

ARTICLE

# Behavior and Reproductive Ecology of the Sicklefin Redhorse: An Imperiled Southern Appalachian Mountain Fish

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## Abstract

Many nongame fishes are poorly understood but are essential to maintaining healthy aquatic ecosystems globally. The undescribed Sicklefin Redhorse *Moxostoma* sp. is a rare, imperiled, nongame fish endemic to two southern Appalachian Mountain river basins. Little is known of its behavior and ecology, but this information is urgently needed for conservation planning. We assessed the spatial and temporal bounds of spawning migration, quantified seasonal weekly movement patterns, and characterized seasonal and spawning behavior using radiotelemetry and weir sampling in the Hiwassee River basin, North Carolina–Georgia, during 2006 and 2007. Hiwassee River tributaries were occupied predominantly during the fish's spawning season, lower reaches of the tributaries and the Hiwassee River were primarily occupied during the postspawning season (i.e., summer and fall), and lower lotic reaches of Hiwassee River (upstream from Hiwassee Lake) were occupied during winter. Adults occupied Hiwassee Lake only as a movement corridor during spawning migrations. Both sexes conducted upstream spawning migrations simultaneously, but males occupied spawning tributaries longer than females. Sicklefin Redhorse exhibited interannual spawning-area and tributary fidelity. Cold water temperatures associated with hypolimnetic releases from reservoirs and meteorological conditions influenced spawning migration distance and timing. During 2007, decreased discharges during the spawning season were associated with decreases in migration distance and spawning tributary occupancy duration. Foraging was the dominant behavior observed annually, followed by reproductive behaviors (courting and spawning) during the spawning season. No agonistic reproductive behavior was observed, but females exhibited a repetitious postspawning digging behavior that may be unique in the family Catostomidae. Our findings suggest that protection and restoration of river continuity, natural flow regimes, seasonally appropriate water temperatures, and geographic range expansion are critical components to include in Sicklefin Redhorse conservation planning. Fisheries and ecosystem managers can use our findings to justify sensitive management decisions that conserve and restore critical streams and rivers occupied by this imperiled species.

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North America hosts the largest, most diverse, and well-studied temperate freshwater fish fauna globally (Abell et al. 2000; Warren and Burr 2014). Cumulatively, approximately 39% of described North American fishes are categorized as imperiled (i.e., endangered, threatened, or vulnerable: Jelks et al. 2008), and the southeastern

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United States hosts a large proportion of those imperiled fishes (Warren et al. 2000). Threats that face North America's diverse family of suckers (Catostomidae) serve as a microcosm for challenges imposed on North America's imperiled fishes; therefore, suckers can be valuable "canary" species that facilitate aquatic ecosystem conservation (Cooke et al. 2005).

Among suckers, redhorses *Moxostoma* spp. are widely distributed throughout the southeastern United States; however, many nongame redhorse species are imperiled and lack comprehensive management (Cooke et al. 2005). The Sicklefin Redhorse *Moxostoma* sp. is a rare, little-known, sucker species and is among the largest undescribed animals in North America. It is endemic to a relatively small geographic range comprised of only two southern Appalachian Mountain basins, the Hiwassee and Little Tennessee river systems of the upper Tennessee River drainage (Ohio River basin) in the Blue Ridge physiographic province of North Carolina and northern Georgia (Jenkins 1999). Historically, Sicklefin Redhorse likely inhabited a majority of large streams and rivers in the Hiwassee and Little Tennessee basins. Currently, the Sicklefin Redhorse is extant in less than 20% of each occupied basin (Jenkins 1999).

For imperiled species, knowledge of critical life history functions (e.g., spawning) is imperative to stem declining abundance trends and necessary to ensure population recovery and viability. Yet, Sicklefin Redhorse reproductive ecology has been only qualitatively described. The Sicklefin Redhorse is a colorful, medium-sized fish that has a deeply falcate (sickle-shaped) dorsal fin that is adapted to swift waters of moderate to high gradient. The species is potamodromous (i.e., migration entirely in freshwater: Myers 1949); adults ascend large tributaries to spawn from late April to mid-May in water temperatures from 10°C to 16°C (Jenkins 1999). Distinct from other redhorses, the Sicklefin Redhorse is strictly a roaming, troupe and pod-forming, gang-spawner. Males display no overt agonistic behavior during courting or spawning. Oviposition site (i.e., spawning location) preparation is absent, and females exhibit high fidelity for oviposition sites.

Several integrated environmental cues (e.g., water temperature and stream discharge) are believed to trigger mass spawning migrations for lotic potamodromous fishes (Kwak and Skelly 1992; Grabowski and Isely 2006; Fisk et al. 2015). Among anthropogenic changes, large river dams exact the most profound ecological consequences on migratory fishes (Waples et al. 2007). In addition to delaying and disrupting environmental cues of the spawning migration (Lucas and Baras 2001), hydroelectric dams can be migration barriers that decrease a species' geographic range (Holden 1979; Cooney and Kwak 2013). During the first half of the 20th century, extensive dam construction

occurred within the Hiwassee and Little Tennessee river systems (Etnier and Starnes 1993). Dams and resulting reservoirs fragmented populations, isolated gene pools, and drastically altered habitat previously inhabited by the Sicklefin Redhorse (Jenkins 1999).

Implementing sound management and conservation strategies for the Sicklefin Redhorse and other potamodromous fishes requires an understanding of current spatial and temporal movement and reach occupancy patterns. Our research objectives were to identify and describe Sicklefin Redhorse seasonal movement, reach occupancy, and behavior patterns (with a focus on reproductive behavior) to guide future management decisions. Characterization of seasonal movement patterns and reproductive ecology of this species may justify designating specific stream reaches for restoration, conservation, or reintroduction initiatives designed to improve the quantity and quality of the geographic range of the Sicklefin Redhorse.

