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ARTICLE

Effects of Regulated River Flows on Habitat Suitability for the Robust Redhorse

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Abstract
The Robust Redhorse *Moxostoma robustum* is a rare and imperiled fish, with wild populations occurring in three drainages from North Carolina to Georgia. Hydroelectric dams have altered the species' habitat and restricted its range. An augmented minimum-flow regime that will affect Robust Redhorse habitat was recently prescribed for Blewett Falls Dam, a hydroelectric facility on the Pee Dee River, North Carolina. Our objective was to quantify suitable spawning and nonspawning habitat under current and proposed minimum-flow regimes. We implanted radio transmitters into 27 adult Robust Redhorses and relocated the fish from spring 2008 to summer 2009, and we described habitat at 15 spawning capture locations. Nonspawning habitat consisted of deep, slow-moving pools (mean depth = 2.3 m; mean velocity = 0.23 m/s), bedrock and sand substrates, and boulders or coarse woody debris as cover. Spawning habitat was characterized as shallower, faster-moving water (mean depth = 0.84 m; mean velocity = 0.61 m/s) with gravel and cobble as substrates and boulders as cover associated with shoals. Telemetry relocations revealed two behavioral subgroups: a resident subgroup (linear range [mean ± SE] = 7.9 ± 3.7 river kilometers [rkm]) that remained near spawning areas in the Piedmont region throughout the year; and a migratory subgroup (linear range = 64.3 ± 8.4 rkm) that migrated extensively downstream into the Coastal Plain region. Spawning and nonspawning habitat suitability indices were developed based on field microhabitat measurements and were applied to model suitable available habitat (weighted usable area) for current and proposed augmented minimum flows. Suitable habitat (both spawning and nonspawning) increased for each proposed seasonal minimum flow relative to former minimum flows, with substantial increases for spawning sites. Our results contribute to an understanding of how regulated flows affect available habitats for imperiled species. Flow managers can use these findings to regulate discharge more effectively and to create and maintain important habitats during critical periods for priority species.

The Robust Redhorse *Moxostoma robustum*, a catostomid that is restricted to the southeastern United States, has recently received attention due to its rediscovery, rarity, and imperilment (Bryant et al. 1996). It is the largest of the redhorses *Moxostoma* spp. and exhibits potamodromous behavior (Breder and Rosen 1966; Grabowski and Isely 2006). The only known wild

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populations are found in the Pee Dee River (North Carolina and South Carolina), Savannah River (South Carolina and Georgia), and Altamaha River (Georgia) drainages; stocked populations exist in the Ogeechee River, Georgia, and in upper portions of the Savannah and Altamaha River drainages.

The Robust Redhorse has been negatively affected by degraded water quality, habitat modification, and habitat fragmentation as a result of hydroelectric dams (Warren et al. 1997, 2000; Ricciardi and Rasmussen 1999; Cooke et al. 2005). Specific detrimental effects may result from sedimentation, nest superimposition, and dewatering of spawning redds (Grabowski and Isely 2007a, 2007b; Jennings et al. 2010; Fisk et al. 2013). Altered flows from dams have also been implicated in (1) reducing the seasonal variation that can affect seasonal cues for fish (Cushman 1985), (2) losses of spawning habitat (Tyus and Karp 1990), (3) degradation of nursery habitat (Robinson et al. 1998), and (4) reduced larval growth rates (Weyers et al. 2003).

Historically, the Robust Redhorse was found over 200 river kilometers (rkm) upstream from its extant range in the Pee Dee River downstream of Blewett Falls Dam (Figure 1) to where Cope (1870) first described the species near Winston-Salem, North Carolina. Blewett Falls Dam is the terminal dam among eight main-stem dams on the Yadkin–Pee Dee River. It is a 23-m-high concrete structure that has no fish passage device to allow for upstream migration. Blewett Falls Dam is operated as a hydropeaking facility, where the units are operated at peak efficiency (204 m^3/s) as well as at intermediate flows. The 30-year (1979–2009) mean annual flow downstream of the dam was 215 m^3/s (SE = 15 m^3/s; USGS 2014).

Little is known about the reproductive ecology of the Robust Redhorse in the Pee Dee River and how it is impacted by regulated flows. The flows associated with hydropeaking power generation rapidly increase and inundate areas that previously were covered by little or no water; therefore, redhorses or other fish species may utilize such areas for spawning or other ecological functions, but those areas become dewatered when hydroelectric production ceases and flows are reduced. This phenomenon is considered a type of "ecological trap" (Battin 2004) that has been documented for several salmonid species (Bauersfeld 1978; Hawke 1978; Stober and Tyler 1982; Becker et al. 1985; Pender and Kwak 2002; McMichael et al. 2005) and for the Robust Redhorse (Grabowski and Isely 2007b; authors' personal observation). Although habitat is temporarily suitable while water levels are elevated, it becomes degraded as water levels recede, and redds become dewatered. The specific effects of redd dewatering have been studied primarily in salmonids, but a laboratory study found that redd dewatering was detrimental to Robust Redhorse eggs and larvae (Fisk et al. 2013). The dewatering of redds and spawning habitat in general may be the ecological bottleneck leading to further reductions in the small Robust Redhorse population of the Pee Dee River.

An environmental assessment associated with Federal Energy Regulatory Commission (FERC) relicensing for Blewett Falls Dam included an instream flow analysis and prescribed minimum flows (Progress Energy 2006). The augmented minimum flows, which were proposed to take effect in 2009, were 68 m^3/s from February 1 to May 15; 51 m^3/s from May 16 to May 31; and 34 m^3/s from June 1 to January 31 (Progress Energy 2006). The proposed minimum flows did not take effect in 2009, but an experimental minimum flow of 34 m^3/s was applied from April 15 to May 15, 2009.

A memorandum of understanding was signed in 1995 by public, private, conservation, state, and federal agencies and academic stakeholders, establishing the Robust Redhorse Conservation Committee to direct the recovery of this species. The Pee Dee River adult population is small; estimates from open-model mark–recapture studies range from a low of 34 individuals (95% CI = 21–47) in 2013 to a high of 58 individuals (95% CI = 36–80) in 2008 (RRCC 2014). Habitat fragmentation from dams and habitat alteration due to regulated flows from hydroelectric power production have restricted and altered spawning and nonspawning habitat for Robust Redhorses, and the quality and quantity of spawning habitat likely constitute a factor limiting Robust Redhorse recruitment. An understanding of habitat requirements is vital for the long-term survival of the Robust Redhorse, providing critical information about the ecology of this rare and imperiled species and allowing evaluation of flow management. Our objective was to characterize habitat suitability for the Robust Redhorse and quantify suitable spawning and nonspawning habitat under the current and augmented minimum flows in the Pee Dee River.

METHODS

Study area.—This research was conducted on the Pee Dee River, North Carolina–South Carolina (Figure 1). The Pee Dee River originates as the Yadkin River in Wilkes and Caldwell counties, North Carolina (Blue Ridge physiographic province), and flows through growing urban areas between Charlotte and Raleigh, North Carolina (NCDWQ 2008). The confluence of the Yadkin and Uwharrie rivers forms the Pee Dee River. Below Blewett Falls Dam, the river flows southeast for 302 km through the lower Piedmont region in North Carolina and the Coastal Plain region in South Carolina until it drains into the Atlantic Ocean through Winyah Bay near Georgetown, South Carolina. The Yadkin–Pee Dee River drainage in North Carolina is the second-largest river drainage in the state at 18,702 km^2 and flows through 22 counties and 93 municipalities (NCDWQ 2008).

