar was not part of the original study in 2004, but the chance observation of a large robust redhorse spawning aggregation there in May 2004 led to its inclusion in 2005. Observations were made every other day in spring 2005.

Data collection

A combination of methods was used to assess how these habitats are partitioned and used by spawning catostomids, but I primarily relied on visual observation. Visibility was such that fish could be observed from the surface with the use of polarized sunglasses. The positions of fish that were spawning, staging, and holding position near the spawning grounds were recorded with a global positioning system (GPS) receiver while drifting over the deeper (>1.5 m) areas of the gravel bar in a boat. Boat observations were conducted over two 15-minute periods every day when conditions allowed. I observed fishes in shallower water from a 3-m tall observation tower placed on the gravel bar. Tower observations typically lasted 60 minutes and were conducted 2-3 times each day when conditions allowed. The positions of fish were marked with

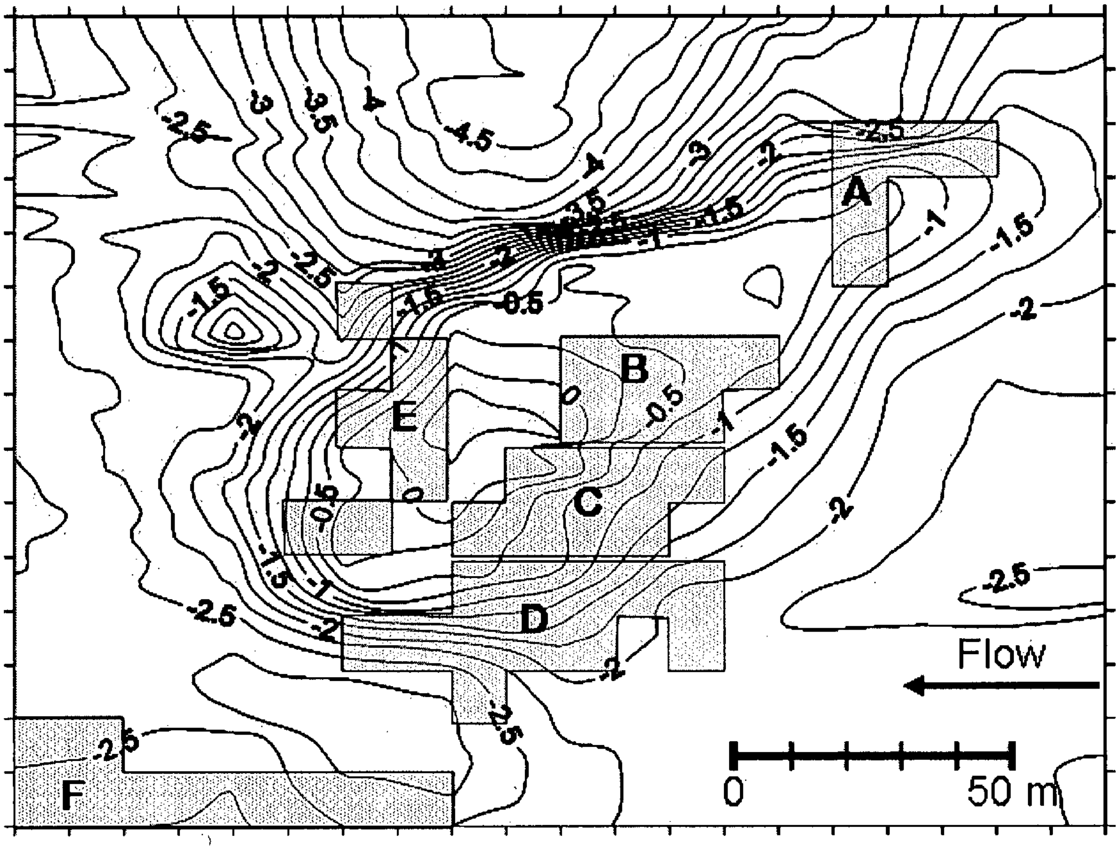

Figure 8. Bathymetric map of the upper gravel bar at river kilometer 299.4 on the lower Savannah River. Contour lines represent a change in depth of 0.25 m. Depths indicate water depth under low flow conditions (approx. 3000 cfs). The locations where catostomids were observed or captured (zones A-F) are delineated by shaded boxes.