## METHODS

*Study area.*—The upper Hiwassee River basin of the southern Blue Ridge Province in the southern Appalachian Mountains of western North Carolina and northern Georgia supports six species of redhorse and one of only two known Sicklefin Redhorse populations (Figure 1). The Hiwassee River is a highly regulated system that originates on the northwestern slopes of the Blue Ridge Mountains in northern Georgia (Figure 1). At the confluence of the Hiwassee and Valley rivers, the Hiwassee River drains approximately 1,092 km<sup>2</sup>. The Hiwassee River, from its origin to the Valley River confluence, is approximately 79.4 km long and has a maximum headwater elevation of 1,422 m. The confluence of the Hiwassee and Valley rivers is periodically inundated by Hiwassee Lake when reservoir levels are at full pool. Hiwassee Lake is impounded by the Hiwassee Dam, which was completed in 1940 for recreation, hydroelectric power generation, and flood control. Hiwassee Lake is a 2,464-ha, oligotrophic impoundment with 262 km of shoreline, a drainage area of 2,507 km<sup>2</sup>, a mean depth of 47 m, and hydraulic retention time of 116 d (NCDEQ 2002).

The Valley River, an unregulated Sicklefin Redhorse spawning stream, is a moderate gradient tributary of the upper Hiwassee River and drains approximately 303 km<sup>2</sup>. The Valley River is approximately 47.1 km long and has a maximum headwater elevation of 1,339 m at its origin in the Snowbird Mountains (Figure 1). The high-gradient watershed that encompasses the tributaries and headwaters of the Valley River is primarily composed of deciduous forest, while the lower Valley River is largely surrounded by agricultural land.

*Radiotelemetry.*—Twenty-five adult Sicklefin Redhorses were surgically implanted with radio transmitters

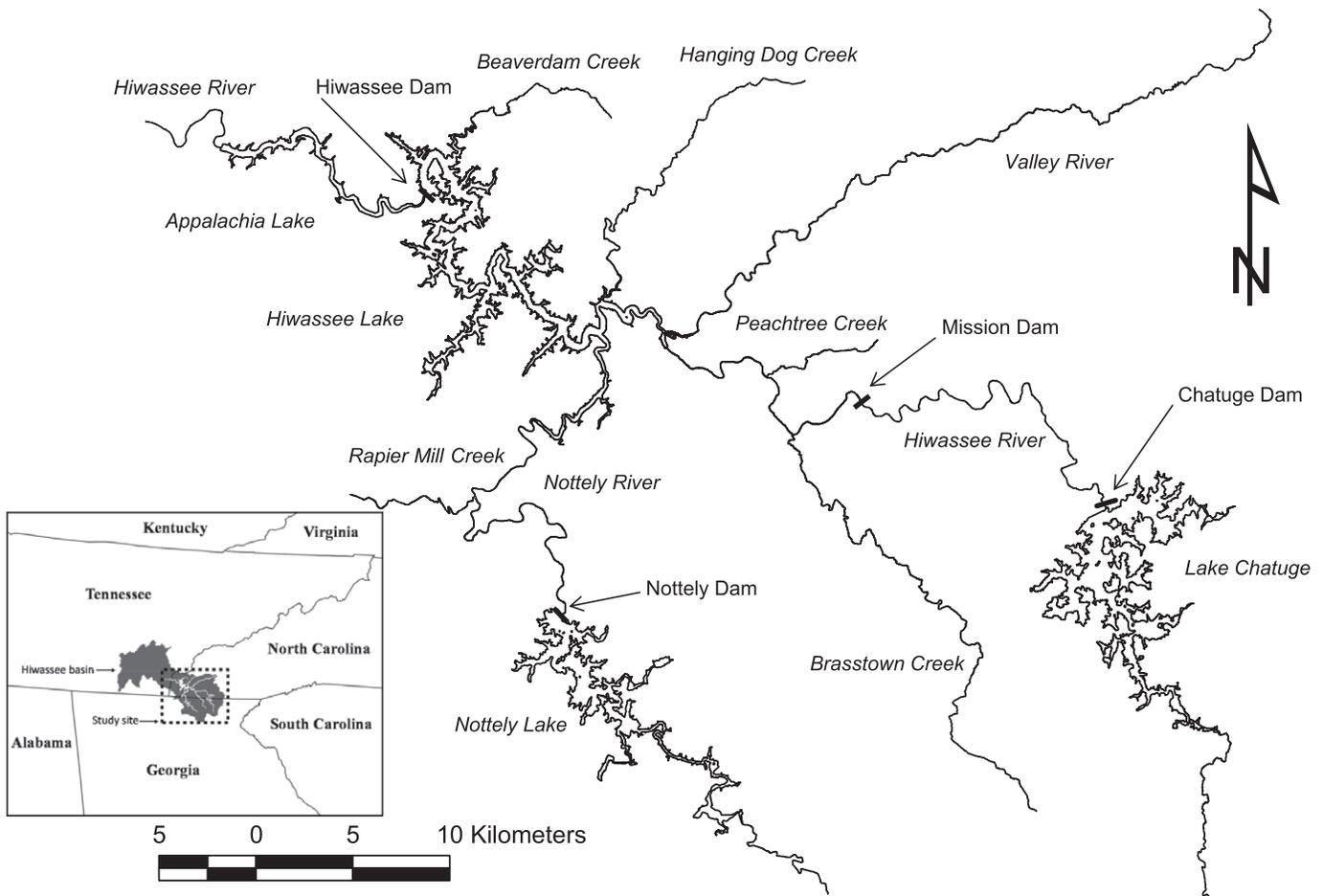


FIGURE 1. The upper Hiwassee River basin with the study area bounded downstream by the Hiwassee Dam and upstream by the Mission and Nottely dams.