Blewett Falls Dam, located near the town of Rockingham in south-central North Carolina, is regulated by FERC. The dam is a six-unit, 22-MW facility that was constructed in 1912 for purposes of flood control and hydropower production (Progress Energy 2006). Blewett Falls Lake is approximately 1,036 ha and

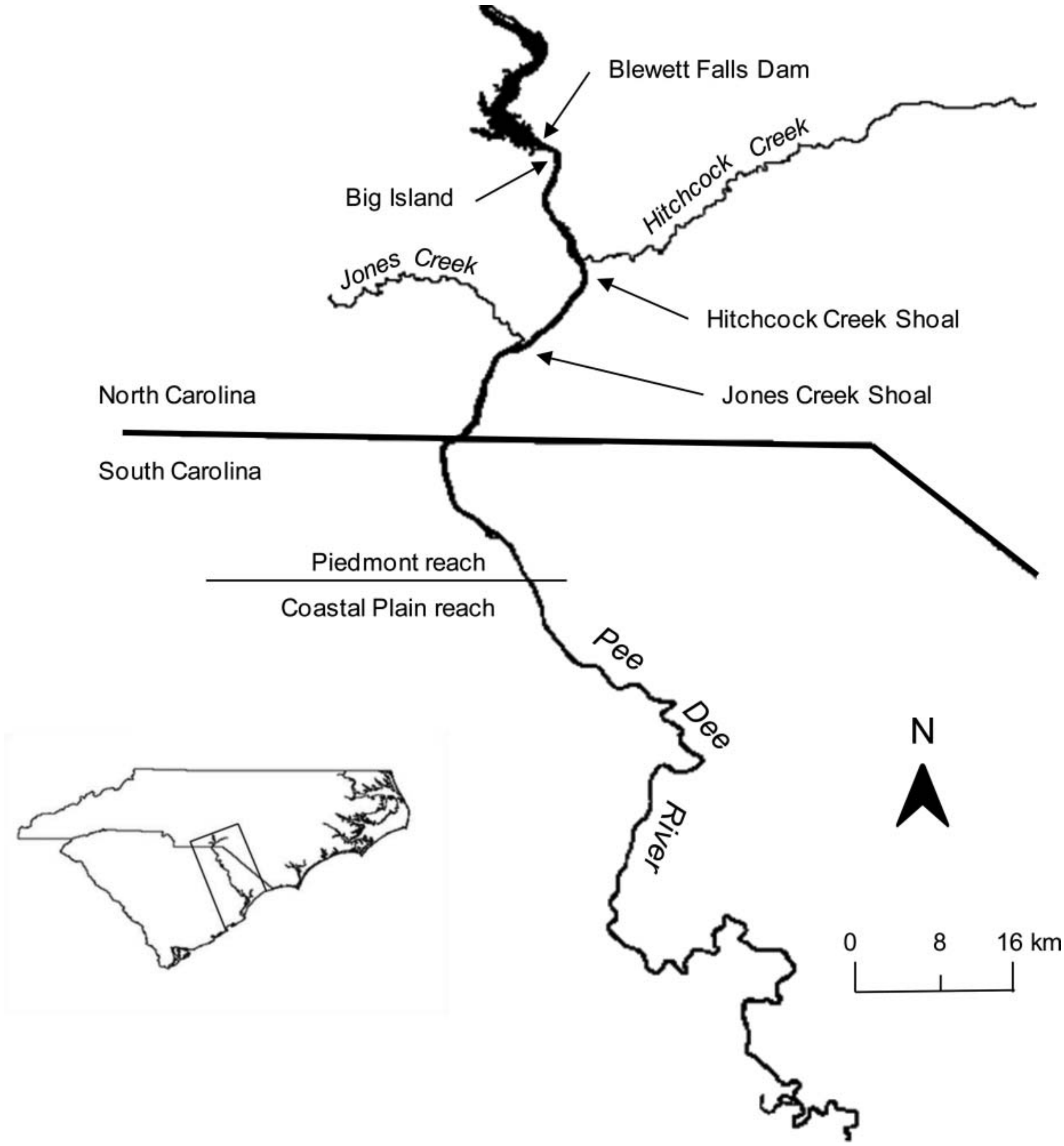

FIGURE 1. Map of the study area on the Pee Dee River, North Carolina–South Carolina, where habitat suitability for the Robust Redhorse was examined.

is the terminal impoundment of eight main-stem dams on the Yadkin–Pee Dee River. The 1958 operating license for the dam prescribed a minimum flow of 4.2 m^3/s; however, when power generation ceases, the spillage over the dam is approximately 11.3 m^3/s. We considered 11.3 m^3/s to be the baseline minimum flow for comparison with augmented flows in our habitat modeling projections.

The study reach of the Pee Dee River extended from rkm 302 (the Blewett Falls Dam tailrace near Rockingham, North Carolina) downstream to rkm 265 at Cheraw, South Carolina (Figure 1). This reach of the river (~37 rkm) flows through the Piedmont physiographic region and the fall zone, which is composed of large, complex systems of shoals, runs, and pools. Downstream of Cheraw, the river flows through the Coastal Plain region and creates more uniform habitats with lower velocities and finer substrates.

Radiotelemetry.—Sampling of Robust Redhorses during this 2-year study was part of the monitoring goals of the Robust Redhorse Yadkin–Pee Dee River Technical Working Group. Adult Robust Redhorses were captured by using multiple electrofishing boats with puslsed DC (120 Hz) at 4.0–5.0 A. Captured fish were weighed (g) and measured (TL, mm).

The sex and reproductive condition of each fish were determined by gamete expression and tuberculation. An Advanced Telemetry Systems Model F1850 radio transmitter (frequency = 40.000–41.999 MHz; weight [mean ± SD] = 23.5 ± 0.60 g; displacement [mean ± SD] = 15.1 ± 1.3 cm^3) with a trailing wire antenna was surgically implanted into the peritoneal cavity. To conduct the surgery, we anesthetized the fish in an aerated cooler containing 40 L of river water and 52 mL of benzocaine stock solution (1 g powdered benzocaine [Sigma E1501] per 30 mL of ethyl alcohol) for 3–5 min or until the fish lost equilibrium. The fish was then placed into a plastic container filled with 20 L of river water and 13 mL benzocaine stock solution. Four to six scales were removed, an incision was made just large enough to accommodate the transmitter's diameter, and the transmitter was inserted into the peritoneal cavity with the wire antenna oriented toward the caudal fin. We inserted the wire antenna of the transmitter inside the peritoneal cavity, where it was loosely coiled so that all components of the transmitter were inside the fish. The tip of each transmitter's wire antenna was coated with 3-mm Scotchcast resin to prevent peritoneal irritation. Incisions were sutured every 4–6 mm by using sterile, synthetic, absorbable suture material (coated Vicryl) with a 36-mm, 0.5-cm reverse cutting needle. Once the incision was closed, fish were placed into an aerated tank of river water to regain normal equilibrium and opercular movement. Fish were released into calm water in the same general area from which they were captured.

Seasonal habitat use.—To quantify microhabitat characteristics, undisturbed Robust Redhorses were relocated by radiotelemetry. Telemetered individuals were relocated by boat using an Advanced Telemetry Systems Model R2100 receiver and a hand-held loop antenna. Fish were relocated starting in 2008: (1) weekly from March into April; (2) every other day during the spawning period (April 15–May 15); (3) weekly from the end of May to August; and (4) monthly from September to March. This tracking cycle was repeated until its termination in July 2009. The spawning period of April 15–May 15 was delineated based on the following criteria: Robust Redhorses made a distinct upstream migration and occupied shallow, fast-flowing habitats; water temperatures were between 16°C and 22°C (the known spawning range for Pee Dee River Robust Redhorses); and captured fish displayed physical characteristics indicative of spawning, such as tubercles, loss of mucus, bruised and worn anal and caudal fins, and expression of gametes with little or no manual pressure. Nonspawning period habitat relocations were differentiated based on when Robust Redhorses made a distinct downstream migration or migrated off the spawning shoals and into deeper waters.