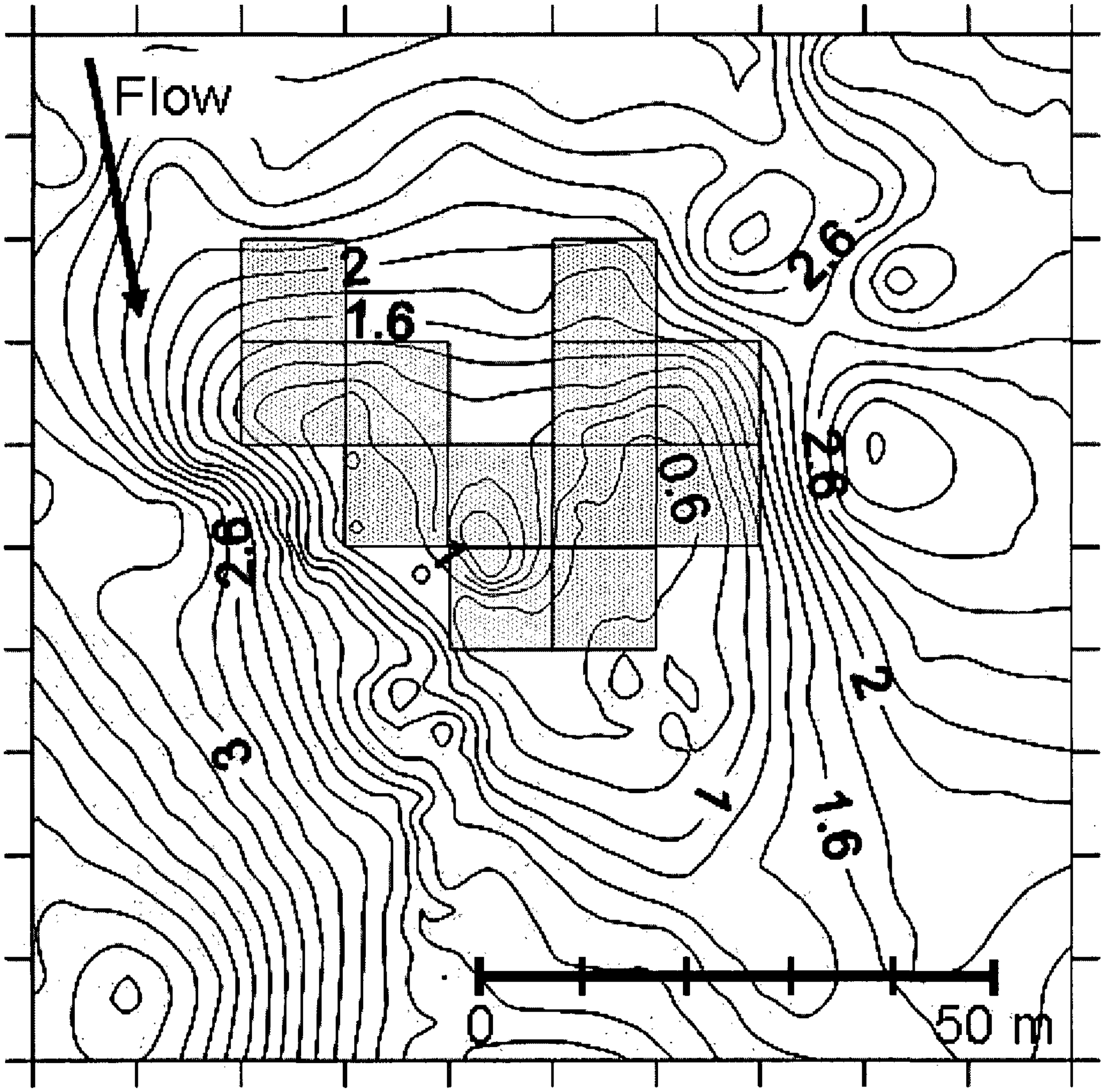

Figure 9. Bathymetric map of the lower gravel bar at river kilometer 283.7 on the lower Savannah River. Contour lines represent a change in depth of 0.2 m. Depths indicate water depth under average flow conditions (approx. 7000 cfs). The 10 m X 10 m areas in which catostomids were observed or captured are indicated by shaded boxes.

individually numbered weighted flags that were dropped upon the locations occupied by fish. The fish responded by moving a few meters away but generally returned within two to three minutes. Upon retrieval, the position of each flag was recorded using GPS and microhabitat variables were recorded. Depth was measured to the nearest 0.01 m using a meter stick. Current velocity was measured using a digital stream flow meter (Great Atlantic Flow Meters, Cornwall, United Kingdom) and a hand-held compass was used to determine current direction. Substrate particle size distribution at each flag was determined in the field using a modified Wolman pebble count procedure (Wolman 1954) with a hand-held size analyzer (gravelometer). This device consists of an aluminum plate with 14 square holes corresponding in size to common ½ phi unit classes and yields results effectively similar to sieving. Water temperature was measured everyday on site and recorded hourly approximately midway between the two gravel bars at river kilometer 289.7 by a Hobo Water Temperature Pro v.1 (Onset Computers, Bourne, Massachusetts) data logger. River discharge in cubic feet per second (cfs) was acquired from US Geological Survey gauging station 02197000 (available online at http://waterdata.usgs.gov/ga/nwis/uv?02197000).

Prepositioned grid electrofishers were deployed as described by Grabowski and Isely (2005) to capture spawning and staging fishes. A GPS waypoint, depth, current direction, current velocity, and substrate particle size distribution was taken at each grid prior to retrieval. The primary purpose in capturing fish was to confirm my above-water species identifications and reproductive condition of individuals. However, a passive integrated transponder (PIT) tag (Biomark, Inc., Bosie, Idaho) was implanted into the musculature immediately posterior to the dorsal fin in order to assess residence time on the spawning grounds, interannual site fidelity to a gravel bar, and number of individuals comprising a spawning aggregation. The sex of all captured catostomids was determined based upon the expression of gametes and secondary sex characteristics (presence of nuptial tubercles in males, loss of mucus in females) in reproductively active individuals and by the shape of the pelvic fins in individuals not reproductively active (W. C. Starnes, North Carolina State Museum of Natural Sciences, personal communication). At least one digital photograph was taken of each individual captured to serve as a voucher before releasing all fish alive.

Emergent larvae were captured as they left the gravel bar using 1,000 μm mesh, square frame plankton nets with a 0.125 m^2 opening. Five to six nets were deployed about each bar and allowed to fish for approximately one hour before retrieval. Depending upon conditions, this was repeated two to three times during each visit to the gravel bars. Ichthyoplankton samples were fixed in a 3.0% formalin solution, rinsed, and stored on 95% ethanol. Larval catostomids were identified to lowest taxa possible using Hogue and Buchanan (1977), Buynak and Mohr (1978, 1979), Fuiman (1979), Kay et al (1994), and Bunt and Cooke (2004).

Data analysis

Mixed model analysis of variance with Dunnett's comparison tests was used to compare mean depths, current velocities, slopes, and particle size among species (fixed effects) while controlling for year and location (random effects) (Zar 1996). A paired t-test was used to test the hypothesis that species found on both gravel bars used areas with different depths, current velocities, slopes, or particle sizes. Principle component analysis was performed to visualize the interaction of these habitat variables by species and location. Spatial analysis of habitat partitioning on the upper bar was three-tiered. First, a 50 X 50-m grid was established and chi-square analysis was performed to test for the uniform distribution of individuals over the upper bar. If fish distribution proved to be non-uniform on this coarse scale, then a 10 X 10-m grid was established. Only boxes with observations of fishes were considered for further analysis. Chi-square tests analysis was used to test for uniform fish distribution among the areas that were used. These 10 X 10-m boxes were then used to establish zones A - F (Figure 8) on the basis of proximity, shared physical features, and similar hydrologic conditions. Pairwise chi-square tests were employed to test the null hypotheses that distributions within the zones did not differ both among species and between 2004 and 2005 within species. Analysis of variance with Dunnett's comparison tests were used to confirm that each zone differed in at least one variable (depth, slope, mean particle size). Additionally, paired chi-square tests were conducted to compare particle size distributions among zones. A similar analysis was completed for the lower bar with the exception of the coarse 50 X 50-m grid. This step was performed using a 20 X 20-m grid because of the smaller size of the lower bar. A finer scale 10 X 10-m grid was then established for areas occupied by fishes (Figure 9) and was analyzed as described for the upper bar. A significance level of $\alpha = 0.05$ was used for all tests.

Results

Conditions on the Savannah River varied considerably between 2004 and 2005 (Figure 10). There were two major flood pulses in March 2005 caused by water releases from upstream reservoirs in an attempt to raise water levels in the river to allow fish passage at NSBLD. These were followed by a major natural flood pulse in April. Spring was a relatively dry in 2004 with flows rarely exceeding the median daily streamflow except for a minor flood pulse in March 2004. Temperatures were depressed and exhibited less fluctuation in 2005 relative to those in 2004.

A total of 268 adult suckers was captured during the two- year study consisting of 39 northern hogsuckers, 58 notchlip redhorse, 22 spotted suckers, and 149 robust redhorse. The sex ratio for all species was heavily biased towards males (northern hogsucker: 2.3:1; notchlip redhorse: 7.3:1; robust redhorse: 4.5:1) except for spotted sucker (1:1). Each individual of all species except for northern hogsucker displayed signs of being reproductively active such as full tubercle development, loss of body slime, expression of gametes with the application of mild abdominal pressure, and wounds such as split fins and scale loss consistent with those found on spawning catostomids in other systems (R. E. Jenkins, Roanoke College, personal communication). Two notchlip redhorse, two spotted suckers and 57 robust redhorse were recaptured in 2005. These individuals were all recaptured from the same gravel bar on which they were originally tagged in 2004 or earlier in 2005. An additional 553 observations of adult catostomids were made during tower and boat observation periods in the course of this study. A total of 52 larval fishes were captured yielding an overall catch per unit effort of 0.14 larvae per net hour. The majority of larva (*n*=42) consisted of catostomids represented by one unidentifiable individual, two *Carpiodes* sp., two northern hogsucker, two spotted sucker, and 35 redhorses. Cyprinids (unidentified species; *n*=4), clupeids (*Alosa* sp.; *n*=1), percid darters (*n*=2), and three unidentifiable larvae comprised the remainder of the ichthyoplankton samples.

