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[Article]

Seasonal and Diel Movements and Habitat Use of Robust Redhorses in the Lower Savannah River, Georgia and South Carolina

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Abstract.—The robust redhorse *Moxostoma robustum* is a large riverine catostomid whose distribution is restricted to three Atlantic Slope drainages. Once presumed extinct, this species was rediscovered in 1991. Despite being the focus of conservation and recovery efforts, the robust redhorse's movements and habitat use are virtually unknown. We surgically implanted pulse-coded radio transmitters into 17 wild adults (460–690 mm total length) below the downstream-most dam on the Savannah River and into 2 fish above this dam. Individuals were located every 2 weeks from June 2002 to September 2003 and monthly thereafter to May 2005. Additionally, we located 5–10 individuals every 2 h over a 48-h period during each season. Study fish moved at least 24.7 ± 8.4 river kilometers (rkm; mean ± SE) per season. This movement was generally downstream except during spring. Some individuals moved downstream by as much as 195 rkm from their release sites. Seasonal migrations were correlated to seasonal changes in water temperature. Robust redhorses initiated spring upstream migrations when water temperature reached approximately 12°C. Our diel tracking suggests that robust redhorses occupy small reaches of river (~1.0 rkm) and are mainly active diurnally. Robust redhorses were consistently found in association with woody debris and gravel streambed sediments along the outer edge of river bends. Fish exhibited a high degree of fidelity to both overwintering and spawning areas. Our observations of long-distance seasonal migrations suggest that successful robust redhorse conservation efforts may require an ecosystem management approach.

The 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 United States. This species was originally described from the Yadkin River within 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 1991 prompted conservation efforts to prevent further population decline and prompted 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 the Pee Dee River system (North Carolina and South Carolina). Robust redhorses probably occurred in 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 to be extirpated. The decline of robust redhorses, 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 (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 redhorses before 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 the water temperature is 18–22°C (Freeman and Freeman 2001). Anecdotal reports suggest that adults are generally collected in association with woody debris and swift current throughout much of the year. To date, there have been few

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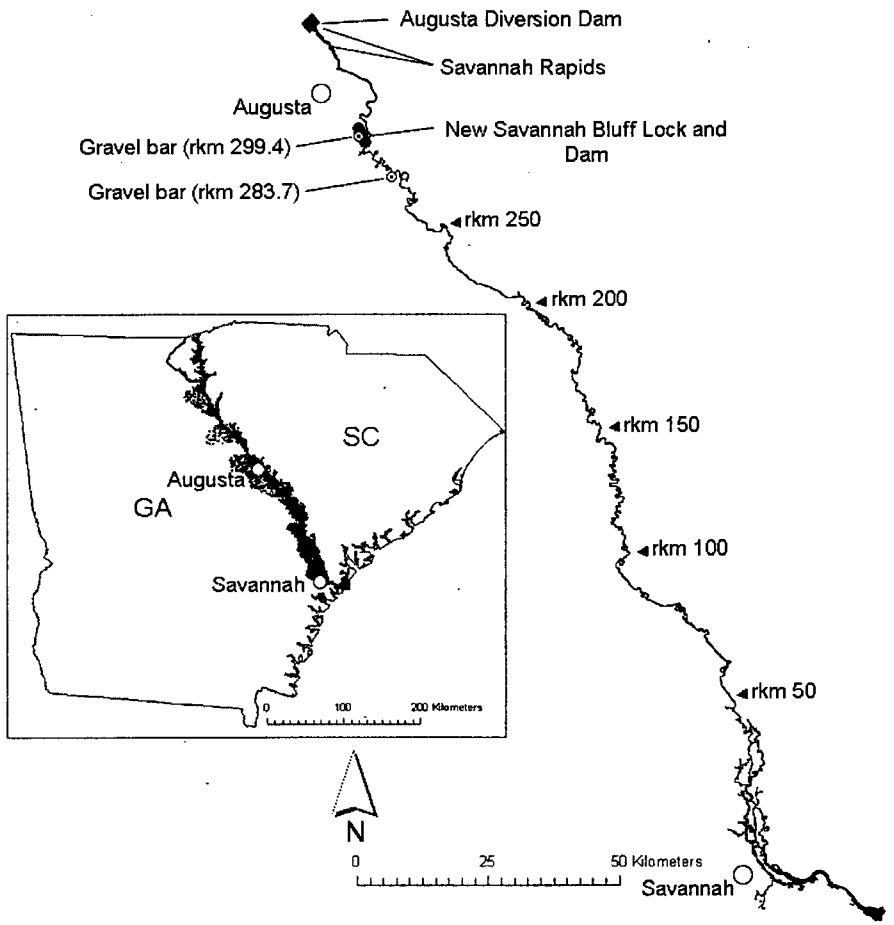

FIGURE 1.—Map of the study area, consisting of the lower Savannah River below the Augusta Diversion Dam, where the movements and habitat use of robust redhorses were monitored. River kilometers (rkm) below New Savannah Bluff Lock and Dam are indicated by solid triangles. The inset shows the Savannah River watershed; the cities of Augusta and Savannah, Georgia, are indicated by open circles.

comprehensive, long-term telemetry studies of the movement or habitat use of catostomids and no such studies of adult robust redhorses.

Our objectives for this study were to characterize seasonal migration, diel movement patterns, and essential habitat of the robust redhorse in the Savannah River. We assessed the effects of temperature and flow as cues for seasonal upstream and downstream migrations. We 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 acts as the first barrier to upstream migration. It is passable only during lock operation and high-water events, when river discharge exceeds 566.34 m^3/s. Upstream of NSBL&D is a 26.7-river-kilometer (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 redhorses were captured during June 2002 by use of standard electrofishing

techniques. We sampled once immediately below Savannah Rapids and twice near a main-channel gravel bar at rkm 283.7 (measuring from the river's confluence with the Atlantic Ocean). We 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. We also measured total length (TL, mm) and weighed (g) each fish. Fish were anesthetized in a 100-mg/L buffered tricaine methanesulfonate (MS-222) solution, and a passive integrated transponder 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, we 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 d was used for fish smaller than 500 mm TL, and a 26.0-g transmitter with a minimum battery life of 912 d was used for larger fish. Both transmitters were detectable at a range of approximately 500 m when submerged. We 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 3 min, and fish were allowed to recover for approximately 30 min in an aerated holding tank before release. Water temperatures in the Savannah River were less than 20°C during the surgeries.

We established the locations of radio-tagged robust redhorses by means of a Lotek SRX-400 telemetry receiver (Lotek Wireless) 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) with a handheld global positioning system receiver. Additionally, we 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 cutoffs. Using these charts, we calculated movement to within 0.1 rkm and verified the calculations with ArcView 3.2 (ESRI, Redlands, CA). We recorded the position of the fish relative to the bank or center of the channel. Fish were located approximately every 2 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 per 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 we track these fish from shore.