Once a fish's position was determined, we collected a suite of location and habitat measurements. A hand-held Global Positioning System unit was used to determine geographic coordinates. Depth in nonwadeable habitats was measured to the nearest centimeter with a boat-mounted winch and a suspended 22.6-kg torpedo weight; a top-set wading rod was used to measure depth in wadeable habitats. A Marsh-McBirney Model 2000 digital flowmeter was attached to either the torpedo weight or the wading rod to measure water velocity (m^3/s). Mean column velocity was measured at 60% of the water column at depths up to 0.75 m; at depths greater than 0.75 m, velocities were measured at 20% and 80% of the water column, and the values were averaged. Bottom velocity was measured at the substrate. Substrate was sampled at each location with a petite Ponar dredge, and dominant substrate was visually estimated and classified by using a modified Wentworth particle size scale (Bovee and Milhous 1978). Physical cover was tactically sampled with either the petite Ponar dredge or a metal rod in a 1-m^2 area around the relocation point; any substrate material or object that could be used as overhead cover or velocity refuge by a Robust Redhorse was considered cover.

Spawning habitat.—Spawning of Robust Redhorses could not be observed visually during this study due to the high turbidity that occurred with suitable spawning flows. At each electrofishing capture location during the spawning period, a weighted buoy marker was deployed and microhabitat characteristics were measured. The precision of this location relative to the fish's undisturbed microhabitat was probably variable. The location of the fish may have been influenced by the electrical field from the boat electrofisher and by the movement of fish before succumbing to narcosis and capture (Larimore and Garrels 1985). To account for variable precision, microhabitat characteristics were measured in a 20- × 20-m grid every square meter (N = 400 points) to describe spawning habitat. Habitat variables were depth (m), bottom velocity (m/s), mean velocity, substrate, and cover. After scrutinizing all of the spawning capture locations based on suitable spawning habitat for Robust Redhorses (Freeman and Freeman 2001; Grabowski and Isely 2006; Straight et al. 2014), we omitted 5 of 20 locations as atypical outliers.

Microhabitat use and availability.—Habitat suitability is typically calculated as habitat use divided by availability, with the resulting value standardized to a maximum index of 1.0. To quantify available habitats, we used existing data from hydroelectric relicensing surveys, during which habitat data were collected along cross-sectional transects throughout the study reach at multiple flow rates (Progress Energy 2006). These data were applied to calibrate the instream flow model and to estimate total available habitats from the Piedmont and Coastal Plain reaches in 5-m^3/s flow increments from 10 m^3/s up to 400 m^3/s by using RHABSIM software (Thomas R. Payne and Associates 1998). Microhabitat data for each fish relocation (i.e., habitat use) were stratified spatially into two reaches (Piedmont and Coastal Plain) and were stratified temporally into the spawning period (April 15–May 15) and the nonspawning period (the remainder of the year). The Piedmont and Coastal Plain reaches are physically distinct, which warranted their treatment as separate sites. The U.S. Highway 1 Bridge (rkm 265) at Cheraw, South Carolina, was used to delineate the Piedmont reach (upstream) versus the Coastal Plain reach (downstream; Fisk 2010).

Microhabitat data were compared between seasons, sexes, and the 2008 and 2009 spawning periods. In 2009, Duke Energy provided a higher minimum flow of 34 m^3/s during the spawning period, thereby mimicking the June 1–January 31 minimum flow proposed in the relicensing agreement. A Kolmogorov–Smirnov two-sample test was used to detect differences in microhabitat use distributions between seasons, sexes, and study years.

The approximate flow at the time of each telemetry relocation in the Piedmont reach was obtained from U.S. Geological Survey (USGS) gauging station 02129000 at the U.S. Highway 74 Bridge near Rockingham, North Carolina. We incorporated a time lag for discharge estimates at downstream locations (Fisk 2010). For fish relocations in the Coastal Plain reach, we obtained discharge data from USGS gauging station 02130561 near Bennettsville, South Carolina. The morphology of the Coastal Plain and the distance from the upstream dam made river fluctuations less intense and less predictable; thus, we did not incorporate a time lag for those discharge estimates.

To quantify available habitat at specific flows associated with fish relocations, all fish microhabitat use data were partitioned into evenly spaced bins according to flow from the corresponding gauging station at the time of fish relocation; this was done for each habitat variable. We then calculated the proportion of a particular bin range (e.g., depth = 0.0–0.5 m at a 20-m^3/s flow) relative to total available habitat in that flow range. Next, we calculated the proportion of fish microhabitat use measurements for each bin range relative to the total number of measurements for the reach (e.g., Piedmont reach during the nonspawning period). The proportional microhabitat use value was then divided by microhabitat availability to yield a proportional suitability value for that specific flow range. For each flow range, the process was repeated with depth, mean velocity, substrate, and cover. Finally, each bin was summed across all flow ranges to obtain the proportion of microhabitat used relative to the available microhabitat for each bin of that variable, and the proportions were standardized to 1.0 (i.e., habitat suitability). The suitability data for the nonspawning period in the Coastal Plain and Piedmont reaches were combined and standardized to 1.0 to represent an overall nonspawning habitat suitability function.

Microhabitat comparisons.—All continuous microhabitat variables were analyzed with principal components analysis (PCA) to determine random or nonrandom habitat use in a multivariate approach. The PCA extracted linear combinations from a correlation matrix of the original untransformed variables that explained the maximum amount of variation in the data without axis rotation. Components with an eigenvalue greater than 0.90 were retained as a practical break point in each data set examined (Stevens 2002; Kwak and Peterson 2007). Microhabitat use component scores were calculated from habitat availability component functions, and the component scores of occupied and available habitat were plotted and compared statistically. A Kolmogorov–Smirnov two-sample test was used to detect significantly different distributions of microhabitat use and availability data. Due to the variability of available habitat among flow rates, PCA was not performed on all microhabitat use data. Instead of running individual PCAs throughout the entire flow range (10–400 m^3/s), we selected four flows (17, 34, 68, and 204 m^3/s) for use in available habitat analyses. These were selected because they represented flows throughout the range of Blewett Falls Dam's normal operations and because they incorporated two of the three proposed minimum flows. Since few relocations fell exactly on the four flows, a range of microhabitat use data was used to increase the sample size and to yield a more robust analysis. This included 576 of 814 relocations (71% of all microhabitat use data). Flows of 34 and 68 m^3/s were omitted from statistical analysis because of low sample sizes (Table 1).

Weighted usable area.—RHABSIM (Thomas R. Payne and Associates 1998) was used to model the amount of available suitable habitat for Robust Redhorses at varying flow rates, quantified as weighted usable area (WUA; m^2/1,000 m). The WUA was modeled throughout the entire flow range (10–400 m^3/s). Resulting estimates are based on the habitat available and a species' habitat suitability function or more specific behavior (e.g., spawning and feeding; Bovee 1978; Stalnaker et al. 1995).

Along with habitat availability data, a habitat suitability criteria function must be developed based on life history characteristics of the selected species (Bovee 1986). It can be based on habitat use from any component of the species' life cycle (i.e., juvenile, spawning adult, or seasonal). We created criteria functions from optimal ranges (i.e., suitability = 1.0) for each variable by using habitat suitability indices for specific spawning sites and for the nonspawning period.

Spatial analyses.—Kernel density home range estimates and linear ranges were calculated annually for tagged fish with at least 30 relocations ($N = 14$ fish) by using methods similar to those of Vokoun (2003). Linear range was defined as the distance between the upstream-most and downstream-most relocations for a specified time period. Fish location coordinates were imported into ArcMap version 9.3.1. A flow line layer from the National Hydrology Dataset was used to delineate the river center line starting at Blewett Falls Dam and going beyond the farthest downstream fish relocation. The center line was divided into 10-m segments (beginning with zero at Blewett Falls Dam), and the nearest segment endpoint was identified for each location. The ArcMap output was imported into SAS version 9.2 (SAS Institute 2010), where seasonal linear ranges and kernel density estimates of home range (99, 95, and 50% levels) were calculated using PROC KDE. The percentages are estimates of where a fish utilizes a certain area for that specific kernel density level. The default bandwidth procedure (Sheather–Jones plug-in) was selected as recommended by Vokoun (2003), and grid points were set at

TABLE 1. Principal component (PC) loadings for Robust Redhorse microhabitat use and availability, eigenvalues, and cumulative variance explained for specified flow ranges (Q_{avail} = microhabitat availability flow, m^3/s; Q_{use} = microhabitat use flow range, m^3/s); number of locations (N) is given in parentheses. Principal components were derived based on microhabitat availability measurements; PC scores were then calculated for field measurements of both microhabitat use and availability under the corresponding flow ranges.