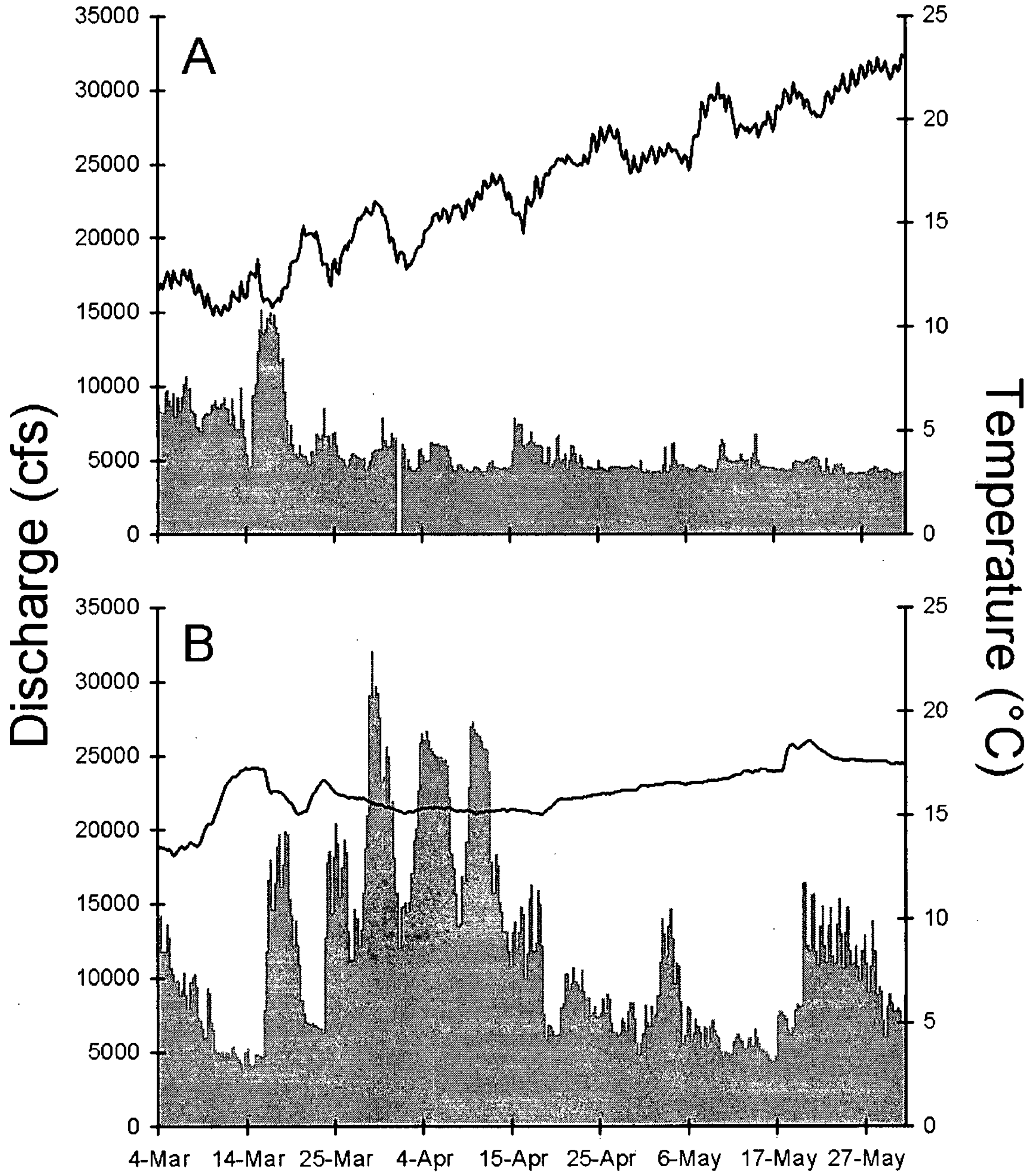

Figure 10. Water temperature and discharge (cubic feet per second) in the lower Savannah River at New Savannah Bluff Lock and Dam (rkm 299.4) from 04 March to 01 June in 2004 (A) and 2005 (B). Water temperature is represented by the solid line and river discharge is represented by gray bars.

Spawning catostomids showed a considerable amount of temporal overlap in their use of Savannah River main channel gravel bars in 2004 and 2005 (Figure 11). Northern hogsucker were present at each gravel bar throughout the duration of observations both years. However, individuals in spawning condition were encountered only in early spring during both 2004 (early April) and 2005 (late March-early April). Spawning behavior was not observed for northern hogsucker and only two larvae of this species were captured during the study both at the upper bar on 13 April 2004. Their continuous presence at both locations throughout the duration of the study in both 2004 and 2005 suggests resident populations of this species are present on each gravel bar. Notchlip redhorse were present and spawning on the upper bar for a longer period of time than all other species except for northern hogsuckers. Notchlip redhorse were observed over a 23-day period from 02-25 April in 2004 and a 56-day period from 14 March to 09 May in 2005.

Larval *Moxostoma* sp. presumed to be notchlip redhorse were captured as late as 09 May 2004 and 13 May 2005. Two other species spawned on the upper bar during the period notchlip redhorse were present. Spotted suckers were observed or captured for 12 days between 13 and 25 April 2004 but larvae were captured one week after the last adults were observed. This species was not seen at either location in 2005. Carpsuckers were observed from 02-07 May 2005 and the last larvae were captured on 09 May. Unfortunately, I was unable to capture any adult carpsuckers; and therefore, am unable to confirm which *Carpiodes* species was present. Robust redhorse were present 13 days in 2004. They were present earlier and remained for a longer period of time at the lower bar (02-15 May) than at the upper one (09-15 May).). Although this difference between the