Additionally, we used the protocol described above to locate a subset of individuals once every 2 h during a consecutive 48-h 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 redhorses. Diel tracking was conducted once per calendar season on 18–20 October 2002 (fall), 27 February–1 March 2003 (winter), 11–13 June 2003 (spring), and 12–13 and 20 September 2003 (summer). The summer diel tracking was interrupted because of mechanical problems with the boat.

Data analysis.—We 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 upstream-most and downstream-most locations within a season or day. Displacement was calculated as the net distance moved (upstream movements were positive, and downstream movements were negative). Estimates of minimum daily movement were calculated only for the seasonal data and are equal to the absolute distance moved between subsequent observations divided by the number of days elapsed. These above values were similarly calculated for diel movement data. We used *t*-tests to evaluate the null hypothesis that these values did not differ from zero (Zar 1996). The hypothesis that these values differed seasonally among sexes (fixed effects) was tested with a mixed-model analysis of variance (ANOVA) while controlling for individuals and year (random effects). The hypothesis that these values differed among seasons (fixed effect) was tested with a mixed-model ANOVA while controlling for individuals, sex, and year (random effects; Zar 1996). Diel data were analyzed in a similar manner wherein photoperiod (daytime, nighttime, twilight) and season were used as fixed effects and individuals and sex were used as random effects. Season was used as a random effect when testing the null hypothesis that diel movement patterns did not differ among photoperiods. We used Dunnett's multiple comparisons of the least-squares means to perform pairwise comparisons of each season or photoperiod (Zar 1996). A significance level (α) of 0.05 was used for all tests.

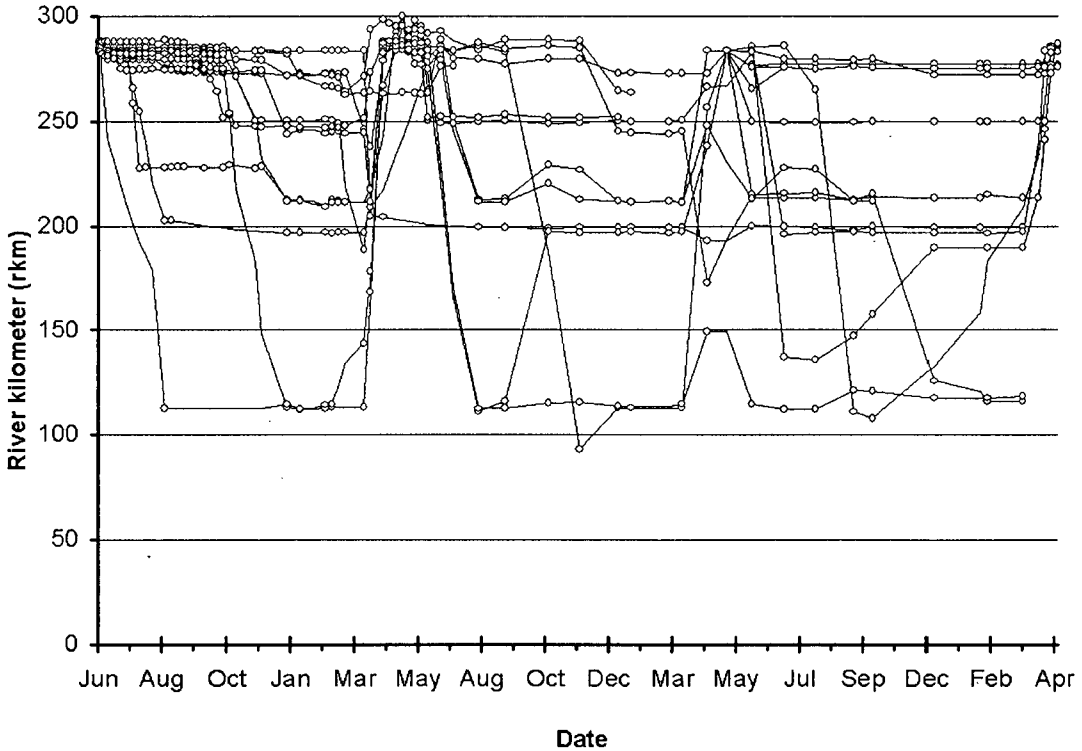

FIGURE 2.—River kilometer (rkm) positions of individual radio-tagged robust redhorses in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to April 2005. The solid lines connecting points indicate the movements of individual fish.

Results

We captured a total of 19 adult robust redhorses that ranged in size from 460 to 690 mm TL during June 2002. Two males were captured immediately below Savannah Rapids at rkm 324.2. Another 17 individuals (12 males, 5 females) were captured below 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 redhorses died or shed their transmitters within the first 2 weeks after release, and one female died or shed the transmitter after 21 months. An additional five individuals (4 males, 1 female) were captured at the same gravel bar in May 2004. Two of these fish died or shed transmitters within 2 weeks of release.

Between June 2002 and April 2005, we relocated radio-tagged robust redhorses 1,182 times. Diel tracking accounted for 515 of these observations. Individuals were relocated from 10 to 165 times. Individual females were relocated an average (±SE) 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 number 48, were not incorporated in at least one of the diel tracking transects.

Most of the robust redhorses remained near (within 6.5 rkm of) their release sites throughout summer 2002 (Figure 2). However, one individual moved 172.8 rkm downstream within 1 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 redhorses showed a high degree of overwintering-site fidelity (Figure 2), returning to the same 100–200-m lengths of shoreline each year. These