	$Q_{avail} = 17$ (N = 9,032); Q_{use} = 11–23 (N = 324)		$Q_{avail} = 34$ (N = 9,032); Q_{use} = 28–40 (N = 45)		$Q_{avail} = 68$ (N = 9,039); Q_{use} = 56–79 (N = 39)		$Q_{avail} = 204$ (N = 10,670); Q_{use} = 158–249 (N = 168)	
Variable or statistic	PC1	PC 2	PC1	PC 2	PC1	PC 2	PC1	PC2
Distance-to-bank (m) loading	0.64	−0.12	0.63	0.29	0.688	0.102	0.671	0.003
Depth (m) loading	−0.47	−0.43	0.12	−0.71	−0.087	−0.707	−0.348	−0.002
Mean velocity (m/s) loading	−0.17	0.89	−0.36	0.61	−0.156	0.698	−0.168	0.967
Substrate loading	0.58	0.04	0.68	0.18	0.703	−0.033	0.631	0.254
Eigenvalue	1.53	1.04	1.27	1.15	1.27	1.14	1.36	0.99
Cumulative variance explained (%)	38.3	64.2	31.8	60.7	31.7	60.2	34.2	59.2

10-unit intervals, which corresponded with the 10-m resolution of the data. Each kernel density estimate level and associated 10-m reference points were used to determine the corresponding utilized river sections for each fish. The utilization distribution points were then counted and multiplied by 10 to obtain an annual linear range in meters.

RESULTS

Fish Catch and Telemetry

Electrofishing capture rates of Robust Redhorses were low during the 2008 and 2009 spawning seasons despite substantial sampling effort. In 2008, 21 adult fish were captured from April 22 to May 8 with 82.3 h of sampling effort (CPUE = 0.27 fish/h) in the Piedmont reach near spawning areas. One additional adult was captured downstream in the Coastal Plain reach on October 6, 2008 (27.2 h of effort; CPUE = 0.03 fish/h). In 2009, 19 Robust Redhorses were captured from April 29 to May 14 with 124.0 h of effort (CPUE = 0.15 fish/h) in the Piedmont reach. Radio transmitters were implanted into 20 of the Robust Redhorses that were captured in 2008: 11 females with a mean TL of 685.1 mm (SE = 12.7; range = 627–766 mm) and a mean weight of 5,126.8 g (SE = 304.6; range = 4,280–7,395 g); and 9 males with a mean TL of 626.9 mm (SE = 13.9; range = 576–715 mm) and a mean weight of 3,568.9 g (SE = 236.4; range = 2,630–4,925 g). In 2009, 11 additional fish received radio transmitters: six females with a mean TL of 658.7 mm (SE = 6.0; range = 646–685 mm) and a mean weight of 4,887.5 g (SE = 234.8; range = 4,325–5,650 g); and five males with a mean TL of 648.8 mm (SE = 7.6; range = 624–665 mm) and a mean weight of 3,919.2 g (SE = 252.8; range = 2,986–4,425 g). Seven radio-tagged females survived from previous (2007) sampling and tagging efforts, resulting in a total of 39 telemetered adult Robust Redhorses. Of these 39 individuals, 12 expelled their transmitters or died within the 2-month period after implantation and were therefore excluded from analyses, leaving 27 individuals that were tracked throughout the study.

Microhabitat Use

Characteristics of the microhabitat occupied by relocated Robust Redhorses (N = 814 relocations; 195 during the spawning period, 619 during the nonspawning period; 14–57 relocations/fish) and the capture locations during spawning (N = 4,850 point measurements of 15 capture locations) varied, with overlap among ranges (Table 2). Robust Redhorses spawned in shallow habitats (mean depth = 0.84 m) but occupied moderate depths during the spawning period (mean = 1.97 m) and nonspawning period (mean = 2.30 m). Mean column velocity was lower during the nonspawning period (0.23 m/s) in comparison with spawning sites (0.61 m/s) and the spawning period (0.62 m/s), but mean velocity ranges were greater during the spawning period. Sandy substrates were occupied most frequently during the nonspawning period, whereas gravel was utilized most often at spawning sites and throughout the spawning period. Boulders were the dominant associated cover during the spawning period, but fish had no association with cover at spawning sites; woody debris was the most prevalent cover during the nonspawning period.

Seasonal comparisons of microhabitat use revealed differences between spring (including the spawning period) and summer–winter (nonspawning period), but microhabitat use was generally similar for summer and winter. Microhabitat

TABLE 2. Robust Redhorse microhabitat use data for the spawning period, spawning capture sites, and the nonspawning period; the number of locations (*N*) is given in parentheses. Mean and SE are presented for continuous variables, and mode is presented for categorical variables (Min = minimum; Max = maximum; Temp = temperature).

Period	Statistic	Depth (m)	Mean velocity (m/s)	Bottom velocity (m/s)	Temp (°C)	Substrate	Distance to bank (m)	Cover
Spawning period ($N = 195$)	Mean or mode	1.97	0.62	0.17	20.5	Gravel	37.5	Boulder
	SE	0.07	0.03	0.02	0.2		2.2	
	Min	0.20	0.01	−0.02	15.1		1.0	
	Max	7.00	2.00	1.40	24.2		122.0	
Spawning sites ($N = 4{,}850$)	Mean or mode	0.84	0.61	0.26	21.1	Very coarse gravel	15.9	No cover
	SE	0.34	<0.01	<0.01	0.1		4.2	
	Min	0.00	0.09	−0.27	17.5			
	Max	1.62	0.87	1.12	22.1			
Nonspawning period ($N = 619$)	Mean or mode	2.30	0.23	0.14	23.6	Sand	52.2	Coarse woody debris
	SE	0.03	0.01	0.01	0.3		1.5	
	Min	0.79	−0.02	−0.18	6.0		2.5	
	Max	5.90	1.85	2.20	32.1		156.0	

use was significantly different ($P < 0.0001$) between spring ($N = 376$ relocations) and summer ($N = 392$ relocations) for all continuous variables, including mean column velocity, bottom velocity, depth, substrate, and distance to the bank. Mean velocity and depth were significantly different ($P < 0.0001$) between spring and winter ($N = 42$ relocations). None of the continuous microhabitat variables was significantly different between summer and winter, and the cover type in occupied microhabitats was similar among all seasons.

Males and females utilized similar microhabitats throughout the year, and few differences were detected among the variables. During spring, females utilized deeper, lower velocities and habitats farther from the bank, but mean velocity was the only variable that was significantly different between males and females ($P < 0.05$). Microhabitat use during summer and winter was generally similar, but females occupied deeper water than males in winter ($P < 0.05$).

Microhabitat use was significantly different for some variables between the spawning periods in 2008 (minimum flow = 11 m^3/s) and 2009 (minimum flow = 34 m^3/s). Relative to 2008, the 2009 relocations of Robust Redhorses occurred in microhabitats with higher bottom velocity (2008: 0.16 m/s; 2009: 0.21 m/s; $P < 0.0001$) and higher mean velocity (2008: 0.28 m/s; 2009: 0.31 m/s; $P < 0.0001$) and were closer to the bank (2008: 41.6 m; 2009: 33.4 m; $P < 0.023$). Depth, substrate, and cover were similar between the two years.