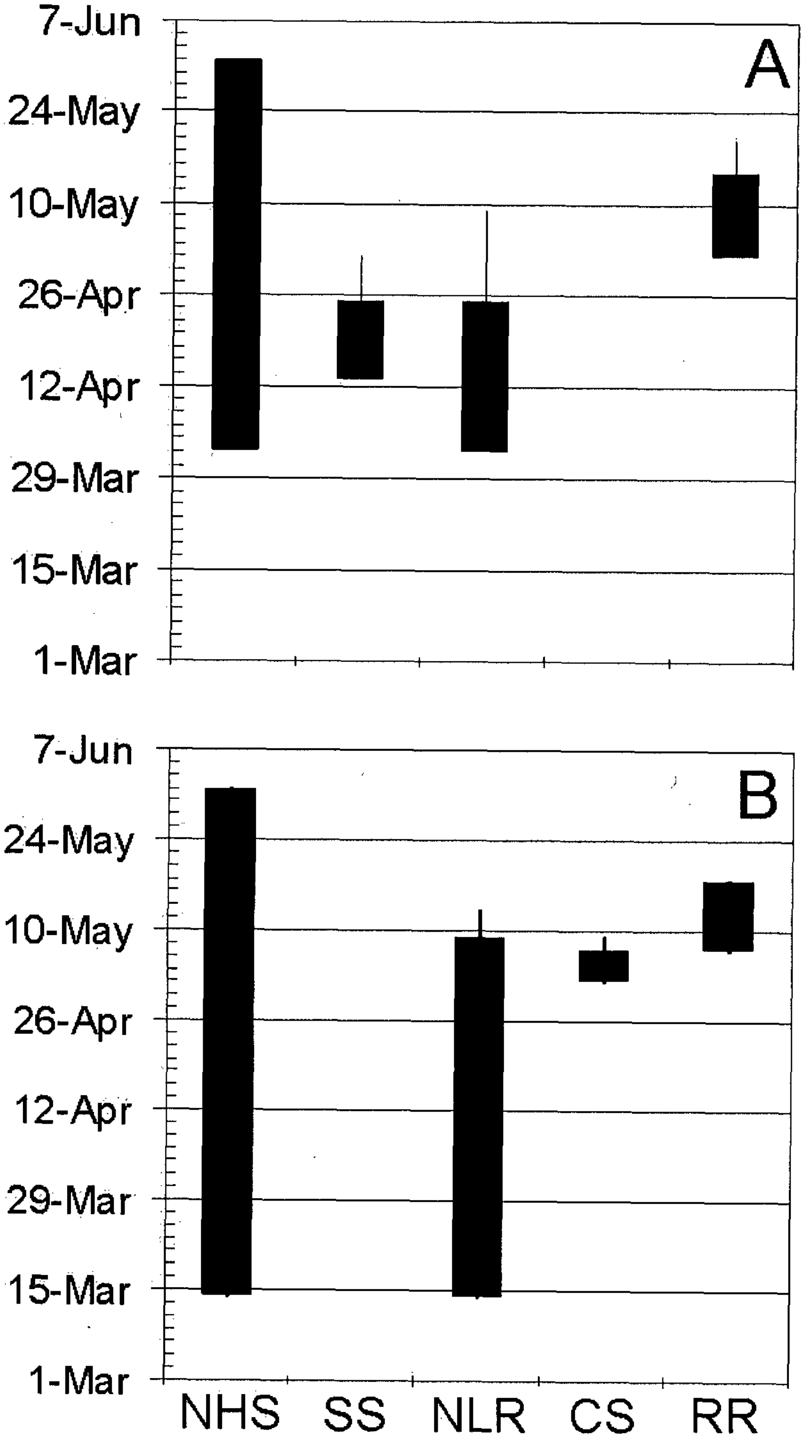

Figure 11. Dates northern hogsucker (NHS), spotted sucker (SS), notchlip redhorse (NLR), carpsucker (CS), and robust redhorse (RR) were observed on the gravel bars in the lower Savannah River in 2004 (A) and 2005 (B). Vertical lines indicate the latest date larvae of that species were captured.

two bars was not as great in 2005, robust redhorse were again present earlier and longer at the lower bar (07-18 May) than at the upper one (09-16 May). Larvae presumed to be robust redhorse were captured as late as 20 May in 2004. No larval robust redhorse were captured in 2005 after the departure of adults due to a dramatic increase in flows on the Savannah. However, a large number (n=97) of pre-hatching robust redhorse embryos at various stages of development were captured when ichthyoplankton nets were set behind actively spawning adults.

Overlap in the temperatures at which species were present appears to correspond to observed temporal overlap (Figure 12). In general, catostomids were present at the gravel bars through a wider temperature range in 2004 than 2005. Northern hogsuckers were found on the upper bar throughout the range of observed temperatures in 2004 (12.7-23.3°C) and 2005 (13.4-18.4°C). Spotted suckers (14.4-19.7°C) exhibited complete overlap with notchlip redhorse (12.7-19.7°C) in 2004, but were not observed in 2005. In 2005 carpsuckers (16.4-16.6°C) also showed complete overlap with notchlip. redhorse (15.0-17.3°C). Robust redhorse (2004: 17.6-21.8°C; 2005: 16.6-18.4°C) and notchlip redhorse overlapped slightly on the upper bar both years.

Spawning catostomids were not distributed uniformly on the upper gravel bar based on a 50 X 50 m grid ($\chi^2 \geq 36.12$; d.f.=11; $p \leq 0.0002$) nor distributed uniformly among the 100-m^2 areas in which they did occur ($\chi^2 \geq 22.46$; d.f.=5; $p \leq 0.0004$). While species demonstrated some spatial overlap among the zones of the upper gravel bar (Table 1), their distributions were different from one another ($\chi^2 \geq 28.71$; d.f.=5; $p<0.0001$). There was no difference between 2004 and 2005 in the distributions