(Advanced Telemetry Systems, model F1820) on March 30, March 31, and April 5 in 2006. An additional nine adults were radio-tagged on March 9 in 2007 (Table 1). Tagged fish were captured by boat electrofishing, using a Smith-Root 2.5 GPP electrofishing unit with pulsed DC current. Telemetered fish were captured from both the Hiwassee River and the Valley River to reduce capture location bias. For each adult, total length (TL, mm), weight (g), water temperature ( $^{\circ}\text{C}$ ), and capture location geographic coordinates (datum, projection; NAD83, universal transverse mercator) were recorded. Determination of sex was accomplished by gamete expression, percent tubercle development, and length of the inner portion of the pelvic fin (Jenkins 1999). Gamete expression was classified based on gamete maturation stage (i.e., not ripe, hard-squeeze ripe, slight-squeeze ripe, running ripe), and percent tubercle development was visually and tactilely estimated.

Fish weighing greater than 425 g were selected for tagging to ensure that tag burden did not exceed 2% of body

weight (Table 1; Winter 1996); mean tag burden was 0.7% (SE = 0.0003). Transmitters operated at frequencies of 48–49 MHz, with a 12-h/d duty cycle and signal emission rate of 34 pulses/min, and had a mean weight of 8.19 g (SE = 0.05) in air. Fish were exposed to benzocaine concentrations of 35–40 mg/L until fish experienced a loss of equilibrium and a reduced opercular rate was observed. Following the observation of stage 4 anesthesia (Summerfelt and Smith 1990) (mean = 4.5 min, SE = 0.17), a sterilized transmitter was inserted intraperitoneally through a 1.5-cm incision anterior to the pelvic girdle and offset 1.5 cm left of the ventral midline. The transmitter wire antenna was inserted into the body cavity to minimize mortality (Matheney and Rabeni 1995). The wire antenna included a 3-mm Scotchcast resin bead at the tip to prevent peritoneal irritation. After transmitter implantation, sterile, nonabsorbable, monofilament suture material (Monosof 3–0) with a 24-mm, 3/8 circle, reverse-cutting needle was used to close the incision. Mean total surgery time was 7.9 min (SE = 0.35). Following surgery, fish

TABLE 1. Characteristics of radio-tagged adult Sicklefin Redhorses from the Hiwassee River basin, North Carolina and Georgia, during 2006 and 2007. Transmitter frequencies presented in bold font represent tagged fish that did not survive the entire study.

Transmitter frequency (MHz)	Capture year	Capture stream	Spawning tributary	Sex	TL (mm)	Weight (g)	Number of relocations
48.041	2006	Hiwassee River	Hanging Dog Creek	Male	501	1,048	18
<b>48.101</b>	2006	Hiwassee River	Unknown	Male	466	902	0
<b>48.122</b>	2006	Hiwassee River	Hanging Dog Creek	Male	483	898	7
48.201	2006	Hiwassee River	Valley River	Female	496	1,068	24
48.221	2006	Valley River	Valley River	Male	454	786	26
<b>48.251</b>	2006	Valley River	Valley River	Male	436	768	0
48.271	2006	Valley River	Valley River	Female	505	1,270	15
<b>48.291</b>	2006	Valley River	Unknown	Male	505	1,120	0
48.352	2006	Valley River	Nottely River	Male	485	1,086	7
48.371	2006	Valley River	Brasstown Creek	Male	505	1,256	11
48.422	2006	Valley River	Valley River	Female	486	1,224	28
48.731	2006	Hiwassee River	Valley River	Male	510	986	15
48.751	2006	Valley River	Valley River	Male	460	934	17
48.771	2006	Valley River	Valley River	Male	501	1,082	22
48.791	2006	Valley River	Valley River	Female	512	1,228	24
48.811	2006	Hiwassee River	Valley River	Male	458	896	25
48.832	2006	Valley River	Valley River	Male	495	1,098	16
<b>48.851</b>	2006	Valley River	Unknown	Female	504	1,168	0
48.871	2006	Valley River	Valley River	Female	489	1,004	21
48.891	2006	Valley River	Valley River	Male	434	785	26
<b>48.911</b>	2006	Valley River	Valley River	Female	532	1,278	0
48.931	2006	Valley River	Valley River	Female	493	1,130	18
<b>48.951</b>	2006	Valley River	Valley River	Female	560	1,564	9
48.971	2006	Valley River	Valley River	Male	492	960	27
48.991	2006	Valley River	Valley River	Female	494	1,252	24
48.011	2007	Hiwassee River	Valley River	Female	541	1,300	12
48.031	2007	Hiwassee River	Valley River	Female	523	1,386	11
48.051	2007	Hiwassee River	Valley River	Male	479	993	10
48.071	2007	Hiwassee River	Brasstown Creek	Female	511	1,360	12
48.081	2007	Hiwassee River	Brasstown Creek	Male	553	1,588	7
48.122 <sup>a</sup>	2007	Hiwassee River	Unknown	Female	560	1,410	12
48.251 <sup>a</sup>	2007	Hiwassee River	Valley River	Male	550	1,396	13
48.911 <sup>a</sup>	2007	Hiwassee River	Unknown	Female	533	1,265	10
48.951 <sup>a</sup>	2007	Hiwassee River	Unknown	Female	472	993	12

<sup>a</sup>Transmitter from previous fish mortality reimplanted during 2007.

were placed into a tank containing aerated water until normal equilibrium and operculum rate were displayed (mean = 2.6 min, SE = 0.27). Following recovery, implanted fish were transferred to and held in a 2.12-m<sup>3</sup>, coated, wire-mesh, instream cage (mean = 3.2 h, SE = 0.16) to ensure postsurgery survival prior to release. Fish were tagged and released on the day of capture in the same stream reach where they were captured.