Multivariate PCA revealed two contrasting habitat gradients. Principal component 1 (PC1) represented a gradient of fine substrates (low scores) at the riverbank increasing to coarse substrates (high scores) at mid-channel. Principal component 2 described a gradient from low velocity and deep water (pools; low scores) to high velocity and shallow water (shoals; high scores), except in the 204-m^3/s analysis, for which velocity was the only significantly loaded variable (Table 1). For each of the flow ranges analyzed, PC1 and PC2 explained at least 59% of the cumulative variance. Distributions of PC1 and PC2 scores for fish microhabitat use and habitat availability were significantly different ($P < 0.0001$) for the 17-m^3/s flow (i.e., 11–23 m^3/s), indicating highly specific (nonrandom) habitat use (Figure 2). Similarly, PC1 distributions were marginally significant ($P < 0.075$) and PC2 distributions were significantly different ($P < 0.0001$) for the 204-m^3/s flow. The PC score distributions at other flows were not significantly different ($P < 0.05$). Robust Redhorses were typically restricted to deep pools with low velocity when river flow was minimal (Figure 2a). Due to the geomorphology of the Pee Dee River, these deep pools were typically near shore. The fish occupied a wider range of available microhabitats as flow increased, which was demonstrated by an increase in the PC score variance of occupied microhabitats relative to available microhabitats as flow rate increased (Figure 2).

Microhabitat Suitability

Habitat suitability was calculated separately for the spawning period, spawning sites, and nonspawning period based on Robust Redhorse microhabitat use relative to habitat availability in the Pee Dee River. Suitable depth range during the spawning period (April 15–May 15), which includes spawning, staging, and resting behaviors, was 0.5–3.9 m; suitable

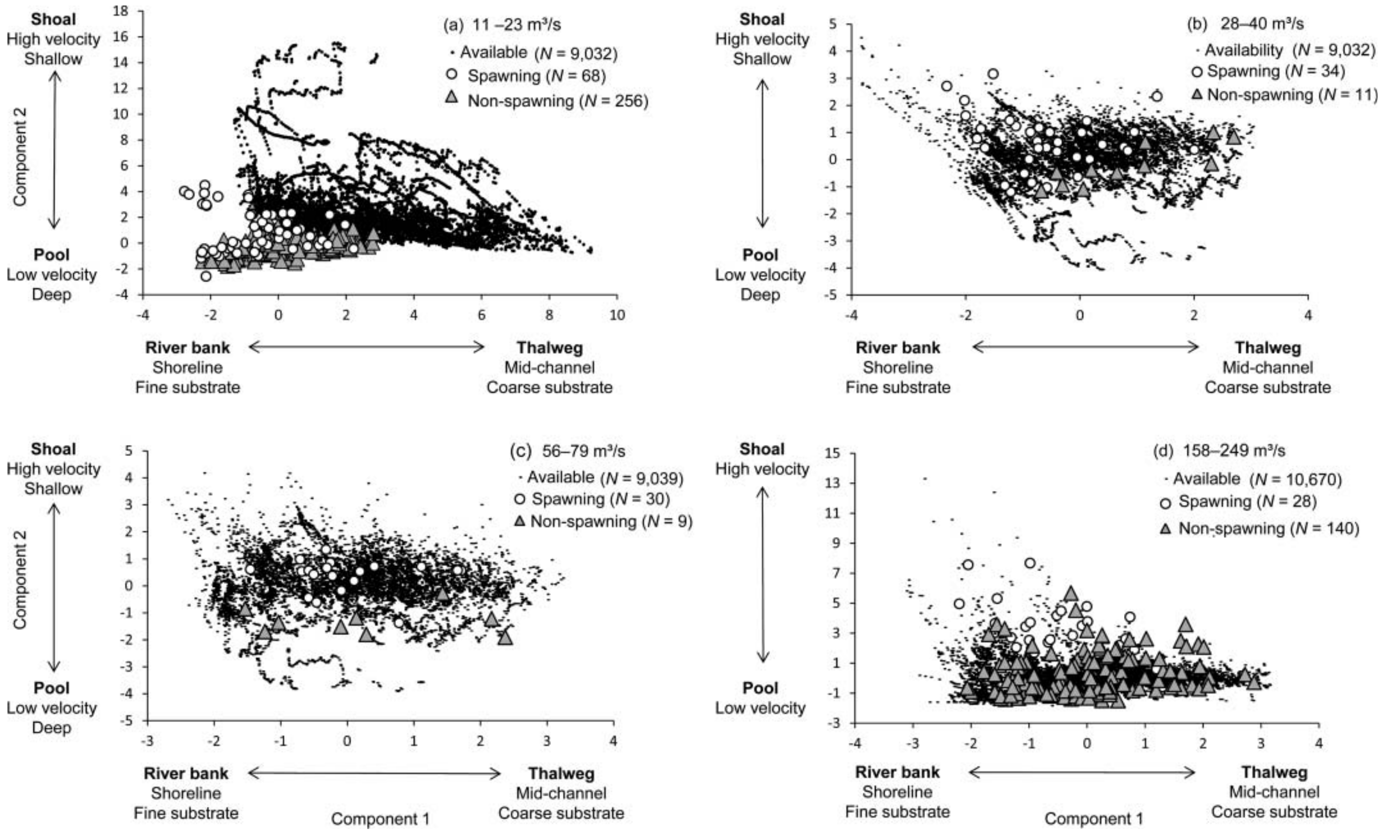

FIGURE 2. Plots of principal component scores for Robust Redhorse microhabitat use and available microhabitat under varying flow ranges in the Pee Dee River: **(a)** 11–23 m^3/s; **(b)** 28–40 m^3/s; **(c)** 56–79 m^3/s; and **(d)** 158–249 m^3/s. Principal component loadings and sample sizes are presented in Table 1.

mean velocity was 0.00–1.19 m/s; substrates spanned all categories; and coarse woody debris was the most suitable as cover (Figure 3). Suitable spawning sites (capture grid microhabitat) had a depth of 0.0–1.9 m, a mean velocity of 0.20–1.49 m/s, substrates spanning all categories, and "no cover" as the most frequently encountered cover category. During the nonspawning period, the suitable depth range was 0.5–4.9 m, the suitable mean velocity was 0.00–0.89 m/s, substrates spanned all categories, and coarse woody debris was most suitable as cover. For both periods (spawning and nonspawning), Robust Redhorse relocations were most frequently not associated with cover; when present, the most suitable cover was woody debris, even though boulders were most frequently utilized (Figure 3). Spawning period suitability included resting, staging, and spawning behaviors, which were represented by a trimodal depth distribution and a bimodal mean velocity distribution (Figure 3). In contrast, suitability during the nonspawning period reflected similar behavior throughout the period and unimodal distributions for depth and velocity.

Weighted Usable Area

Habitat criteria (optimal ranges) applied to estimate WUA under a variety of flow conditions differed substantially between spawning and nonspawning habitats. Suitable spawning site criteria comprised a depth range of 1.0–1.5 m, a mean velocity of 0.5–0.8 m/s, medium and large gravel substrate, and no cover. Nonspawning habitat criteria included a depth of 2.0–3.0 m, a mean velocity of 0.11–0.30 m/s, sand substrate, and woody debris and boulders as cover.

For both spawning and nonspawning habitats, WUA increased at all proposed seasonal augmented minimum flows relative to the 11.3-m^3/s minimum flow (Figure 4). No suitable spawning habitat was projected (i.e., WUA = 0) at the 11.3-m^3/s minimum flow; WUA was 56 m^2/1,000 m at a minimum flow of 34 m^3/s. The WUA then increased by 21% at 51 m^3/s, by 59% at 68 m^3/s, and by 1,137% at the peak efficiency flow of 204 m^3/s. Weighted usable area for the nonspawning period increased by 102% at 34 m^3/s, by 58% at 51 m^3/s, by 81% at 68 m^3/s, and by 35% at the peak efficiency flow in comparison with the 11.3-m^3/s minimum flow.