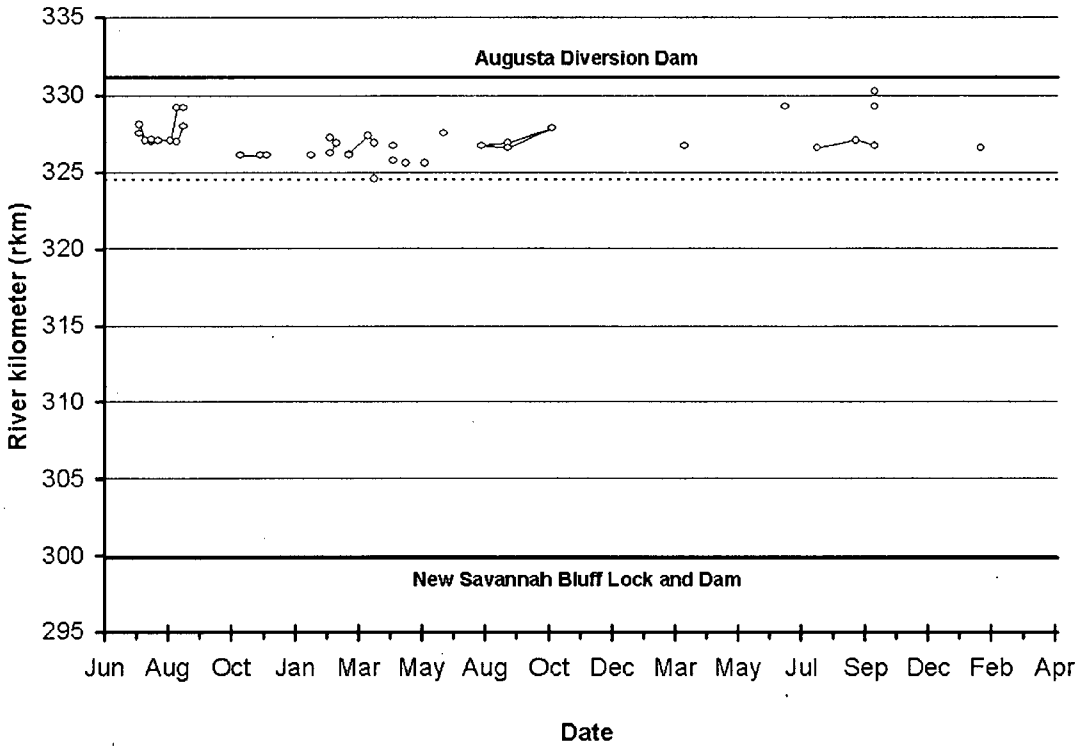

FIGURE 3.—River kilometer (rkm) positions of individual radio-tagged robust redhorses in the Savannah River between the Augusta Diversion Dam and New Savannah Bluff Lock and Dam from June 2002 to April 2005. The dashed line represents the downstream limit of Savannah Rapids. The solid lines connecting points indicate the movements of individual fish.

overwintering areas were distributed along the outside edge of river bends in water 3.0–5.0 m in depth. Observations with an underwater camera system showed coarse-gravel streambed sediment and structurally complex habitats consisting of large woody debris. During 2003–2005, fish began to make upstream migrations in early to mid-March (Figure 2), when water temperatures were approximately 10–12°C. Most individuals made upstream migrations each year. However, one or two individuals in each year did not make a migration (Figure 2). These individuals were not the same from year to year and were observed to make spawning migrations the following year. Radio-tagged robust redhorses 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, when flows rarely exceeded the median daily streamflow. During high water, radio-tagged robust redhorses accessed the floodplain and occupied flooded forest habitats, particularly in areas at rkm 200–250 and rkm 100–125. Individuals frequently moved far enough onto the floodplain to be just barely detectable with our telemetry receiver. This was the only time during the study when we observed robust redhorses out of the main river channel. Our fish did not use any of the smaller-order streams that flow into the Savannah River, regardless of flow conditions. Spawning-habitat fidelity also appeared to decrease during high water. Radio-tagged robust redhorses 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 number 51 was last observed below the dam at rkm 276.2 on 28 June 2003 and was not seen again until it was relocated above NSBL&D on 9 August 2004 at rkm 326.6 in the Savannah Rapids.

Radio-tagged robust redhorses above NSBL&D did

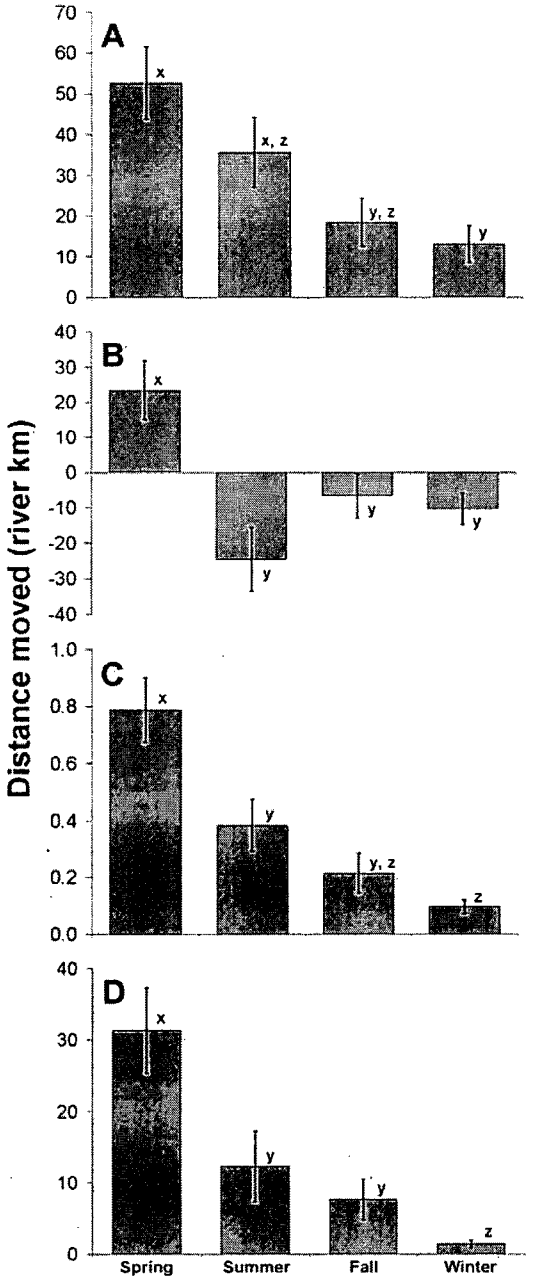

FIGURE 4.—Mean (±SE) seasonal (A) absolute movement, (B) displacement, (C) minimum estimate of daily movement, and (D) range of radio-tagged robust redhorses in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to May 2005.

not exhibit any seasonal movement patterns (Figure 3). These individuals remained in the shoal and pool habitats of the Savannah Rapids. Gaps in the data are presumed to occur when fish moved out of 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 redhorses were most active in spring ($F_{3,155} = 7.27$, $P = 0.0001$), exhibiting mean (±SE) absolute movement of 52.7 ± 8.9 rkm (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 (±SE) distance of 23.4 ± 8.4 rkm upstream in spring and returned 24.6 ± 9.0 rkm downstream in summer (Figure 4). Minimum (mean ± SE) estimates of daily movement rate were highest in spring ($F_{3,155} = 14.02$, $P < 0.0001$) and ranged from 0.8 ± 0.1 rkm/d in spring to 0.1 ± 0.02 rkm/d in winter (Figure 4). Radio-tagged robust redhorses also exhibited the greatest seasonal range in spring ($F_{3,155} = 9.23$, $P < 0.0001$) and had a mean (±SE) distance of 31.3 ± 6.0 rkm between the furthest upstream and downstream locations (Figure 4). Interannual differences in absolute movement, seasonal range, and minimum estimates of daily movement rates were assessed between 2003 and 2004 (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 in 2004 ($t_{132} = 2.30$, $P = 0.0229$), moving, on average, 22.6 ± 9.5 rkm more in 2003 than in 2004.