Following a 14-d postsurgical period to ensure normal behavior (Stasko and Pincock 1977), radio-tagged fish were relocated weekly during the spawning migration

period (April–June). Additional tracking occurred on October 12–13 in 2006, January 11–14 in 2007, and January 14–17 in 2008 to obtain postspawning and winter relocations.

Fish in the four stream reaches (Brasstown Creek [23.8 km], Hanging Dog Creek [14.4 km], Hiwassee River [17.1 km], Valley River [32.2 km]) were tracked by means of a canoe weekly in 2006. In addition, fish in Nottely River (24.0 km), Hiwassee Lake, and several smaller tributary streams were tracked by using a canoe and on foot during 2006 and 2007 (Favrot 2009). A total of 1,092

river kilometers (rkm) (for a total of 503 h) and 903 rkm (450 h) were tracked in 2006 and 2007, respectively. A total of 106 tracking sessions were conducted resulting in 264 and 215 relocations and 149 and 67 visual observations during 2006 and 2007, respectively.

We assumed that all tagged fish in streams tracked were detected based on shallow depths and narrow stream widths; however, this assumption was less justified for Hiwassee Lake due to extreme depths (Freund and Hartman 2002). Thus, on June 9, 2007, a radio transmitter was suspended from a buoy and deployed to a depth of 35 m at a location 100 m upstream from Hiwassee Dam (Figure 1). A strong signal was detected while conducting test tracking transects 100 m from the buoy, suggesting that our tracking methods would detect tagged fish from even the deepest areas of Hiwassee Lake.

Radio-tagged fish were relocated using an Advanced Telemetry Systems model R2100 receiver and a handheld loop antenna. Upon signal reception, the canoe was maneuvered to the stream bank and the precise fish location was determined using triangulation techniques. Trackers then attempted to visually observe undisturbed behavior (i.e., courting, spawning, foraging, resting, and migrating). Geographic coordinates were obtained using a hand-held global positioning system unit (Garmin GPS 5). Identical data were also obtained for any untagged and undisturbed adult Sicklefin Redhorses observed while radio-tracking.

*Spawning behavior, timing, and conditions.*—Observers used binoculars with polarized lenses to locate courting and spawning adult Sicklefin Redhorses. Upon observing reproductive behavior, identified depressions were categorized as either courting or spawning oviposition sites, and reproductive behavior was documented, quantified, and photographed or video recorded with associated GPS coordinates noted. Quantified reproductive behaviors included number of fish engaged, quivering duration time, pre-spawning and post-spawning behavior, and participating species.

Two modified two-way resistance board weirs were installed and monitored in the Valley River from April 15 to June 30, 2006, and from March 20 to June 9, 2007, to describe directional movement of Sicklefin Redhorses associated with spawning migration (Favrot 2009; Favrot and Kwak 2016). Weirs were located 11.8 km and 22.4 km upstream from the confluence of the Valley and Hiwassee rivers. Concurrent 24-h samples were collected from both weirs twice per week in 2006 and four times per week in 2007. For all Sicklefin Redhorses collected by weir, TL (mm), weight (g), sex, maturation stage, tubercle development, and migration direction (upstream or downstream) were recorded. Captured fish were released in the direction they were migrating.

In addition to measuring instantaneous water temperature at each fish location, continuous hourly water

temperature data were collected using HOBO Water Temp Pro version 2 Loggers (Onset Computer Corporation) from January 11, 2007, to January 11, 2008, from Hanging Dog Creek and Valley River (Figure 1). Daily water temperature data were also obtained for Hiwassee River (from January 1, 2006 to December 31, 2007) from the water treatment plant at Murphy, North Carolina. Valley River discharge data were acquired from U.S. Geological Survey gauging station 03550000 (available online at <http://waterdata.usgs.gov/nwis/uv?03550000>).

*Spatial analyses.*—Annual and seasonal linear home range estimates and median weekly linear ranges were calculated for all tagged fish (i.e., the stream distance between the downstream-most and upstream-most locations) using methods similar to those described by Vokoun (2003). Median weekly linear ranges were directionally categorized as either upstream or downstream movement. Fish location coordinates were imported into ArcView 9.2. The thalweg was then delineated using a flow line data layer from the National Hydrology Dataset obtained from the U.S. Geological Survey (available online at <http://viewer.nationalmap.gov/viewer/nhd.html?p=nhd>). Four thalweg data layers composed of one of the spawning tributaries and the Hiwassee River were created for subsequent manipulation using shareware arcscripts Add Points Evenly Along a Line (Lead 2002) and Nearest Neighbor 3.1 (Weigel 2002). Points, spaced 10 m apart, were added to each thalweg data layer beginning at the headwaters of each spawning tributary, and the nearest 10-m point to each fish location was identified using Nearest Neighbor 3.1. The accumulation of 10-m thalweg points was used to calculate total linear stream distance between relocation points.

Between years (2006 and 2007), annual and seasonal linear home ranges were compared using the Mann–Whitney rank-sum test. For each year, seasonal linear home ranges were compared using a Kruskal–Wallis nonparametric ANOVA test with a post hoc Dunn’s test for multiple comparisons. Between years, seasonal and annual median weekly movements (upstream and downstream) were compared using the Mann–Whitney rank-sum test. For each year and in aggregate, spawning season upstream and downstream median weekly movements were compared using the Mann–Whitney rank-sum test. For each year and in aggregate, spawning and post-spawning season upstream and downstream median weekly movements were compared using the Mann–Whitney rank-sum test (Zar 1996).