Linear Ranges and Kernel Density Estimates of Home Range

Linear ranges of Robust Redhorses differed among seasons. Overall, linear ranges were largest during the spring, followed

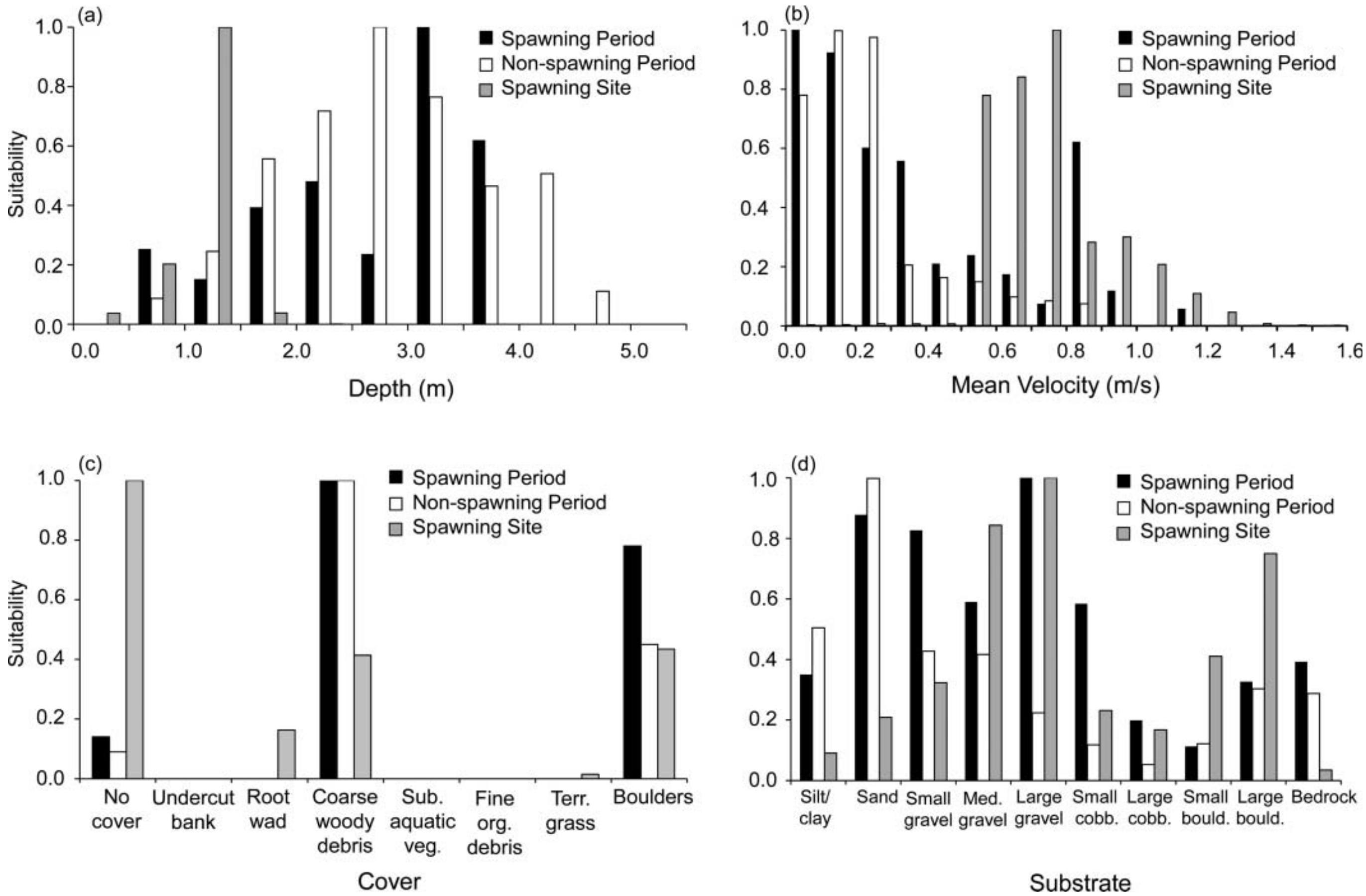

FIGURE 3. Suitability values for **(a)** depth, **(b)** mean column velocity, **(c)** cover (sub. aquatic veg. = submerged aquatic vegetation; fine org. debris = fine organic debris), and **(d)** substrate (cobb. = cobble; bould. = boulder) during the spawning period, during the nonspawning period, and at spawning sites for Robust Redhorses in the Pee Dee River based on capture locations and telemetry relocations.

by summer and then winter. Linear ranges varied widely among individual Robust Redhorses, and two subgroups with distinct behavioral patterns were evident: a resident subgroup and a migratory subgroup (Table 3; Figure 5). The resident subgroup stayed in the Piedmont reach throughout the year and exhibited localized movements during the spawning season. The migratory subgroup made substantial downstream migrations into the Coastal Plain reach of South Carolina during the nonspawning period and migrated back upstream into the Piedmont reach during the spawning period. The number of individuals in the migratory subgroup ($N = 7$) was smaller than the number of fish in the resident subgroup ($N = 20$); overall, the migratory subgroup had substantially larger linear ranges, as expected. Fish belonging to the migratory subgroup were slightly larger than fish of the resident subgroup. The migratory subgroup had a mean TL of 665.3 mm (SE = 23.5) and a mean weight of 4,288.0 g (SE = 593.6), whereas the resident subgroup had a mean TL of 638.6 mm (SE = 9.1) and a mean weight of 4,138.6 g (SE = 188.4). Significant size differences between subgroups were not detected ($P > 0.05$), but this may have been the result of the limited sample sizes.

Individual spawning migrations varied widely, as some fish moved upstream quickly over long distances, while others moved upstream incrementally. Timing was also variable; some fish arrived near spawning areas in February, whereas others waited until May—during the peak of the spawn—to move into these areas. We found no difference in migratory timing between male and female Robust Redhorses. High site fidelity between years was evident, with several fish occupying the same locations during the nonspawning period over the 2-year study.

Kernel density estimates were considerably smaller than linear ranges (Table 3). Mean 50% kernel density estimates were 5% of the mean linear range among all fish, 10% of the mean linear range for the resident subgroup, and 4% of the mean linear range for the migratory subgroup (Table 3). At the 99% kernel density level, the mean home range was 50% of the linear range for all fish, 60% of the linear range for the resident subgroup, and 48% of the linear range for the migratory subgroup. This demonstrates the sedentary nature of Robust Redhorses, with the exception of intermittent and seasonal migratory movements.

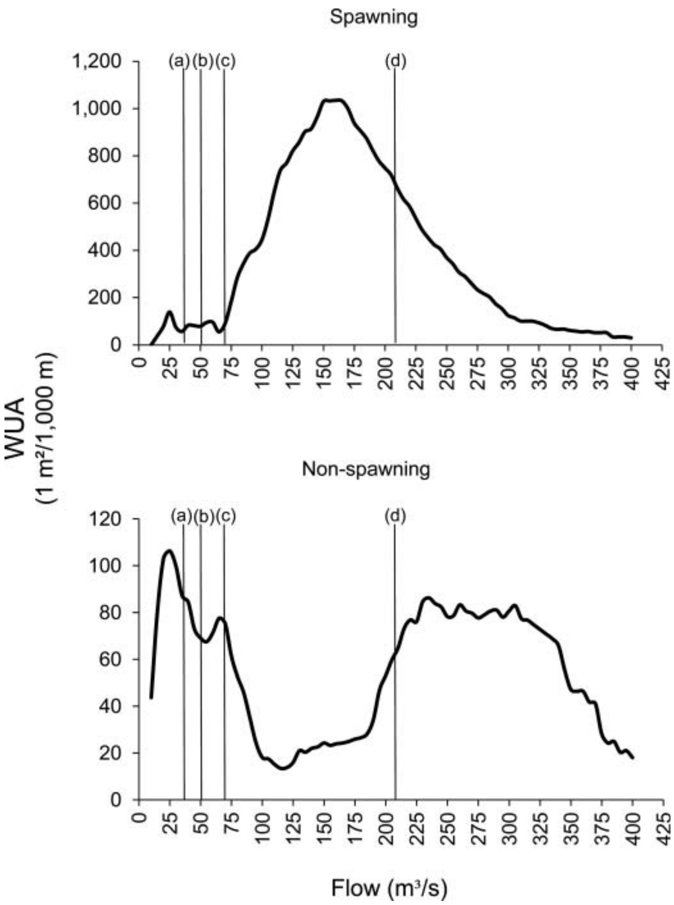

FIGURE 4. Weighted usable area (WUA; m^2/1,000 m) of spawning habitat (upper panel; based on spawning site suitability) and nonspawning habitat (lower panel; based on nonspawning period suitability) for Robust Redhorses in the Pee Dee River. Letters correspond to (a) a proposed minimum flow of 34 m^3/s for June–January; (b) a proposed minimum flow of 51 m^3/s for late May; (c) a proposed minimum flow of 68 m^3/s for February to mid-May; and (d) the peak generator efficiency flow (204 m^3/s) from Blewett Falls Dam.