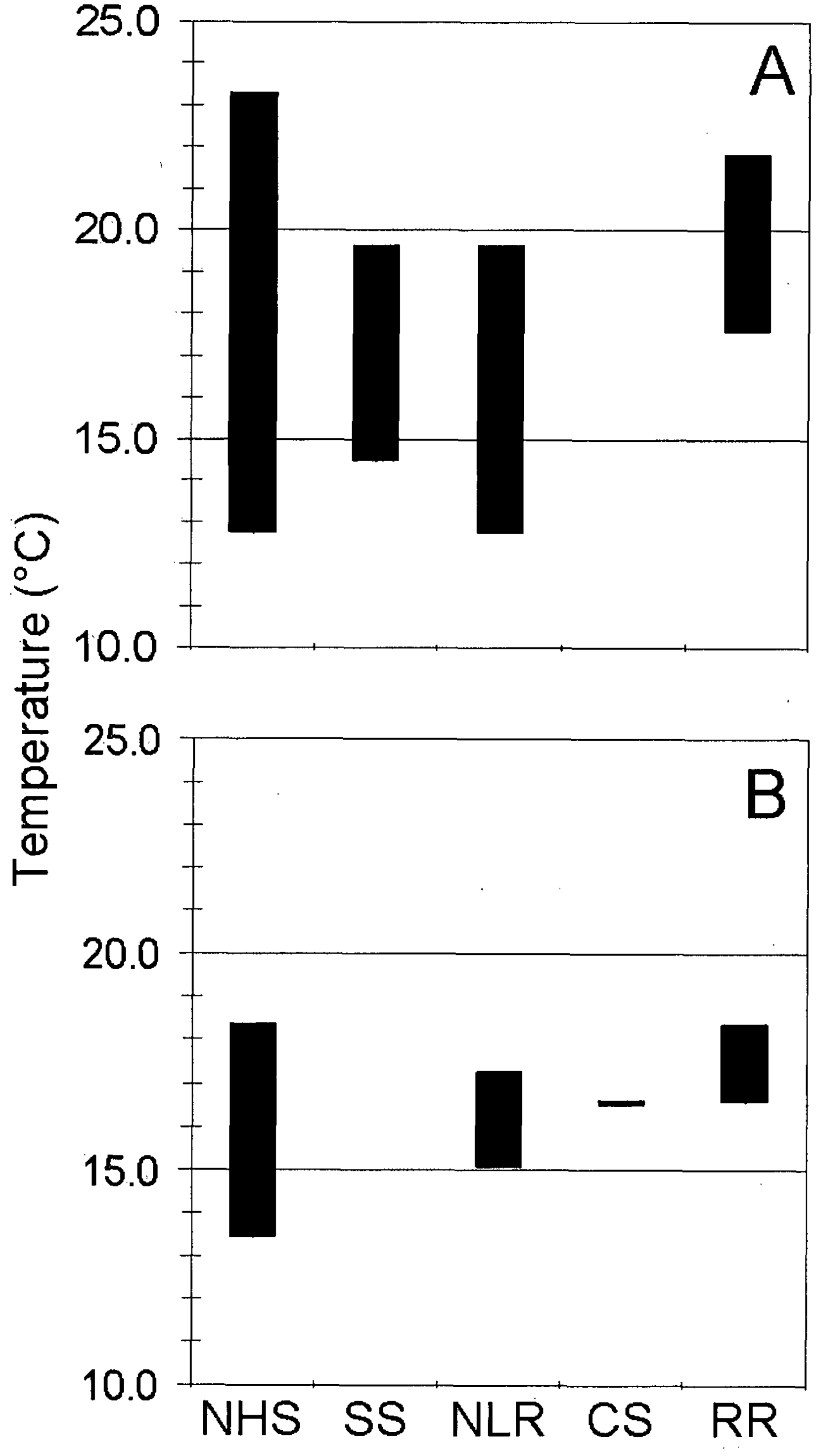

Figure 12. Temperatures northern hogsucker (NHS), spotted sucker (SS), notchlip redhorse (NLR), carpsucker (CS), and robust redhorse (RR) were observed on the gravel bars in the lower Savannah River in 2004 (A) and 2005 (B).

Table 3. Percentage of individuals of each catostomid species found in the zones of the upper gravel bar in the Savannah River during spring 2004 and 2005.

		Zone					
Species	*n*	A	B	C	D	E	F
Carpsucker	40	0.0%	0.0%	7.5%	0.0%	92.5%	0.0%
Northern hogsucker	108	0.0%	13.9%	33.3%	8.3%	5.6%	38.9%
Spotted sucker	34	0.0%	0.0%	5.9%	2.9%	0.0%	91.2%
Notchlip redhorse	610	2.6%	27.9%	39.0%	20.8%	0.7%	9.0%
Robust redhorse	29	0.0%	6.9%	3.4%	75.9%	3.5%	10.3%
Total	821	1.9%	22.8%	34.1%	19.4%	5.9%	15.9%

of notchlip redhorse ($\chi^2=11.38$; d.f.=5; $p=0.056$) or robust redhorse ($\chi^2=4.26$; d.f.=5; $p=0.489$). Notchlip redhorse aggregated primarily on the upstream edge of the gravel bar in zones B and C (Figure 13), but a considerable number of individuals (approx. 20%) used the South Carolina edge (zone D). Robust redhorse spawned predominantly along the South Carolina edge in zone D but smaller aggregations formed on the secondary gravel bar in zone F. Northern hogsucker distribution did differ between years ($\chi^2=31.93$; d.f.=5; $p<0.0001$). A higher percentage of individuals were observed or captured from zones B and E in 2005, as opposed to primarily occupying zones C and F in 2004. In most cases, northern hogsuckers appeared to congregate immediately downstream of spawning individuals of other species. Spotted suckers were observed almost exclusively in deeper areas along the South Carolina bank immediately upstream of the secondary gravel bar in zone F (Figure 13). These fishes were presumably staging at this location and spawning likely occurred in zones C and D. Carpsuckers were encountered almost exclusively on the top and downstream edge of the gravel bar (zone E).

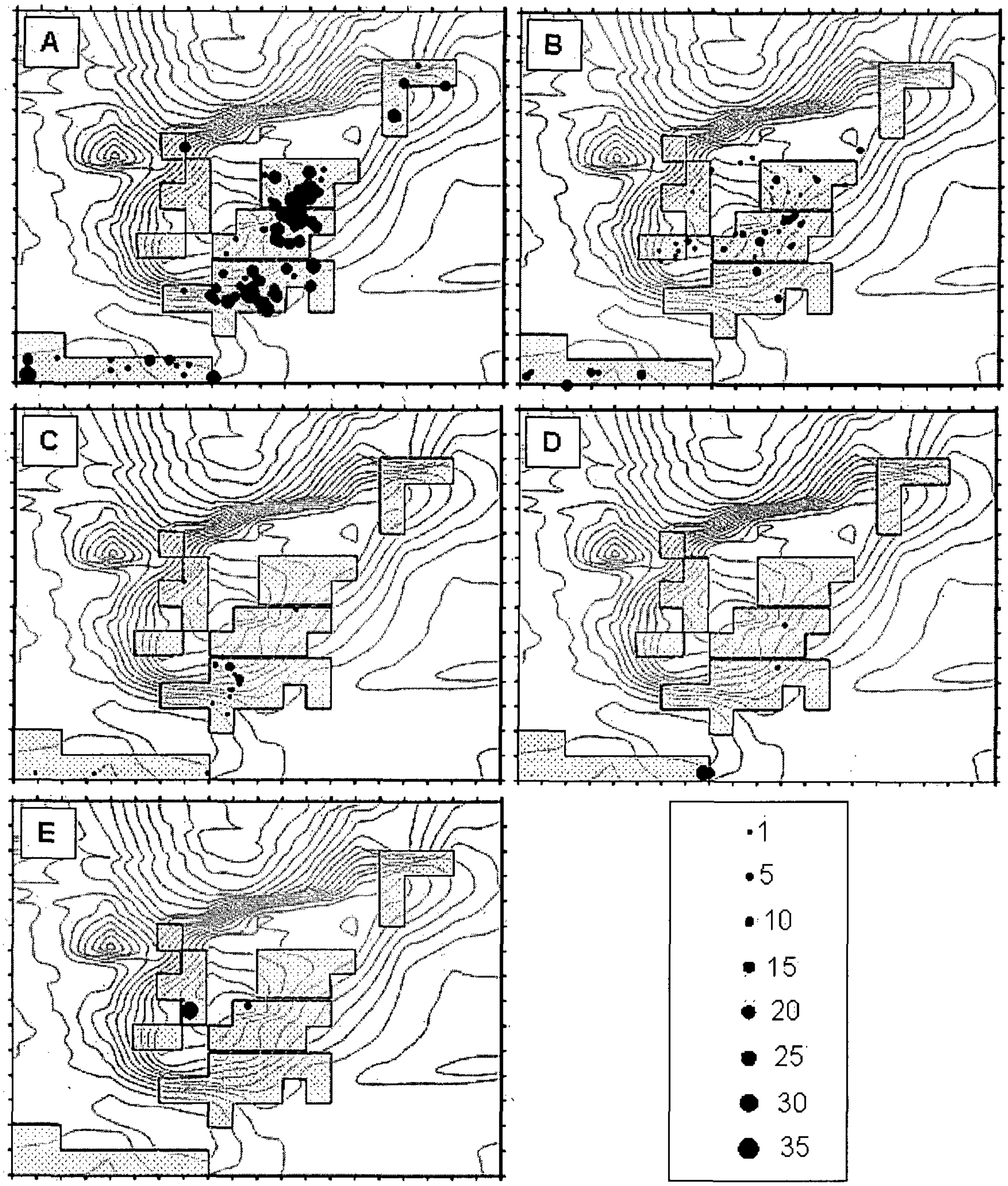

Figure 13. Distribution of notchlip redhorse (A), northern hogsucker (B), robust redhorse (C), spotted sucker (D), and carpsucker (E) on the upper gravel bar at river kilometer 299.4 on the lower Savannah River in 2004 and 2005. Circle diameter represents number of individuals observed or captured at a given point. Zones A-F are delineated by shaded boxes.