Relocations for radio-tagged Sicklefin Redhorses were segregated by sex and then the number of days residing within a spawning tributary was determined. Spawning tributary residence times were subsequently enumerated and stratified into 20-d intervals by sex, and differences were tested between sexes using a Kolmogorov–Smirnov

(KS) two-sample test. Sicklefin Redhorse behavior was classified as occurring during the spawning season or nonspawning period (i.e., postspawning season and winter). A likelihood-ratio chi-square test was performed comparing spawning and nonspawning period behaviors (i.e., foraging, resting, courting, spawning, and migrating). Statistical software packages SAS/STAT 9.1 (SAS Institute 2003) and SigmaPlot version 12.5 (SYSTAT Software 2008) were used to conduct all statistical analyses. A significance level ( $\alpha$ ) of 0.05 was applied to all statistical tests.

## RESULTS

### Radiotelemetry and Two-Way Weirs

In 2006 and 2007, 34 adult Sicklefin Redhorses were implanted with radio transmitters during early spring. From March 30 to April 5, 2006 (water temperature = 14–15°C), 25 adults (15 males, 10 females) were tagged from lower Valley and Hiwassee rivers just upstream from Hiwassee Lake (Table 1). Males had a mean TL of 479.0 mm (SE = 6.6) and mean weight of 973.7 g (SE = 36.4); females had a mean TL of 507.1 mm (SE = 7.2) and a mean weight of 1,218.6 g (SE = 47.8). Male mean tubercle development was 61.0% (SE = 4.6), and females displayed no tubercles. One male fish expressed milt when slightly squeezed, and no females were ripe. On March 9, 2007 (water temperature = 10°C), nine adults (three males, six females) were tagged from the middle Hiwassee River (Table 1). Males had a mean TL of 527.3 mm (SE = 24.2) and a mean weight of 1,325.7 g (SE = 175.3); females had a mean TL of 523.3 mm (SE = 12.3) and a mean weight of 1,285.7 g (SE = 62.5). Male mean tubercle development was 50.0% (SE = 5.8), and females had a mean tubercle development of 8.3% (SE = 8.3). Gamete expression was absent for all adults tagged in 2007.

In 2006, seven (28%) mortalities occurred, and none were observed in 2007 (Table 1). Of the seven mortalities, three occurred in Valley River, three occurred downstream from the confluence of the Hiwassee River and Valley River, and one occurred in Hanging Dog Creek. All tags were recovered, except for those in the Hiwassee River as this reach was impounded after tags were implanted into the fish in 2006. The three mortalities that occurred in the Hiwassee River were assumed as these tags were stationary throughout the study. Not all adults were relocated every week due to the large number and length of streams tracked during this study (Favrot 2009); however, all adults were regularly accounted for during this study.

During 2006, 17 adults made upstream spawning migrations; 14 migrated up the Valley River, two ascended Hanging Dog Creek, and one migrated up Brasstown Creek. In 2007, 12 (66.7%) of the remaining 18 adults from 2006

conducted a spawning migration; 10 ascended Valley River, one migrated up Hanging Dog Creek, and one ascended the Nottely River. Adults that conducted spawning migrations in 2006 and 2007 ascended the same tributary both years. Of the nine adults tagged in 2007, six (66.7%) conducted a spawning migration and three remained in the Hiwassee River for the remainder of the study (Table 1). Of the six migratory adults, four ascended Valley River, and two ascended Brasstown Creek (Table 1).

Weir catches for Sicklefin Redhorses varied between locations and years. During 2006 and 2007, our weirs were effective at sampling immigrating fish, but not effective at sampling emigrating fish. In 2006, 19 Sicklefin Redhorses were captured migrating upstream at each weir (38 total). The female : male sex ratio of fish from the downstream weir was biased toward females (3.8:1), while that in the upstream weir was biased toward males (1:2.2). In 2007, 201 Sicklefin Redhorses were captured in the downstream weir and 28 in the upstream weir. At both weirs, the female : male sex ratio was biased toward females (downstream: 2.7:1, upstream: 2.1:1). During both years, immigrating females were typically larger than males. In 2006, immigrating males exhibited a mean TL of 481.7 mm (SE = 6.0, range = 430.0–520.0 mm) and mean weight of 955.7 g (SE = 26.3, range = 722.0–1,151.0 g). Females had a mean TL of 528.3 mm (SE = 6.1, range = 465.0–580.0 mm) and mean weight of 1,317.0 g (SE = 35.8, range = 1,058.0–1,778.0 g). In 2007, males exhibited a mean TL of 498.5 mm (SE = 3.2, range = 421.0–562.0 mm) and mean weight of 1,092.6 g (SE = 20.0, range = 746.0–1,649.0 g). Females had a mean TL of 522.5 mm (SE = 1.9, range = 462.0–604.0 mm) and mean weight of 1,341.4 g (SE = 15.3, range = 949.0–2,122.0 g).

Adult Sicklefin Redhorses exhibited similar mean weekly percent tubercle development and maturation stages during 2006 and 2007; however, females developed tubercles later in 2007 than in 2006 (Figure 2). Males exhibited 60–80% tubercle development by late March and early April and maturation stages ranging from slight-squeeze ripe to running ripe during mid-April. Male mean weekly tubercle development peaked in mid to late April and then sharply declined during May, whereas maturation stage peaked during late April to mid-May (Figure 2). Female mean weekly tubercle development peaked during early April in 2006, whereas peaking occurred during early May in 2007. Female mean weekly maturation stage was considerably less (not ripe to hard-squeeze ripe) than that in males; however, similar to males, maturation peaked in mid to late April (Figure 2). Between 2006 and 2007, water temperature variation coincided with the tubercle development disparity exhibited by females (Figure 2).