On average, radio-tagged robust redhorses moved between 0.5 and 1.0 rkm over a 24-h period (Figure 5). There was minimal evidence of boat motor noise affecting behavior. On two occasions, fish initially located in shallow water appeared to retreat back to woody debris in deeper water on the opposite side of the channel. 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 rkm in length (Figure 5) and did not

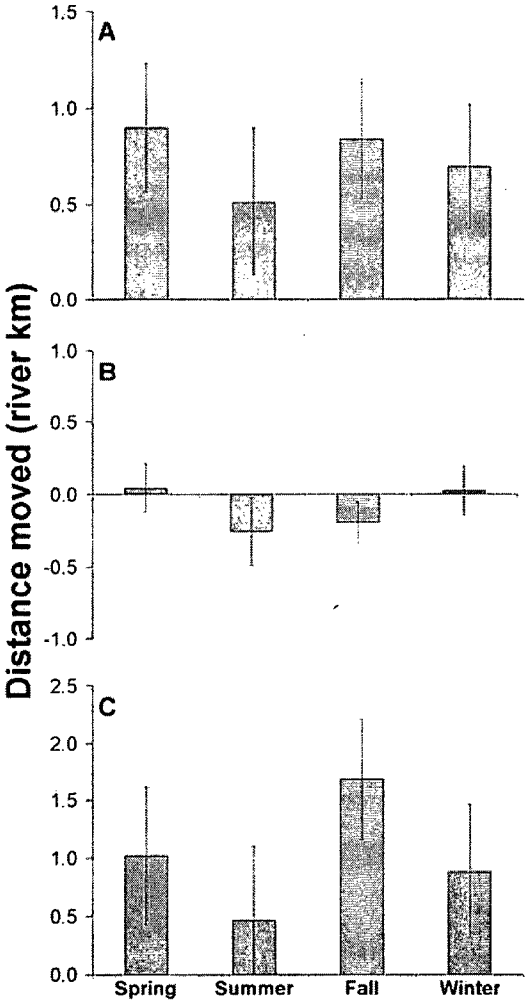

FIGURE 5.—Mean (±SE) diel (A) absolute movement, (B) displacement, and (C) use area of radio-tagged robust redhorses in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to May 2005.

differ among seasons ($F_{3,17}$ = 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); significantly more movement occurred 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 redhorses 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 the razorback sucker *Xyrauchen texanus* (Tyus 1987; Tyus and Karp 1990; Modde and Irving 1998), white sucker *Catostomus commersonii* (Olson and Scidmore 1963), and southeastern blue sucker *Cycleptus meridionalis* (Mettee et al. 1996), the robust redhorses below NSBL&D appears to be potamodromous. Potamodromy (movements occurring entirely within freshwater) is a migratory strategy employed by numerous riverine fishes, including many species of sturgeons *Acipenser* spp. and *Scaphirhynchus* spp. (Bemis et al. 1997), paddlefish *Polyodon spathula* (Bemis et al. 1997; Stancill et al. 2002; Zigler et al. 2003), large tropical catfishes (Barthem et al. 1991; Barthem and Goulding 1997), large cyprinids (Tyus 1990; Lucas and Batley 1996; Allouche et al. 1999; Winter and Fredrich 2003), and some characoids (Bayley 1973; Duque et al. 1998). Specific information on the migratory behavior of other *Moxostoma* species is very limited, but it appears that Savannah River robust redhorses undertake much longer upstream migrations to spawning habitats than do other redhorse species, such as the greater redhorse *M. valenciennesi* (Bunt and Cooke 2001) and river redhorse *M. carinatum* (Hackney et al. 1968). It also is likely that robust redhorses 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 that American shad *Alosa sapidissima* and other anadromous fishes migrated over 614 rkm to the Savannah River 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 that robust redhorses 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 redhorses 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 suckers (Olson and Scidmore 1963; Werner 1979), river carpsuckers *Carpiodes carpio* and common carp *Cyprinus carpio* (Bonneau and Scarnecchia 2002),

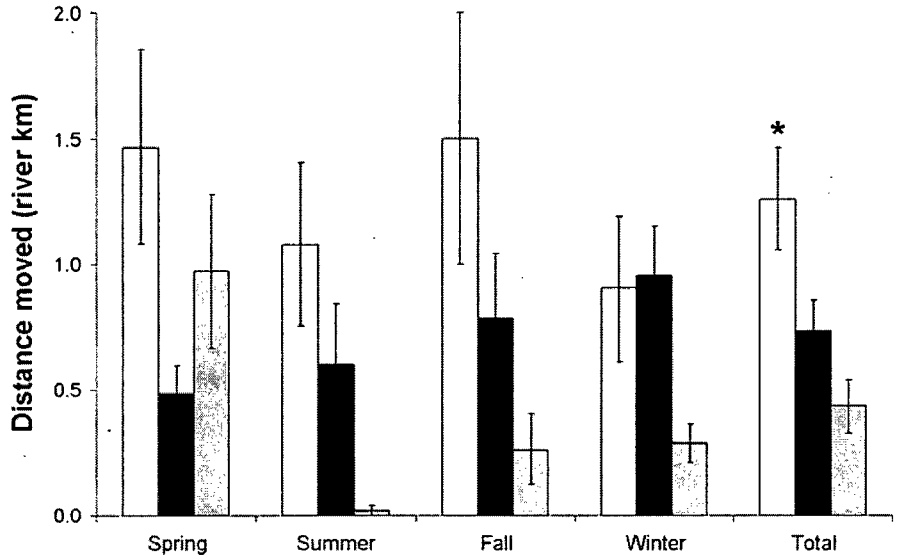

FIGURE 6.—Mean (±SE) absolute movement between 2-h tracking periods for robust redhorses in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to May 2005. The white, black, and gray bars represent daylight, nighttime, and twilight periods, respectively.

Colorado pikeminnow *Ptychocheilus lucius* (Tyus 1990), razorback suckers (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 Johnston 1990), our radio-tagged robust redhorses did not ascend tributaries to spawn. Instead, they used main-channel gravel bars similar to other large riverine redhorses, such as the 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 depth and current velocities on both bars unsuitable for robust redhorse spawning (Freeman and Freeman 2001). This pattern of wandering among a few sites within a relatively small area during the spawning season has been observed in razorback sucker (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 redhorses was unexpected. Radio-tagged robust redhorses often migrated more than 100 rkm 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 of individuals to overwintering and staging areas. However, fidelity to overwintering or oversummering areas has been identified on coarser scales in reservoir populations of striped bass *Morone saxatilis* (Jackson and Hightower 2001; Young and Isely 2002), razorback sucker (Mueller et al. 2000), and Gulf sturgeon *Acipenser oxyrinchus desotoi* (Wooley and Crateau 1985; Clugston et al. 1995; Heise et al. 2005). 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 a similar behavior pattern (Matheney and Rabeni 1995; Bunt and Cooke 2001). It is important to note that these studies were 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 redhorses appear to use their entire home range during the course of a day. In so doing, their behavior and activity are 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). Our results suggest that this species is mostly sedentary and occupies relatively small linear home ranges for extended periods of time interspersed with long-distance seasonal migrations. Infrequently, some individuals were observed to abandon previous home ranges and establish new ones in different locations. This usually occurred during downstream migrations. It was rare for individuals to do so at other times of the year. The razorback sucker (Mueller et al. 2000) was the only catostomid species for which we 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 redhorses moved into previously unused habitats during winter and spring floods on the Savannah River in 2003. High-water events were the only times we observed radio-tagged robust redhorses 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. Movement of riverine fish into these habitats during flood events has been attributed to (1) avoidance of displacement by high current velocities (Matheney and Rabeni 1995; Allouche et al. 1999; David and Closs 2002), (2) foraging on the floodplain (Ross and Baker 1983; Turner et al. 1994; Snedden et al. 1999), or (3) spawning in floodplain habitats (Welcomme 1979; Snedden et al. 1999). We were not able to ascertain the reason that robust redhorses left the main river channel during high-water events, but we hypothesize that they are using the floodplain habitats for feeding in preparation for 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 the behavior of their downstream counterparts. These individuals did not undertake long migrations; instead, they 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 our study adopted a pattern of behavior similar to the two individuals that were originally captured in the Savannah Rapids. We hypothesize that the robust redhorse population above NSBL&D may be confined to a relatively small stretch of river (approximately 8.0 rkm) based on the inability or unwillingness of the radio-tagged fish to move out of the Savannah Rapids. This requires further investigation because of the small sample size and difficulty in locating these fish during our study.