Robust redhorse and northern hogsucker were the only catostomid species observed on the lower gravel bar. More robust redhorse were observed or captured on the lower bar (n=226) than the upper bar (n=29). Their distribution on the lower bar was not uniform (χ^2=210.77; d.f.=24; p<0.0001) as they were found only along the upstream edge of the gravel bar (Figure 14). This is the same area from which this species was observed and captured in 2002 (Grabowski and Isely, *in review*) and 2004 (Grabowski and Isely 2004). Their overall distribution along this edge also was not uniform (χ^2=76.91; d.f.=11; p<0.0001) with the largest concentration occurring along the Georgia edge of the bar. This is also the area where the first spawning individuals were observed in 2005. Northern hogsucker appeared to follow a similar distribution pattern (Figure 8). However, their distribution over the entire gravel bar (χ^2=16.43; d.f.=24; p=0.872) and among the 100 m^2 areas in which they were found (χ^2=1.915; d.f.=5; p=0.861) was uniform. This is likely an artifact of the small number of individuals observed or captured (n=12). Northern hogsuckers on the lower bar exhibited no signs of being reproductively active. Visual observations suggest that northern hogsuckers were present within active robust redhorse redds to feed on eggs and possibly benthic invertebrates dislodged from the substrate.

Catostomids on the upper bar appeared to segregate based on microhabitat conditions of flow, depth, slope, and substrate size (Figure 15, Table 4). The zones of the upper bar where each species was predominantly found were basically defined by these conditions (Table 5). Carpsuckers were excluded from further analysis because only one full set of habitat measurements was taken. Two of the three records of this species were

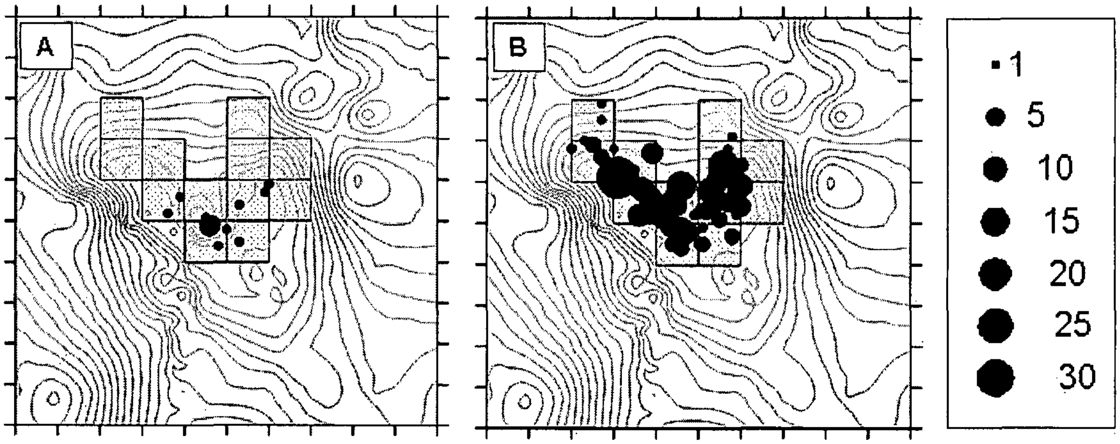

Figure 14. Distribution of northern hogsucker (A) and robust redhorse (B) on the lower gravel bar at river kilometer 283.7 on the lower Savannah River in 2005. Circle diameter represents number of individuals observed or captured at a given point. The 10 m X 10 m areas in which catostomids were observed or captured are indicated by shaded boxes.

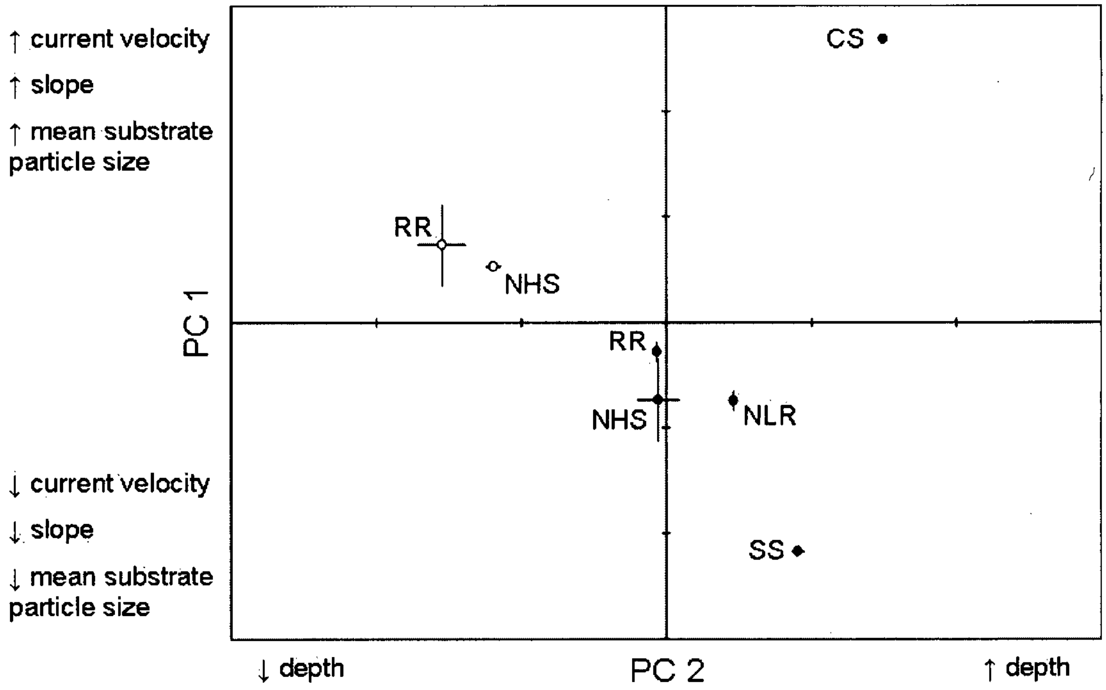

Figure 15. Principle component analysis for habitat conditions in areas used by spawning notchlip redhorse (NLR), northern hogsucker (NHS), robust redhorse (RR), spotted sucker (SS), and carpsucker (CS) in the lower Savannah River in 2004 and 2005. Current velocity, slope, and mean particle size loaded onto the first principle component while depth was the only variable loaded onto second component. Closed circles indicate individuals from the upper gravel bar and open circles represent those from the lower gravel bar. Error bars represent standard error.

Table 4. Mean depth, velocity, slope, and mean and median substrate particle size of the Savannah River gravel bar locations from which catostomid species were captured or observed in spring 2004 and 2005. All means are reported ± SE.