Within the Hiwassee River basin, we identified four spawning tributaries via radiotelemetry techniques (Valley

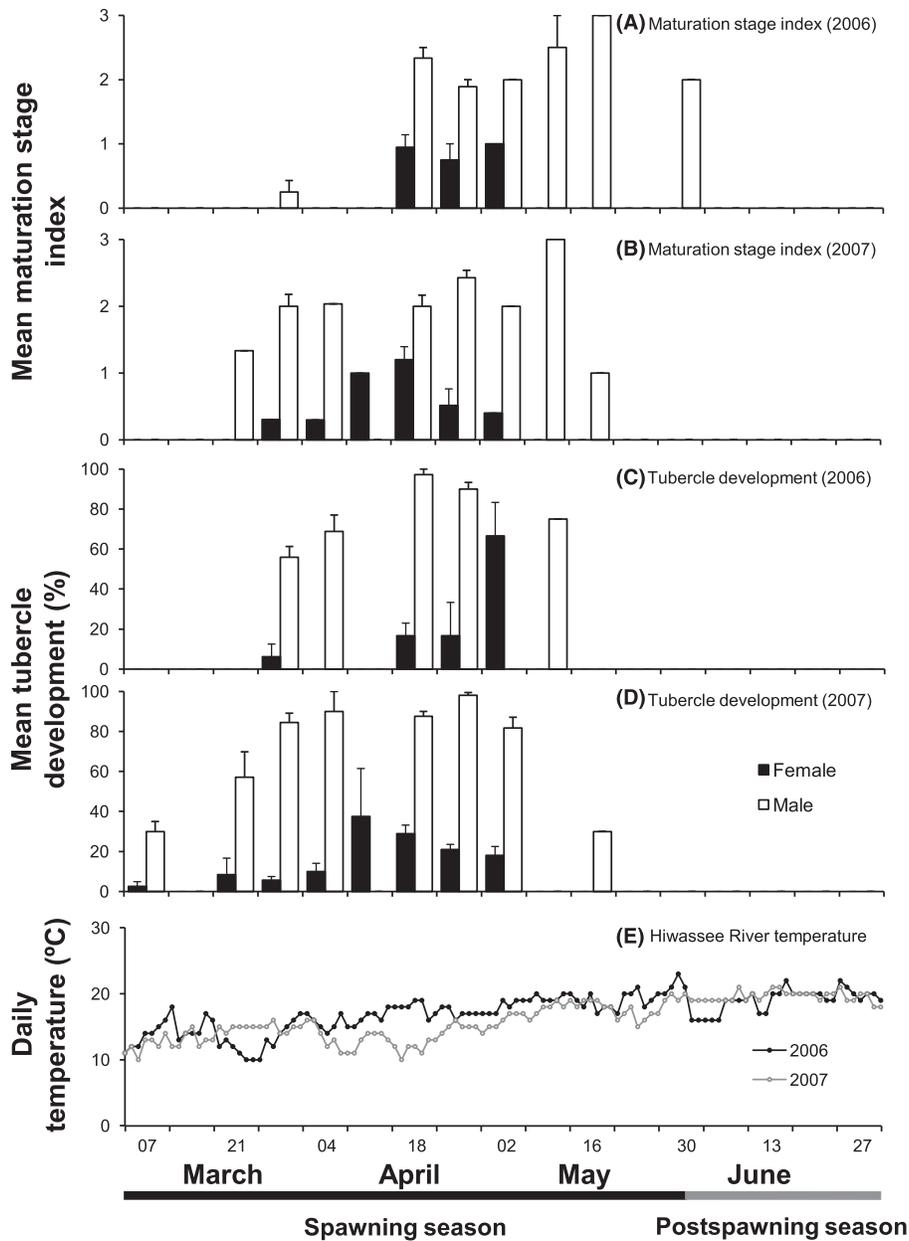


FIGURE 2. (A, B) Mean weekly maturation stage index (not ripe = 0, hard-squeeze ripe = 1, slight-squeeze ripe = 2, and running ripe = 3) and (C, D) percent tubercle development for Sicklefins Redhorses captured in 2006 and 2007. Error bars represent SE. (E) Hiwassee River water temperature is provided for comparison.

River, Brasstown Creek, Hanging Dog Creek, and Nottely River; Figure 3). No spawning was observed in the Hiwassee River; however, the Hiwassee River was intensively occupied during the postspawning and winter seasons. From these five streams and rivers, temporal patterns associated with spawning, tubercle development, maturation stage, and movement patterns discerned from weir and radiotelemetry data were integrated to delineate discrete functional seasons. Spawning season (reproductive migration through spawning) began on March 1 and

ended on May 31, postspawning season was June 1 to November 15, and winter season spanned November 16 to February 29.