Linear ranges differed substantially between the resident subgroup (mean = 7.9 km) and the migratory subgroup (mean = 64.3 km), whereas the kernel density estimates varied relatively less between the subgroups (mean = 0.8 km for the resident subgroup versus 2.5 km for the migratory subgroup; Table 3).

Eight Robust Redhorses (57% of the 14 tagged fish with at least 30 relocations) occupied one continuous core area (50% kernel density estimate), and six fish (43%) occupied two core areas. No fish occupied more than two core areas, but multiple areas were common at higher kernel density levels. Multiple core areas did not translate into larger home ranges. Means of each core area (2.5 and 1.5 km) for the six fish with two core areas were greater than the mean (0.8 km) for the eight fish with a single continuous core area. All core areas were within the limits of 95% areas.

TABLE 3. Mean, median, and SE of linear home range and kernel density estimates of home range (km) for Robust Redhorses with at least 30 relocations (N =14 fish) in the Pee Dee River (for resident and migratory subgroups and for all fish combined; Min = minimum; Max = maximum). Linear range is the distance spanned among relocations for an individual fish. Kernel density estimates represent utilization distributions at the 99, 95, and 50% levels.

		Kernel density		
Statistic	Linear home range (km)	99%	95%	50%
	All fish			
Mean	24.0	12.1	7.4	1.3
Median	10.4	4.6	3.5	0.8
SE	7.4	3.8	2.2	0.4
Min	2.6	2.0	1.8	0.4
Max	79.1	48.8	27.6	7.0
	Resident subgroup			
Mean	7.9	4.7	4.0	0.8
Median	7.3	3.7	3.1	0.7
SE	3.7	3.2	2.6	0.4
Min	2.6	2.0	1.8	0.4
Max	13.6	11.6	8.9	1.4
	Migratory subgroup			
Mean	64.3	30.7	15.9	2.5
Median	68.9	31.1	17.0	1.1
SE	8.4	7.5	5.6	1.5
Min	40.3	11.8	2.1	0.8
Max	79.1	48.8	27.6	7.0

DISCUSSION

Throughout the year, Robust Redhorses in the Pee Dee River occupied pool habitats with low velocities except during April and May, when they spawned in shoal habitats. Movements were localized except during the spawning or postspawning period, as demonstrated by the linear home ranges and kernel density estimates. We confirmed the locations of the primary spawning areas downstream of Blewett Falls

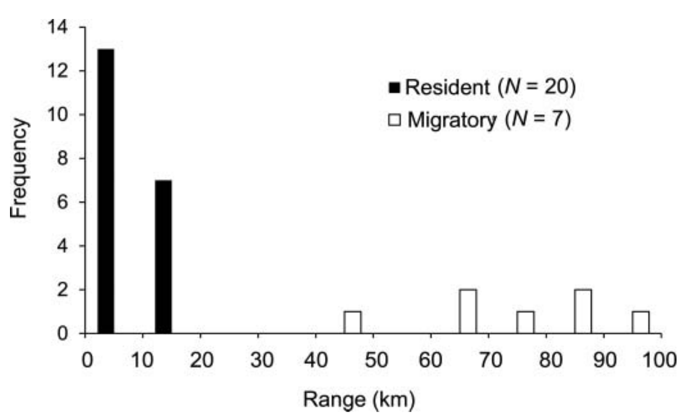

FIGURE 5. Linear home ranges of radio-tagged Robust Redhorses in the Pee Dee River; data are presented separately for the resident and migratory subgroups.

Dam; this information provides opportunities to protect these limited habitats. Our findings reveal that river discharge affects spawning habitat more than nonspawning habitat and that timely flow manipulations can enhance instream habitat for the Robust Redhorse.

Behavior

Robust Redhorses in the Pee Dee River exhibited seasonal potamodromous patterns similar to those of other redhorse species, although behavioral differences among individuals were apparent. Seasonal ranges quantified for the Pee Dee River population were smaller than those reported for the Savannah River (Grabowski and Isely 2006), but it appears that Robust Redhorses occupy the largest home ranges observed among redhorse species (Hackney et al. 1968; Bunt and Cooke 2001; Favrot 2009).

Kernel density estimates showed high within-season site fidelity of Robust Redhorses, as has been observed in other Robust Redhorse populations and in other redhorse species (Grabowski and Isely 2006; Favrot 2009). The holotype used to describe the Robust Redhorse was collected in the Yadkin River near Winston-Salem, North Carolina (Cope 1870), over 200 km upstream of the present Blewett Falls Dam site, but spawning habitat and migratory corridors on the Yadkin–Pee Dee River are now restricted by a series of main-stem dams, thus contributing to the extirpation of the species upstream of Blewett Falls Dam. Unlike other potamodromous redhorses that migrate into tributaries to spawn (Curry and Spacie 1984; Sule and Skelly 1985; Kwak and Skelly 1992; Favrot 2009), Robust Redhorse spawning in the present study was restricted to the main channel and side-channel gravel bars, and the fish resided in the main stem for the remainder of the year. The restriction of Robust Redhorses to main-stem and side-channel river habitat may further explain their extirpation in all but the terminal reach of the Yadkin–Pee Dee River system.

We observed that Robust Redhorses occupied spawning gravel bars only during elevated flows that were associated with hydropower generation or flooding events. The gravel bars located within the two primary spawning shoals were unsuitable for spawning at the 11.3-m^3/s minimum flow, and Robust Redhorses were never located in the shoals during those conditions. In fact, portions of the spawning areas were dewatered at 11.3 m^3/s. Robust Redhorses utilized shoal habitats for staging at higher flows, but when flow was minimal, they typically staged in deeper pools near the shoals.

Robust Redhorse habitat use varied between years with differing minimum flow regimes. Behavioral effects of increased flows have been documented for juvenile Coho Salmon *Oncorhynchus kisutch*, Chinook Salmon *O. tshawytscha*, and Brown Trout *Salmo trutta*, but this topic has been largely neglected for most other species in regulated rivers (Shirvell 1994; Vehanen et al. 2000; Robertson et al. 2004). The between-year behavioral differences of Robust Redhorses in our study highlight the interaction of habitat availability and fish behavior.

Males and females exhibited similar patterns of migration and residence on spawning shoals. However, considerable individual variation existed wherein both sexes arrived and remained on or near spawning areas throughout the spawning period. This finding is contrary to the prevailing notion that arrival at spawning areas is earlier for males than for females (Hackney et al. 1968; Page and Johnston 1990); a similar finding of concurrent migration between sexes was revealed during a study of spawning behavior in the Sicklefin Redhorse *Moxostoma* sp. (Favrot 2009).