Our observations of the behavior of radio-tagged robust redhorses 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) probably contributed to its "disappearance," robust redhorses 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 in 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 the robust redhorse in the Savannah River and throughout the species' range.

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[Management Brief]

Emigration of Fish from Two South Carolina Cooling Reservoirs

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Abstract.—We assessed fish escapement from two South Carolina reservoirs, Par Pond and L Lake, from spring 2002 through summer 2003. Escapement was greatest in the spring and early summer, with lake chubsucker *Erimyzon sucetta* dominating the escapement catch in early spring and several sunfishes *Lepomis* spp. dominating in late spring and early summer. Most of the escaping centrarchids were bluegill *L. macrochirus*, warmouth *L. gulosus*, and redbreast sunfish *L. auritus* in L Lake and warmouths, bluegills, dollar sunfish *L. marginatus*, and spotted sunfish *L. punctatus* in Par Pond. Escapement was enhanced by high reservoir water levels and surface discharge over the spillway. Escapement declined during periods of hypolimnetic release from bottom discharge gates. Location of the Par Pond discharge structure in the littoral zone rather than the pelagic zone as in L Lake contributed to greater escapement of littoral species in Par Pond. Species composition in the escapement catches and reservoirs was not significantly correlated. Relatively low escapement from L Lake and Par Pond compared with that in other reservoirs may have been related to the configuration of the discharge structures, low water levels during 2002, fish habitat preferences, species composition and abundance in the reservoirs, and low rates of discharge.

The emigration of fish from reservoirs by passage over spillways has been a long-standing concern of resource managers. Research in this area was initially motivated by concern over the depletion of sport fishes from reservoir populations (Clark 1942; Louder 1958; Stober et al. 1983) and by fears that escapement of undesirable species could be harmful to downstream fisheries (Holder 1971; Schultz et al. 2003). Recently, the focus of interest has shifted to the passage of juvenile salmonids from reservoirs, where reservoir emigration is viewed positively rather than negatively (Giorgi et al. 1997). However, initial concerns over the loss of sport fish and the downstream effects of emigrating fish persist (Rischbieter 1996, 1998), partly because many questions regarding fish escapement remain unanswered. Manifestations of this concern include a recent review of the related topic of fish loss through water diversion systems (Moyle and Israel 2005) and the frequent inclusion of features to prevent fish loss in guidelines for pond construction.

Previous research on fish passage over spillways demonstrates that escapement is highly variable and influenced by many factors. Most studies show that escapement is seasonal, usually peaking during the spring (Lewis et al. 1968; Powell and Spencer 1979), or in some cases the winter (Clark 1942). Fish movements related to spawning may contribute to escapement, but other factors, such as disease, may also be important (Clark 1942; Holder 1971). Accounts differ regarding spillway discharge, with some sug-

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gesting that the rate of discharge is unimportant within limits (Navarro and McCauley 1993) and others indicating that discharge and depth at the spillway crest are critical (Rischbieter 1996, 1998). Other factors that may influence escapement include fish age (Lewis et al. 1968) and spillway design (Elser 1960). Lastly, some studies suggest that fish escapement is a generalized phenomenon affecting most species in proportion to their abundance in the reservoir (Elser 1960), whereas others indicate selective emigration of particular species (Navarro and McCauley 1993).

We recently evaluated the escapement of fish from two cooling reservoirs in South Carolina to assess the possible importance of the passage of contaminated fish as a mechanism of radionuclide export from the reservoirs. Although our focus was on largemouth bass *Micropterus salmoides* (which were studied as part of a larger inquiry on radionuclide dispersal [Paller et al. 2005a]), we collected all species to obtain an overview of fish escapement. The spillway structures differed between reservoirs, but both structures had multiple release depths. Fish surveys previously conducted in both reservoirs provided insights on escapement selectivity, and historical information was available from one reservoir permitting us to assess changes in escapement over time. Our objective was to describe fish escapement from the reservoirs, compare it with escapement from other reservoirs in the literature, and identify factors that influenced escapement.

Study Site

L Lake and Par Pond are located on the Savannah River Site, a 780 km^2 U.S. Department of Energy reservation located primarily on the upper coastal plain of South Carolina. Par Pond (10.5 km^2 surface area) was constructed in 1958 by impounding the upper reaches of Lower Three Runs Creek; L Lake (4.0 km^2) was constructed in 1985 by impounding the middle reaches of Steel Creek. Both reservoirs were used for reactor cooling until reactor operations ceased in 1988. The watersheds of both reservoirs are relatively small, and reservoir water levels are maintained by pumping in water from the Savannah River. A minimum of about 0.3 m^3/s is discharged from each reservoir to maintain required minimum flows in Lower Three Runs and Steel Creek, although greater discharges occur when watershed runoff is high. Both reservoirs support diverse warmwater fish communities that have been studied extensively (summarized in Paller 2005b).

The L Lake outlet consists of a standpipe located 152 m offshore from the center of the dam with two independent and adjustable release gates at depths of about 3 m and 20.4 m at normal pool elevation (57.9 m mean sea level [msl]). Water is transported to and through the dam by a large culvert that discharges down a sloped concrete slab at the base of the dam into Steel Creek. Water can be released from both gates simultaneously or from either gate individually to maintain minimum flows in Steel Creek (estimated from a gauging station downstream from the outlet).