#### Linear Home Range and Movement Patterns

Annual and seasonal linear home-range estimates were not significantly different between 2006 and 2007 (Mann-Whitney test:  $U \geq 23.0$ ;  $N_1 \geq 9$ ,  $N_2 \geq 10$ ;  $P \geq 0.079$ ), with the exception of the postspawning season ( $U = 25.5$ ;  $N_1 = 17$ ,  $N_2 = 18$ ;  $P < 0.001$ ). Linear home-range estimates

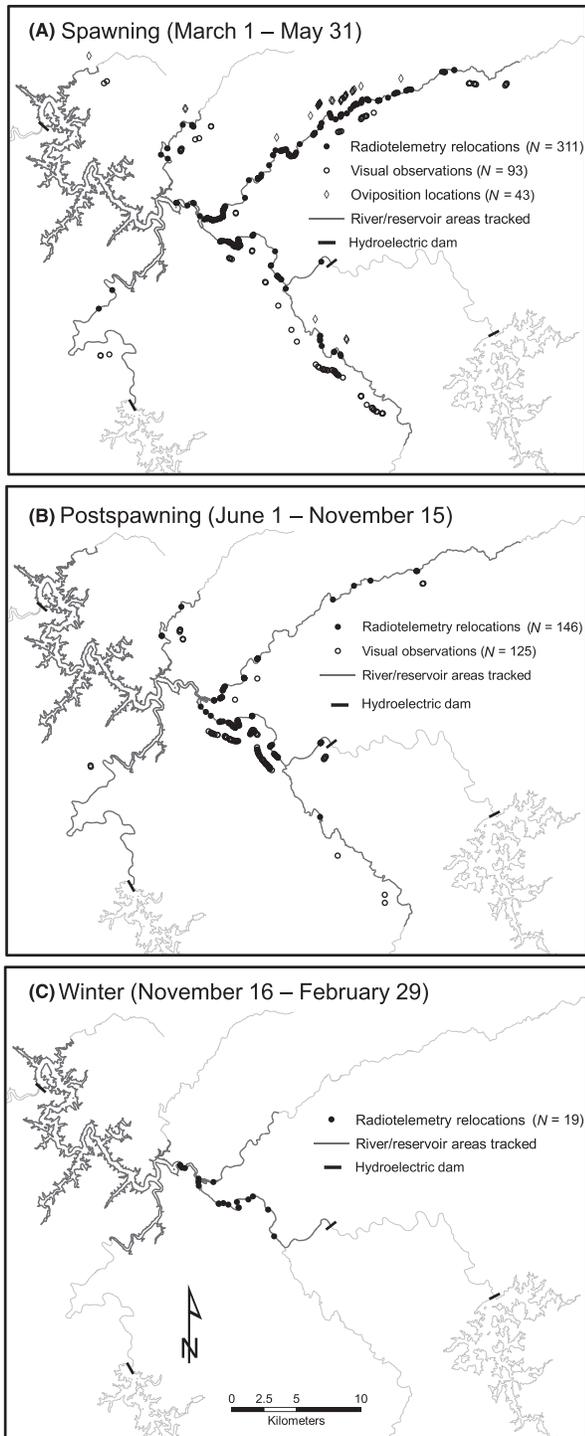


FIGURE 3. Seasonal maps characterizing Sicklefins Redhorse relocations, visual observations, and courting–spawning visual observations for the Hiwassee River basin, North Carolina and Georgia, during 2006 and 2007. Stream, river, and reservoir reaches tracked are denoted with a dark line, while water bodies not tracked are depicted with a gray line. To reduce symbol overlap, radiotelemetry relocation symbols are positioned directly on the stream line, oviposition location symbols are offset north of the stream, and visual observation symbols representing undisturbed adult Sicklefins Redhorse locations are offset south of the stream.

were, however, different among seasons (Kruskal–Wallis test:  $H = 48.18$ ,  $df = 2$ ,  $P < 0.001$ ). Spawning season linear home-range estimates were greater than those from postspawning and winter seasons (Dunn's test:  $Q \geq 4.05$ ,  $P < 0.05$ ); however, postspawning and winter linear home ranges were not significantly different (Dunn's test:  $Q = 6.77$ ,  $P \geq 0.05$ ). Rare high postspawning and winter linear home-range estimates reflected movement to postspawning and overwintering reaches; after the initial relocation, high site fidelity was apparent upon occupancy of postspawning reaches.

Median annual linear home range was slightly greater than that of the spawning season (Table 2). Specifically, 34 (85%) spawning-season, linear home-range estimates were greater than 5.0 km, 14 (35%) were greater than 20 km, and four (10%) were greater than 29 km. Despite significantly greater linear home ranges during the spawning season, relocations indicated high mobility prior to occupancy of spawning areas (i.e., early March), site fidelity following occupancy of spawning reaches (i.e., mid-March–May), and high mobility after spawning areas were abandoned (i.e., late April to late May).

Median postspawning linear home range was low (Table 2). However, four fish occupied postspawning-season linear home ranges greater than 11 km, suggesting delayed emigration from spawning areas. After excluding fish that exhibited prolonged occupancy in spawning tributaries, maximum postspawning linear home range was 4.5 km. Winter median linear home range was intermediate (Table 2), indicating movement from postspawning to overwintering reaches. Twelve fish occupied winter home ranges greater than 1 km, and five fish exhibited a winter linear home range that exceeded 5 km.

During winter 2006, 17 of 18 tagged fish were relocated during mid-January; 16 were in the Hiwassee River, and one was in lower Valley River. Of the 16 fish occupying the Hiwassee River, four (25%) were located 2.5 km downstream from the confluence of the Hiwassee and Valley rivers. The location of these four fish was precisely where the Hiwassee River transitioned to a lentic reservoir habitat that winter (Figure 3).