Based on telemetry findings, we identified two distinct behavioral subgroups of Robust Redhorses. At the termination of the spawning season, 26% of Robust Redhorses made long downstream migrations into the Coastal Plain reach of South Carolina, whereas the remainder stayed within 10 km (most fish within 3 km) of the primary spawning area. The concept of mobile and sedentary subpopulations within a fish species dates back at least to Funk (1957) and is supported by numerous subsequent studies (Heggenes et al. 1991; Freeman 1995; Smithson and Johnston 1999; Schmetterling and Adams 2004). The dichotomy of resident and migratory subgroups has also been observed in Brown Trout and Bull Trout *Salvelinus confluentus*, wherein a portion of the population does not migrate from the natal stream but resides there to complete the life cycle (Northcote 1997; Nelson et al. 2002). Individual size differences between resident and migratory subgroups of Robust Redhorses were not detected, but size differences occurred in Bull Trout, with resident fish being smaller than migratory fish (Al-Chokhachy et al. 2005). Such behavioral differences may be related to food availability, habitat availability, flow patterns, and river connectivity—all of which are influenced by dams and regulated flows.

Based on our telemetry results and kernel density estimates, Robust Redhorses can be characterized as sedentary fish that undertake varying degrees of movement to spawn or to seek nonspawning habitat. The degree of migration varies greatly between the resident and migratory subgroups. The migration distance between spawning and nonspawning habitats is shorter for the resident subgroup than for the migratory subgroup, but the adaptive significance of that movement is unclear.

Microhabitat Use and Suitability

The habitat suitability indices developed from our research are the first published for the Robust Redhorse throughout its range. Robust Redhorse habitat use has been qualitatively described in other studies (Grabowski and Isely 2006; Straight et al. 2014) but was not compared to available habitat. Spatial habitat availability has repeatedly been demonstrated to affect fish habitat use (DeGraaf and Bain 1986; Heggenes and

Saltveit 1990; Heggenes 1991; Rincón and Lobón-Cerviá 1993), thus limiting the relevance of indices that are based on habitat use alone. Our habitat suitability indices are important for the conservation and management of Robust Redhorses, and with additional study they may be transferable and applicable among basins. All three drainages that contain Robust Redhorse populations are regulated by hydroelectric power facilities, and flow releases are critical for maintaining available suitable habitats for Robust Redhorses and other riverine species.

Suitability indices constitute an important biological component of instream flow modeling, particularly the instream flow incremental methodology (Bovee 1986), and the inclusion of all life stages and behaviors of a species is beneficial to river management. For instance, if we only examined nonspawning habitat use, which consists of moderate to deep pools, then the 11.3-m^3/s minimum flows may appear adequate since pools are less sensitive to flow fluctuations (Aadland 1993). However, spawning habitat (riffles and shoals) is more sensitive to flow fluctuations, and without adequate flow during specific time periods, species such as the Robust Redhorse may not successfully spawn or their progeny may not survive.

Bovee (1986) concluded that although visual observation is optimal for describing spawning habitat, a strong argument can be made for the use of other techniques. Deviation from a fish's "normal" behavior is one technique that can be employed to detect spawning. Robust Redhorses have been visually observed spawning in the Savannah River and Altamaha River drainages (Freeman and Freeman 2001; Grabowski and Isely 2007b; Straight et al. 2014), but visual observations are not feasible in the Pee Dee River because Robust Redhorses spawn at moderate to high flows associated with turbid water conditions. For some rare species in turbid waters, alternative methods may be the only feasible way to describe spawning habitats (Tyus and Karp 1990).

Habitat Modeling

The amount of projected suitable habitat (expressed as WUA) fluctuated with an increase in discharge for spawning and nonspawning functions, but WUA increased overall at the three augmented minimum flows proposed in the relicensing agreement and at the peak efficiency flow in comparison with the WUA observed at the 11.3-m^3/s minimum flow (Figure 4). The WUA for spawning was zero at 11.3 m^3/s, which was supported by the fact that none of the telemetered Robust Redhorses utilized gravel bar habitats at this flow. The fluctuations in WUA with flow reflected the spatially heterogeneous habitats of the Pee Dee River. Without these unique habitats (e.g., in a spatially homogeneous, channelized river), habitat would be affected similarly in quality and quantity, and habitat refuges would be scarce or absent (Garner 1997). This is not the case in the Pee Dee River, where distinct habitats (in particular shoal habitats) consist of diverse patches that may or may not exist at varying volumes of discharge (Figure 4). Spawning habitat (shoals) is affected more by flow than nonspawning habitat (pools) and may be a predominant factor limiting the Robust Redhorse's survival, as much of the spawning habitat has been altered and restricted by dam construction and operation and other human activities.

Long-term effects from increases in minimum flow based on habitat modeling estimates similar to those reported here have been documented. For example, spawning salmon utilized habitats farther upstream, the occurrence of redd dewatering decreased, and fry escapement increased in response to minimum-flow increases (Connor and Pflug 2004). Auer (1996) and Freeman et al. (2001) also found an increase in spawning fish farther upstream after the implementation of a minimum-flow regime. In the Pee Dee River, suitable spawning habitat remains available under higher flows at variable durations, and egg incubation and larval rearing habitats are enhanced with minimum flows that reduce mortality associated with redd dewatering (Fisk et al. 2013).

Conservation and Management

The Robust Redhorse is listed as an endangered species by the states of Georgia and North Carolina and is considered a high-priority species in the state wildlife action plans of Georgia, North Carolina, and South Carolina (GADNR 2005; NCWRC 2005; SCDNR 2005). The protective status and associated attention are warranted, as the Pee Dee River adult spawning population is small (35–58 individuals based on open-population mark–recapture model estimates for 2006–2014; RRCC 2014) and its riverine environment has been highly altered by humans. Habitat alteration, especially the construction and operation of dams, is a major detriment to aquatic systems and results in reduced and modified species assemblages (Pringle et al. 2000; Bunn and Arthington 2002; Cooney and Kwak 2013). Thus, optimizing the management of water releases at dams is critical, and the findings presented here can inform that process for imperiled species.

Although our results provide a tool for assessment, long-term monitoring will be required to assess the impacts that an augmented minimum-flow regime will have on Robust Redhorse habitat use and density. Augmented minimum-flow regimes are known to benefit fish assemblages (Lamouroux et al. 2006); Harby et al. (2007) recommended either long-term sampling or waiting multiple years before initiating sampling, as the effects of minimum-flow augmentation on fish assemblages are gradual and exhibit annual variation.

Information on Robust Redhorse abundance (2005–2014; Yadkin–Pee Dee River Technical Working Group; RRCC 2014) provides valuable baseline data to support long-term monitoring under varying flow regimes. Our findings identify suitable habitats during critical time periods for successful spawning and recruitment, along with flow modeling projections to guide management objectives. Once implemented, the proposed augmented minimum flows will inundate all gravel bars throughout the Pee Dee River's Piedmont reach and will provide important habitat for egg incubation and larval rearing (Fisk et al. 2013). Additional research and management focused on other poorly understood ecological aspects of the Robust Redhorse, such as juvenile habitat use and the impacts of endocrine-disrupting compounds, will further enhance management capabilities (Hinck et al. 2009). Currently, no young-of-the-year Robust Redhorses and very few juveniles have been collected in the Pee Dee River. Other critical knowledge gaps involve interactions between Robust Redhorses and nonnative species, including predation by introduced Blue Catfish *Ictalurus furcatus* and Flathead Catfish *Pylodictis olivaris*, competition with introduced Smallmouth Buffalo *Ictiobus bubalus*, and indirect effects from exotic Grass Carp *Ctenopharyngodon idella* and Common Carp *Cyprinus carpio*. Although other native species are likely to benefit from an augmented minimum-flow regime, unforeseen consequences of more stable seasonal flows are possible for both native and nonnative species (Fisk et al. 2013, 2014). The management of releases from Blewett Falls Dam to benefit the Robust Redhorse is a critical aspect of the species' recovery in the Pee Dee River. The results from our research will allow managers to make informed decisions about enhancing and sustaining habitats that are important for the Robust Redhorse.

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