Species	Mean depth (m)	Mean velocity (ms^{-1})	Mean slope	Mean substrate particle size (mm)	Modal substrate particle size (mm)
Carpsucker	1.25	0.63	0.04 ± 0.008	14.8 ± 1.219	5.7, 22.6
Northern hogsucker	0.74 ± 0.034	0.44 ± 0.027	0.05 ± 0.004	11.9 ± 0.492	11.3
Spotted sucker	1.16 ± 0.031	0.17 ± 0.031	0.03 ± 0.013	9.4 ± 0.726	8.0
Notchlip redhorse	0.98 ± 0.016	0.30 ± 0.026	0.04 ± 0.002	12.2 ± 1.126	16.0
Robust redhorse	0.74 ± 0.017	0.24 ± 0.014	0.07 ± 0.003	14.3 ± 0.272	32.0

Table 5. Mean depth, depth range, mean slope, and mean and median substrate diameter of the zones of the upper gravel bar. All means are reported ± SE.

Zone	Mean depth (m)	Depth range (m)	Mean slope	Mean substrate diameter (mm)	Modal substrate diameter (mm)
A	1.66 ± 0.166	0.88 - 4.08	0.051 ± 0.010	10.5 ± 0.597	5.7, 11.3
B	0.23 ± 0.075	0.00 - 0.90	0.039 ± 0.003	9.1 ± 0.512	5.7
C	0.53 ± 0.072	0.00 - 1.10	0.039 ± 0.003	11.5 ± 0.695	5.7
D	1.00 ± 0.094	0.23 - 2.07	0.054 ± 0.008	12.5 ± 0.685	8.0, 16.0
E	0.16 ± 0.071	0.00 - 1.95	0.063 ± 0.012	9.7 ± 0.489	5.7, 8.0
F	0.62 ± .332	0.03 - 1.20	0.025 ± 0.002	10.5 ± 0.535	8.0

made during boat observations over deep water. The mean depth of areas used for spawning differed among all other species ($F_{3,198}$= 26.19; p<0.0001) when controlling for year and location (upper vs. lower gravel bar) despite the occupation of similar mean depths by robust redhorse and northern hogsucker (Table 4). Spotted suckers were found in the deepest water, and robust redhorse and northern hogsuckers were typically observed in the shallowest. Similarly, the mean flow velocity of areas occupied by catostomids differed among all species ($F_{3,190}$= 20.42; p<0.0001) when adjusted for year and location effects. Northern hogsuckers on average were found in the swiftest flowing water and spotted suckers were found in the slowest. The slopes of areas used by catostomids differed among species ($F_{4,230}$= 24.95; p<0.0001). Robust redhorse were captured in areas that were steeper than areas used by other species. Spotted sucker used areas of similar slope to those used by notchlip redhorse and northern hogsucker. However, northern hogsucker used areas with a greater slope than did notchlip redhorse. Both robust redhorse (t_{81}=2.05; p=0.043) and northern hogsucker (t_{48}=7.20; p<0.0001) used areas with a greater slope on the lower gravel bar (robust redhorse: 0.08 ± 0.004; northern hogsucker: 0.09 ± 0.007) than on the upper bar (robust redhorse: 0.06 ± 0.005; northern hogsucker: 0.04 ± 0.006). In general, areas used by these species on the upper bar tended to be shallower with higher current velocities, steeper slopes, and larger substrate (Figure 15).

Depth and flow velocity varied with stream discharge at NSBLD. Spawning catostomids on the upper bar were found consistently in the same areas regardless of spawning intensity or water level. These areas remained underwater and flow was maintained under all observed levels of stream discharge (3,000-30,000+ cfs). On the lower gravel bar, robust redhorse initiated spawning on the Georgia side of the upstream edge and spilled over to the center and South Carolina edge as spawning intensity increased. However, the Georgia edge appeared to remain the area of greatest intensity. Redd sites along the Georgia edge were not exposed or degraded by fluctuating water levels as opposed to areas along the center and South Carolina edge of the bar.

Discussion

The upper and lower gravel bars represent important spawning habitat for catostomids in the lower Savannah River. The biased sex ratios of captured adult fishes and collection of emergent catostomid larva are consistent with the observation of catostomids using the upper and lower gravel bars for spawning and has been noted in other catostomid species (Peterson et al. 2000; Vokun et al. 2003). These fishes are known to primarily spawn as "trembling trios" or triads of a single female flanked by two males (Page and Johnson 1990; Jenkins and Burkhead 1993). Males hold position on the spawning ground and are approached by females arriving from nearby staging areas. Collections in active spawning areas would, therefore, result in the highly biased sex ratios observed in this study. It also suggests that spotted sucker were using the deeper area of zone F as a staging area. The majority of individuals of this species (>90%) were captured here in equal proportions of males and females. Spotted suckers were likely spawning in zones C and D where only males were captured. The larvae of all species observed spawning or captured in spawning condition were captured during the course of this study. It is important to note that at present there is no reliable method of distinguishing between larval robust redhorse and notchlip redhorse aside from a mitochondrial DNA assay (Wirgin et al. 2004). The results presented here are, therefore, conservative estimates of the temporal overlap between notchlip and robust redhorse as larval robust redhorse were not identified as such until five days after the adults were observed. This is well below the time reported by Weyers et al. (2003) of 5-10 days between hatching and emergence of larval robust redhorse under aquarium conditions.

Temporal and spatial overlap occurs between spawning catostomids in the lower Savannah River despite the apparent partitioning of available spawning habitat. This overlap can be broadly divided into two types: temporal overlap of spawning adults of different species, and temporal overlap of spawning adults with the early life history stages of another species. The more common of these was the presence of spawning adults while early life history stages of a previous species were still emerging from the gravel. This occurred in both years between spawning robust redhorse and larval notchlip redhorse. Other studies examining the spawning aggregations of catostomids have not incorporated ichthyoplankton sampling concurrent with sampling of spawning adults. This study confirms that larvae are present for a considerable period of time after spawning activity of other species has initiated. This is true in other fish groups such as salmonids. The long incubation periods and the relative ease of identifying redd sites of salmonids has lead to the recognition of redd site superimposition, both intra- and interspecific, as a serious concern (Sandercock 1991; Essington et al. 1998; Fukushima et al. 1998; Fukushima and Smoker 1998). For example, Fukushima et al. (1998) estimated redd site superimposition accounted for a loss of up to one-third of the daily reproductive output within an Alaskan pink salmon *Oncorhynchus gorbuscha* population.

It is unclear how commonly temporal overlap occurs between spawning adults of two species in the lower Savannah River. Notchlip redhorse overlapped with spotted sucker in 2004 and carpsucker in 2005. However, it is uncertain how often and under what circumstances spotted sucker and carpsucker use the upper bar. These species occupied a limited area on the bar, were there for a short period of time, and were never observed at high densities. In other systems, spotted sucker have been reported to ascend tributaries to form large spawning aggregations (McSwain and Gennings 1972; Mettee et al. 1996) while carpsuckers have been reported to use a variety of different habitats in both the main river channel and in smaller tributaries (Harlan and Speaker 1956; Scott and Crossman 1973; Jenkins and Burkhead 1993). Notchlip redhorse were present on the upper gravel bar in larger numbers, over a greater proportion of the available area, and for a longer period of time during both years. Temporal overlap in spawning between two or more species has been observed in other catostomid assemblages (Curry and Spacie 1984; Kwak and Skelly 1992; Dion and Whoriskey 1993), salmonids (Fukushima and Smoker 1998), and cyprinid nest associates of nest building cyprinids such as *Nocomis* spp. (Johnston 1991). In these cases, authors generally reported a greater degree of spatial segregation than that observed at the gravel bars in the lower Savannah River in the case of catostomids and salmonids or non-invasive deposition of eggs as in the case of cyprinids. As previously mentioned, northern hogsucker did overlap with all other species but were present on the bars as either residents or egg predators and not for reproduction.