Water is released from the Par Pond dam through two outlets, which differ in depth. A lower outlet near the bottom of the dam is equipped with adjustable gates that control the amount of bottom discharge. An upper outlet consisting of an overflow spillway in the dam discharges surface water from the littoral zone when reservoir water levels exceed 60.7 m msl. Water flowing over the spillway drops down a standpipe to a tunnel that passes through the base of the dam. This tunnel is also connected to the lower outlet so that waters from the upper and lower gates mix and are discharged from the tunnel outlet at the base of the dam. Reservoir water level dictates flow from the spillway, so surface discharge occurs during periods of heavy runoff; discharge needed to supply minimum flows to Lower Three Runs is entirely from the bottom outlet when reservoir levels drop below the spillway crest.

Methods

We installed traps below the outlets at the base of each dam to collect fish leaving the reservoirs. Screen fences (plastic-coated wire, mesh 23 mm × 23 mm, 30 mm diagonal) approximately 5 m long and placed diagonally across the outlets guided fish toward a tube that led into a holding cage made of the same material. Water depths were generally less than 20 cm near the L Lake trap but varied from about 30 cm to nearly 100 cm near the Par Pond trap. We removed fish from the traps (from two to three times per week when escapement was high to biweekly when escapement was low) and identified, measured (standard length), and released them below the traps.

We sampled Par Pond from mid-April through late October 2002 and from late March through early July 2003. Elevated flows resulted in a trap outage of 19 d during April/May of 2003; shorter maintenance outages occurred at other times. We sampled L Lake from early June 2002 through early July 2003. A 21-d trap outage occurred during November 2002, and four shorter outages occurred at other times. Dissolved oxygen and water temperature were recorded biweekly near the traps, and dissolved oxygen and water temperature profiles were usually measured twice a month at 1-m depth intervals within each reservoir near the dam.

To compensate for trap outages, we calculated average monthly escapement by dividing the number of fish caught that month by the number of operating

TABLE 1.—Number (*N*) and average standard length (SL) of fish collected in escapement traps below the L Lake and Par Pond dams. Dominant species in both reservoirs are shown for comparison with species that escaped.

Species	L Lake			Par Pond		
	Fish escaping *N* (%)	Average SL (mm)	% in L Lake[a]	Fish escaping *N* (%)	Average SL (mm)	% in Par Pond[a]
Amiidae						
Bowfin *Amia calva*				4 (0.8)	255	
Anguillidae						
American eel *Anguilla rostrata*	12 (11.3)	404				
Cyprinidae						
Golden shiner *Notemigonus crysoleucas*	3 (2.8)	104	3	13 (2.7)	109	10
Catostomidae (total)	20 (18.8)		1	132 (27.7)		11
Lake chubsucker *Erimyzon sucetta*	19 (17.9)	126	1	123 (25.8)	141	11
Spotted sucker *Minytrema melanops*	1 (0.9)	96		9 (1.9)	262	
Ictaluridae (total)	1 (0.9)			3 (0.6)		
Snail bullhead *Ameiurus brunneus*				1 (0.2)	223	
Yellow bullhead *Ameiurus natalis*				1 (0.2)	198	
Flat bullhead *Ameirurs platycephalus*	1 (0.9)					
Unidentified Ictaluridae				1 (0.2)	121	
Escocidae						
Chain pickerel *Esox niger*			5			5
Centrarchidae (total)	67 (63.2)		64	311 (65.1)		64
Mud sunfish *Acantharcus pomotis*				2 (0.4)	89	
Flier *Centrarchus macropterus*				3 (0.6)	112	
Redbreast sunfish *Lepomis auritus*	10 (9.4)	99	7	13 (2.7)	126	
Pumpkinseed *Leponis gibbosus*				2 (0.4)	117	
Warmouth *Lepomis gulosus*	16 (15.1)	109	4	168 (35.3)	120	2
Bluegill *Lepomis macrochirus*	32 (30.2)	99	39	53 (11.1)	124	37
Dollar sunfish *Leponis marginatus*	4 (3.8)	73		32 (6.7)	76	1
Redear sunfish *Leponis microlophus*				1 (0.2)	152	
Spotted sunfish *Lepomis punctatus*	3 (2.8)	68	7	29 (6.1)	100	1
Unidentified *Lepomis* spp.				3 (0.6)	137	
Largemouth bass *Micropterus salmoides*	2 (1.9)	148	7	3 (0.6)	177	23
Black crappie *Pomoxis nigromaculatus*				2 (0.4)	159	
Percidae						
Yellow perch *Perca flavescens*			22	13 (2.7)	145	5
Unidentifiable species	3 (2.8)					
Total	106 (100)			476 (100)		

[a] From Paller 2005b; excludes very small species such as brook silverside *Labidesthes sicculus* and coastal shiner *Notropis petersoni*.

trap days and multiplying by the number of days in the month. These numbers probably underestimated actual escapement because trap outages sometimes precluded measurement of fish passage during peak discharges (discussed in greater detail later). We tested monthly differences in $\log_{10} + 1$–transformed escapement between L Lake and Par Pond for significance ($P \leq 0.05$) with a dependent *t*-test.

Long-term electrofishing surveys in L Lake and Par Pond (Paller 2005b) provided data on fish assemblages in these reservoirs for comparison with the escapement trap catches. The most recent reservoir surveys occurred 4 to 6 years before the escapement study. We assumed these results were indicative of fish assemblages during the escapement study because species composition was relatively stable in the reservoirs near the end of the survey period. The similarity between species composition in the escapement catches and the reservoir assemblages was assessed with Spearman rank correlation coefficients.

Results and Discussion

We collected 106 fish representing 12 species from the L Lake escapement trap and 476 fish representing 20 species from the Par Pond trap (Table 1). Numerically dominant species in the L Lake catch included bluegill, lake chubsucker, warmouth, redbreast sunfish, and American eel. Numerically dominant species in the larger Par Pond catch included warmouths, lake chubsuckers, bluegills, dollar sunfish, and spotted sunfish and lesser numbers of redbreast sunfish, golden shiner, yellow perch, and spotted sucker. Other species were present at low frequencies. These totals exclude small fish that passed through the screens on the escapement cages and fish that escaped during trap outages. By pushing preserved specimens diagonally through a sample of the screen, we determined that only *Lepomis* spp. greater than about 65–70 mm standard length (SL) and lake chubsuckers greater than about 90–100 mm SL were likely to be retained. Small, elongate species such as the brook silverside and coastal shiner were missed entirely.

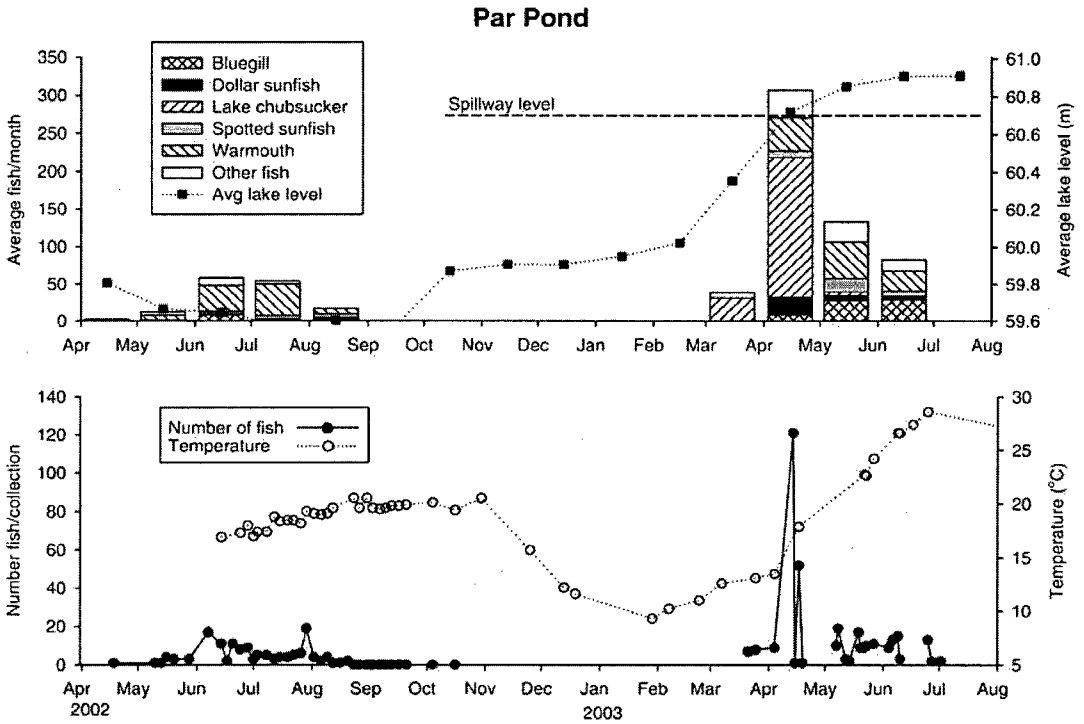

FIGURE 1.—Seasonal changes in fish escapement from Par Pond in relation to temperature and water level.

Differences in total escapement between Par Pond and L Lake were probably greater than indicated by total escapement numbers (Table 1) because of the longer trap outages in Par Pond (total number of trap days: 259 for Par Pond and 344 for L Lake). Particularly significant was a 19-d trap outage that occurred in Par Pond during a period of increased water discharge in April and May 2003. Large numbers of lake chubsuckers that may have emigrated from Par Pond were observed in the pool below the dam at that time. The average number of fish escaping per month was 60.9 (0.0–303.3) for Par Pond and 10.6 (0.0–46.5) for L Lake. When adjusted to include only the months sampled in both reservoirs, average monthly escapement was 71.7 for Par Pond and 14.5 for L Lake, but this difference was not statistically significant because of small sample size and high variability.

Seasonal Effects

Escapement from both L Lake and Par Pond was seasonal, peaking in the spring and early summer when water temperatures and levels were rising and declining to low levels in the late summer and winter. Escapement from Par Pond peaked during May-July 2002 and March–June 2003, the latter peak being substantially higher than the former (Figure 1). The 2002 peak, which began when the trap was installed, was dominated by warmouths, whereas lake chubsuckers dominated the early part (March and April) and warmouths and bluegills the latter part (May and June) of the 2003 peak. Like Par Pond, escapement from L Lake peaked strongly in the spring (April and May) of 2003, with lake chubsuckers again dominating early and sunfishes (bluegill, redbreast sunfish, and warmouth) dominating later. L Lake sampling did not begin early enough to determine whether a spring peak occurred in 2002, but only a few bluegills and warmouths were collected there during June through November 2002 (Figure 2). Regardless of season, escapement from both L Lake and Par Pond was episodic, with periods of low catch interspersed with periods of high catch.

Maximum escapement during the spring has been observed in other studies (Louder 1958; Lewis et al. 1968) and attributed to increased movement associated with spawning (Clark 1942; Holder 1971). However, it could also result from increased foraging activity as the result of rising temperatures. Lewis et al. (1968) observed maximum escapement of sexually immature largemouth bass from Chautauqua Lake, Illinois, during spring high water periods, and Clark (1942) observed maximum escapement of adult bluegills and

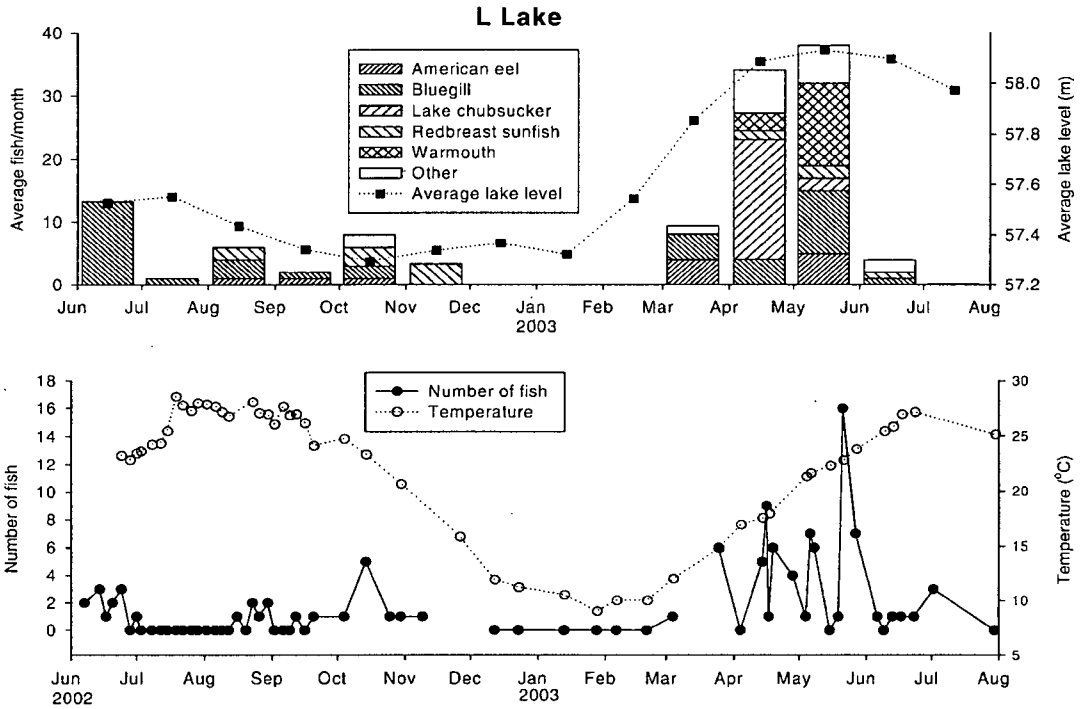

FIGURE 2.—Seasonal changes in fish escapement from L Lake in relation to temperature and water level.

white crappie *Pomoxis annularis* from Lake Loramie, Ohio, when substantial spillway overflow occurred during the "height of the spawning season." Both authors recorded escapement was minimal at other times despite considerable spillway overflow. Escapement peaks for lake chubsuckers, warmouths, and bluegills in Par Pond and L Lake corresponded to the expected spawning periods for these species in South Carolina (Marcy et al. 2005), although many of the escaping lake chubsuckers and bluegills appeared to be subadults, which suggests they were not actually spawning. In contrast, Clark (1942) observed gizzard shad *Dorosoma cepedianum* leaving Lake Loramie, Ohio, during high water in February and March as a possible result of "winter kill," and Jahn et al. (1987) observed impingement of gizzard shad on spillway screens at Spring Lake, Illinois, during the winter. In the latter two cases, escapement apparently resulted from the passive entrainment of fish debilitated by severe winter conditions.