The sequence of species arrival and the time spent spawning on gravel bars in the lower Savannah River is likely heavily influenced by photoperiod and water temperature.

These factors have been identified as important cues for initiating spawning migrations (Quinn and Adams 1996; McCormick et al. 1998) and maturation of gonads (Huber and Bengston 1999). Catostomids in the lower Savannah River have to cope with a temperature regime that is dramatically altered from its natural state as water temperatures in the lower Savannah River tend to be consistently cooler (Paller and Saul 1996). Fishes may be spawning outside their preferred temperature range based on records for these species in other river systems in the southeastern US (Freeman and Freeman 2001, D. J. Coughlan, Duke Power, personal communication). Alternatively, they may be delaying reproduction to later in the spring when temperatures are within this range which would likely have severe negative effects on young of year age class strength and survival due to failure in acquiring the energy reserves necessary to survive winter (Kipling and Frost 1970, Buckley et al. 1991). Species sequences and reproductive chronology can be highly variable among river systems (McHugh and Budy 2004) necessitating comparative studies on larger geographic scales or site specific models. Complicating matters is the difference in annual temperature regimes such as that observed in 2004 and 2005. Fishes were present on the gravel bar at lower temperatures and narrower temperature ranges in 2005 than 2004. This may increase the likelihood of temporal overlap among species by decreasing the time between species or increasing the time early life history stages are present on the gravel bar. However, some species such as robust redhorse arrived on the gravel bar at approximately the same time in 2004 and 2005 suggesting photoperiod may be just as important. Further investigation of the stability of the observed sequence of catostomids both in the Savannah River and throughout the southeastern US will be required to determine the relative role of photoperiod and temperature or perhaps intrinsic factors not yet considered.

Despite the considerable amount of both temporal and spatial overlap between notchlip redhorse and the other species, spatial segregation under observed conditions appears to be sufficient to prevent excessive mortality of early life history stages due to interspecific nest site superimposition. For example, robust redhorse, considered the least abundant species in this assemblage, appears to have the lowest risk. This species not only spawns later in the spring than the other species, but also appears to be the only species to use the lower gravel bar. Spotted sucker is one of the most common large fish species in the Savannah River (Marcy et al. 2005). However, the relatively low number of individuals observed at the study sites suggests the majority of individuals in the Savannah River population ascend tributaries to spawn as in other systems (McSwain and Gennings 1972) or utilize as of yet unidentified habitat. Notchlip redhorse appear to be the predominant species spawning on the upper bar both in terms of number of individuals and time present on the bar. There is the potential for a relatively small proportion of their nests to be disturbed by spawning robust redhorse and spotted sucker. However, a much greater potential exists for intraspecific nest site superimposition for fishes in the lower Savannah River dependent upon main channel gravel bars as their primary spawning habitat such as notchlip redhorse and robust redhorse. Based upon mark-recapture data, there may be as many as 400-800 robust redhorse spawning in an approximately 1200 m^2 area on the lower bar and as many as several thousand notchlip redhorse using an approximately 2600 m^2 area on the upper bar (Grabowski and Isely, unpublished data). While this may appear to be sufficient area, it is important to note that fishes are not uniformly distributed within it.

Species tended to spawn in areas within a narrow range of conditions such as depth, slope, current velocity, and substrate size distributions. This degree of spawning microhabitat specificity has been noted in other catostomids (Curry and Spacie 1984; Kwak and Skelly 1992). In fishes, this specificity probably has several functions ranging from acting as a reproductive isolating mechanism (Kwak and Skelly 1992) to maximizing reproductive success (Hall 1972; Itzkowitz 1991; Maurakis and Green 2001). Spawning habitat specificity may be a contributing factor to the spawning site fidelity observed in robust redhorse and notchlip redhorse during this study and in a radio telemetry study of Savannah River robust redhorse (Grabowski and Isely *in review*). The microhabitat specificity demonstrated by spawning catostomids is likely the underlying reason for the observed differences in spatial distribution among species. For example, robust redhorse was the only species observed spawning on the lower gravel bar. This species used areas with the largest modal substrate particle size and slope relative to those used by the other catostomid species. The lower gravel bar would seem to be the logical choice for robust redhorse to meet these conditions. Spawning microhabitat specificity is also likely to partially explain why some species distributions varied between 2004 and 2005. Some of the microhabitat variables such as slope and substrate size remained relatively constant over the duration of this study. On the other hand, depth and current velocity changed by the hour in relation to water discharge upstream of the gravel bars. Hyporheic discharge, or upwelling water passing through the substrate, has been demonstrated to be a critical factor in spawning habitat selection in other species, such as brook charr *Salvelinus fontinalis* (Benson 1953; Bernier-Bourgault and Magnan 2002; Blanchfield and Ridgway 2005). Attempts to locate similar areas of hyporheic discharge at areas used by spawning catostomids using piezometers failed. Hyporheic flow is likely minimal if such areas are present on the gravel bars and probably not a major factor in habitat selection. Other factors likely to have contributed to the selection of spawning habitat by Savannah River catostomids include presence of spawning conspecifics (Essington et al. 1998; Danchin et al. 2004) and competitive exclusion from preferred sites by larger conspecifics or other species (Ming and Noakes 1984; Essington et al. 2000).

The availability of suitable spawning habitat appears to have the potential to be a major limiting factor in the conservation and long term viability of catostomid populations in the lower Savannah River. Species dependent upon the two main channel gravel bars in the Savannah River are subject to intraspecific nest disturbance and site superimposition. This is illustrated by the developing embryos that were captured behind active nest sites on the lower bar in 2005. This number would have likely been higher, but there were also large numbers of cyprinids, such as bannerfin shiner *Cyprinella leedsi*, whitefin shiner *Cyprinella nivea* and spotfin shiner *Notropis hudsonius*, blackbanded darters *Percina nigrofasciata*, and northern hogsuckers present on the lower bar. These fishes were presumably feeding on dislodged embryos and eggs. Captured individuals had guts that were filled with eggs. Egg predators have been reported occasionally from assemblages of spawning catostomids in other systems (Kwak and Skelly 1992; Dion and Whoriskey 1993). This study did not have sufficient spatial resolution to assess the extent and impact of intraspecific nest site superimposition.

Using the methods employed by this study, it was not possible to localize where the eggs had been deposited with the degree of accuracy necessary to reliably quantify intraspecific nest superimposition. However, the overlap in fish positions and the amount of disturbed gravel observed in this study suggests that a high degree of superimposition occurs and warrants investigation into effects of intraspecific interactions on reproductive success. Species using these bars are also vulnerable to stochastic events and anthropogenic influences such as pollution and siltation (Acornley and Sear 1999; Spromberg and Birge 2005), boat traffic and groundings (Boussard 1981; Bettoli and Clark 1992; Amoser et al. 2004), fishing pressure (Whaylen et al. 2004; Claydon 2005), and fluctuations in current velocities and water levels due to hydropower generation or conservation at upstream reservoirs (Baxter 1977; Bain et al. 1988; Weyers et al. 2003). Further, the small area readily available to Savannah River species may exacerbate these risks.

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