Water Level and Outlet Design

Escapement from Par Pond was influenced by water level, which affected the mode of water release (surface spill versus bottom release). Water was released into Lower Three Runs through the bottom discharge gates throughout 2002 and early 2003, because Par Pond surface levels remained below 60.7 m msl (Figure 1). The bottom gates opened below the thermocline that developed during the summer, with the result that the water discharged was relatively cold hypolimnetic water. Water temperatures near the Par Pond escapement cage were comparable with Par Pond hypolimnetic temperatures (as indicated by temperature profiles measured near the Par Pond dam) and more than 10°C lower than Par Pond surface temperatures. Low escapement during 2002 could have resulted from the use of these bottom gates, which were probably less accessible or attractive to potential emigrants because of their depth, particularly when stratification occurred and fish had to move through anoxic water to reach the gates. However, dissolved oxygen levels below 6.2 mg/L were never recorded near the escapement cage, probably because Par Pond discharge was aerated as it passed through the outlet structure.

Surface discharge over the Par Pond spillway did not begin until early April 2003, when heavy rains raised the lake surface level above 60.7 m msl (Figure 1). These conditions were associated with maximum escapement from Par Pond, although escapement later (July) diminished despite the continuance of high water. Escapement from L Lake also increased with

increasing lake levels (Figure 2). Water leaves L Lake from two sets of gates (about 3 m and 17 m from the surface) rather than by way of a surface discharge spillway, which Par Pond has. Similarity between L Lake surface temperatures and creek temperatures near the escapement cage throughout this study indicated that most of the water entering Steel Creek was from the 3-m-deep gates, which opened above the thermocline that developed during the summer.

Linear regression of log-transformed numbers of escaping fish on reservoir water levels indicated a significant but weak relationship for both reservoirs ($R^2 = 0.22$ and $P = 0.01$ for both reservoirs), suggesting that water level influenced escapement but was not alone in controlling it. High water during the spring appeared to be the critical factor, possibly because this combination created greater potential for fish to leave the reservoir when they were being highly active.

Escapement Selectivity

Relative abundance differed between the escapement catches and reservoir surveys, although this conclusion is weakened by the different timing of the two studies. Differences were observed for warmouths, largemouth bass, lake chubsuckers, and American eels in L Lake and warmouths, dollar sunfish, spotted sunfish, bluegills, and lake chubsuckers in Par Pond (Table 1). Moreover, several species that were common in the reservoirs rarely escaped, including yellow perch and chain pickerel *Esox lucius* in L Lake and chain pickerel in Par Pond. For both reservoirs, the Spearman rank correlations between species abundances in the reservoir and the escapement catches (excluding species too small to be retained in the escapement traps) were low ($r = -0.06$ for L Lake and 0.38 for Par Pond) and not statistically significant ($P > 0.05$).

A remaining characteristic of many escaping fish was their relatively small size. All electrofishing surveys indicated that lake chubsuckers exceeding 250 mm SL were common in Par Pond (Paller 2005), but the average SL of lake chubsuckers in the Par Pond escapement catch was only 141 mm (Table 1). Most other species that dominated the escapement catches were smaller than their average adult size in the reservoirs, although adults of relatively small littoral centrarchid species such as dollar sunfish, spotted sunfish, and warmouths escaped from Par Pond.

Fish habitat preferences and the locations of the discharge structures apparently interacted to produce differences in the number and species composition of fish escaping from L Lake and Par Pond. Because the Par Pond discharge structure was located in the littoral zone, the littoral fishes we observed among the riprap along the dam (warmouths, spotted sunfish, and dollar sunfish) escaped in greater than expected proportions; and bluegills, which occupied somewhat deeper water, escaped in lesser than expected proportions (Table 1). In L Lake, where the discharge structure was offshore, escaping fish were fewer in number, and bluegills were collected in proportion to their abundance in the reservoir. Chain pickerel and yellow perch, which never appeared in the escapement catches from either reservoir, were strongly associated with aquatic vegetation (Paller 2005) and may have avoided the discharge areas because of the lack of this habitat.

Differences in species composition between reservoir assemblages and reservoir escapement were also observed in Lake Chautauqua, Illinois (Lewis et al. 1968); the Okefenokee Swamp, Georgia (Holder 1971); and two Michigan reservoirs (Navarro and McCauley 1993). However, escapement and reservoir species composition were more similar in Maryland ponds (Elser 1960); Lake Loramie, Ohio (Clark 1942); and especially Barren River Lake, Kentucky (Jacobs and Swink 1983). In the latter case, a 75% drawdown may have increased the probability of escapement, regardless of habitat preference and behavior. When smaller volumes of water are released slowly and continuously, species-specific behaviors may result in greater escapement selectivity, as we observed in Par Pond and L Lake.

Conclusions

Our results show that fish escapement was minimal when reservoir discharge was from the hypolimnion; moreover, escapement was lower in L Lake, which had an offshore outlet, than in Par Pond, which had an outlet in the littoral zone, where fish were comparatively abundant. Offshore and hypolimnetic outlets could also minimize escapement from other reservoirs that have seasonally anoxic hypolimnions and lack large numbers of pelagic fish. The configuration of the discharge structures, low water levels during 2002, low discharge, and species composition in the reservoirs probably contributed to relatively low escapement from L Lake and Par Pond compared with most other reservoirs discussed in the literature. However, earlier fish collections showed that thousands of juvenile bluegills escaped when L Lake was first constructed (Paller et al. 1987). At that time, bluegills were reproducing prolifically in L Lake, and juvenile bluegills were common offshore near the discharge structure, creating significant potential for escapement. As the reservoir matured, recruitment diminished and juvenile bluegills remained closer to expanding stands of submerged vegetation that provided cover from a growing bass population (Paller 2005b), thus diminishing the likelihood of escapement and demonstrating

that changeable ecological factors can influence fish escapement.

Fish escapement from reservoirs is affected by weather, species-specific behaviors, reservoir ecology, spillway design, and reservoir operation. Despite decades of study, many of these factors remain imperfectly understood, and the potential interactions among them can be complex and difficult to anticipate. Therefore, apart from broad generalizations, the magnitude of fish escapement from reservoirs remains difficult to predict without site-specific study that encompasses the range of climatic and environmental conditions experienced by the fish populations.

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