Seasonal median weekly directional movements (i.e., upstream and downstream) were not significantly different between years (Mann–Whitney test:  $U \leq 1,366.5$ ;  $N_1 \geq 10$ ,  $N_2 \geq 57$ ;  $P \geq 0.244$ ); however, annual median weekly directional movements were significantly different between years ( $U \geq 3,217.5$ ;  $N_1 \geq 73$ ,  $N_2 \geq 95$ ;  $P \leq 0.023$ ). Annual and aggregated, spawning-season, median weekly directional movements were not significantly different ( $U \leq 5,852.5$ ;  $N_1 \geq 37$ ,  $N_2 \geq 51$ ;  $P \geq 0.444$ ). Annual and aggregated, postspawning-season, median weekly directional movements were significantly less than those from the spawning season ( $U \geq 209.5$ ;  $N_1 \geq 10$ ,  $N_2 \geq 57$ ;  $P \leq 0.024$ ).

TABLE 2. Annual and seasonal median, mean, SE, and minimum and maximum limits of linear home ranges for radio-tagged Sicklefin Redhorses during 2006 and 2007 in the Hiwassee River basin, North Carolina and Georgia.

Season	<i>N</i>	Median linear home range (km)	Mean linear home range (km)	SE (km)	Range (km)
Annual	40	19.4	18.8	1.72	0.37–46.3
Spawning	40	17.8	16.8	1.60	0.20–40.5
Postspawning	35	0.1	2.5	0.98	0.00–25.1
Winter	19	3.4	3.6	0.89	0.06–13.6

The annual, median weekly directional movement of Sicklefin Redhorses was 0.1 km (Table 3). Weekly maximum upstream movement was 21.1 km, and maximum downstream weekly movement was 30.5 km (Table 3). Annual weekly directional movement estimates suggest that Sicklefin Redhorses exhibited high site fidelity throughout the year, except during migrations to occupy spawning and overwintering areas.

Estimates of spawning-season, median, weekly, directional movements were greater than both annual and postspawning estimates (Table 3). Specifically, weekly estimates revealed that 34% and 22% of adults migrated upstream and downstream more than 1 km, respectively. Estimates of postspawning-season, median, weekly, directional movements were less than both spawning and annual estimates (Table 3), indicating high site fidelity behavior during occupancy of the Hiwassee River and lower reaches of occupied spawning tributaries.

Multiple adults appeared to transition between two spawning areas within a season. For example, one female consistently occupied a specific riffle 29.4 km upstream from the Valley River mouth from April 23 to May 18, 2006, but relocated to a riffle 900 m upstream on May 11 and again on May 26 before emigrating to the Hiwassee River before June 2.

Seven fish that conducted two annual spawning migrations in 2006 and 2007 used spawning areas associated with the same stream reach in both years. On average, spawning areas occupied in 2007 were 2.27 km (SE = 1.01, range = 0.20–7.59 km) from those used in 2006. Following occupancy of a spawning area, reduced movement occurred until emigration to the Hiwassee River or lower spawning tributary reaches; mean linear movement while occupying spawning areas was 1.04 km (SE = 0.20, range = 0.02–3.90 km). Similarly, following occupancy of postspawning reaches, site fidelity was high; mean linear movement while occupying postspawning sites was 0.14 km (SE = 0.04, range = 0.01–1.58 km). On average,

TABLE 3. Weekly annual and seasonal median, mean, SE, and range estimates of directional movements (i.e., upstream or downstream) for radio-tagged Sicklefin Redhorses during 2006 and 2007 in the Hiwassee River basin, North Carolina and Georgia.

Direction	<i>N</i>	Median distance (km)	Mean distance (km)	SE	Range (km)
Annual					
Upstream	189	0.09	1.47	0.24	0–21.13
Downstream	197	0.09	2.00	0.35	0–30.47
Spawning					
Upstream	76	0.31	2.12	0.39	0–16.30
Downstream	75	0.15	2.75	0.71	0–30.47
Postspawning					
Upstream	107	0.04	1.00	0.31	0–21.13
Downstream	108	0.06	1.20	0.35	0–21.80

postspawning sites used in 2007 were 0.23 km (SE = 0.17, range = 0.00–1.60 km) from those used in 2006.

Male and female residence times in spawning tributaries were significantly different (KS test:  $D = 0.6349$ ,  $P = 0.0035$ ). Females briefly occupied spawning tributaries, while males exhibited extended spawning-tributary occupancy before returning to the lower Hiwassee River during winter. During 2006 and 2007, males spent a mean of 108 d (range = 0–289 d) occupying spawning tributaries; females spent a mean of 35 d (range = 0–290 d). In total, one (7.1%) male and five (27.8%) females did not undertake a spawning migration in either 2006 or 2007. However, all males conducted at least one spawning migration; whereas, three (16.7%) females were never observed in a spawning migration.

### Movement, Spawning, and Environmental Conditions

Spawning season fish movement appeared to be associated with increased discharge (Figures 4 and 5). In 2006, adults occupying the upper Valley River abandoned spawning reaches and returned to the Hiwassee River during three separate discharge pulses (Figure 4). Similarly, during late March to mid-April 2007, radiotelemetry and weir data revealed that the spawning immigration rate increased and was associated with peaks in discharge (Figures 4 and 5).

During late February to early July 2006, the Hiwassee River basin experienced normal to moderate drought conditions; however, during 2007, moderate to extreme drought conditions occurred (data available online at [http://www.ncwater.org/Drought\\_Monitoring/](http://www.ncwater.org/Drought_Monitoring/)). Discharge in the Hiwassee River basin and specifically that in the Valley River was significantly lower during 2007 (mean = 2.6 m<sup>3</sup>/s, range = 0.5–27.1 m<sup>3</sup>/s) than in 2006 (mean = 3.7 m<sup>3</sup>/s, range = 0.9–30.9 m<sup>3</sup>/s;  $t = 4.68$ ,  $df = 617$ ,  $P < 0.0001$ ). Low discharge was associated with reduced

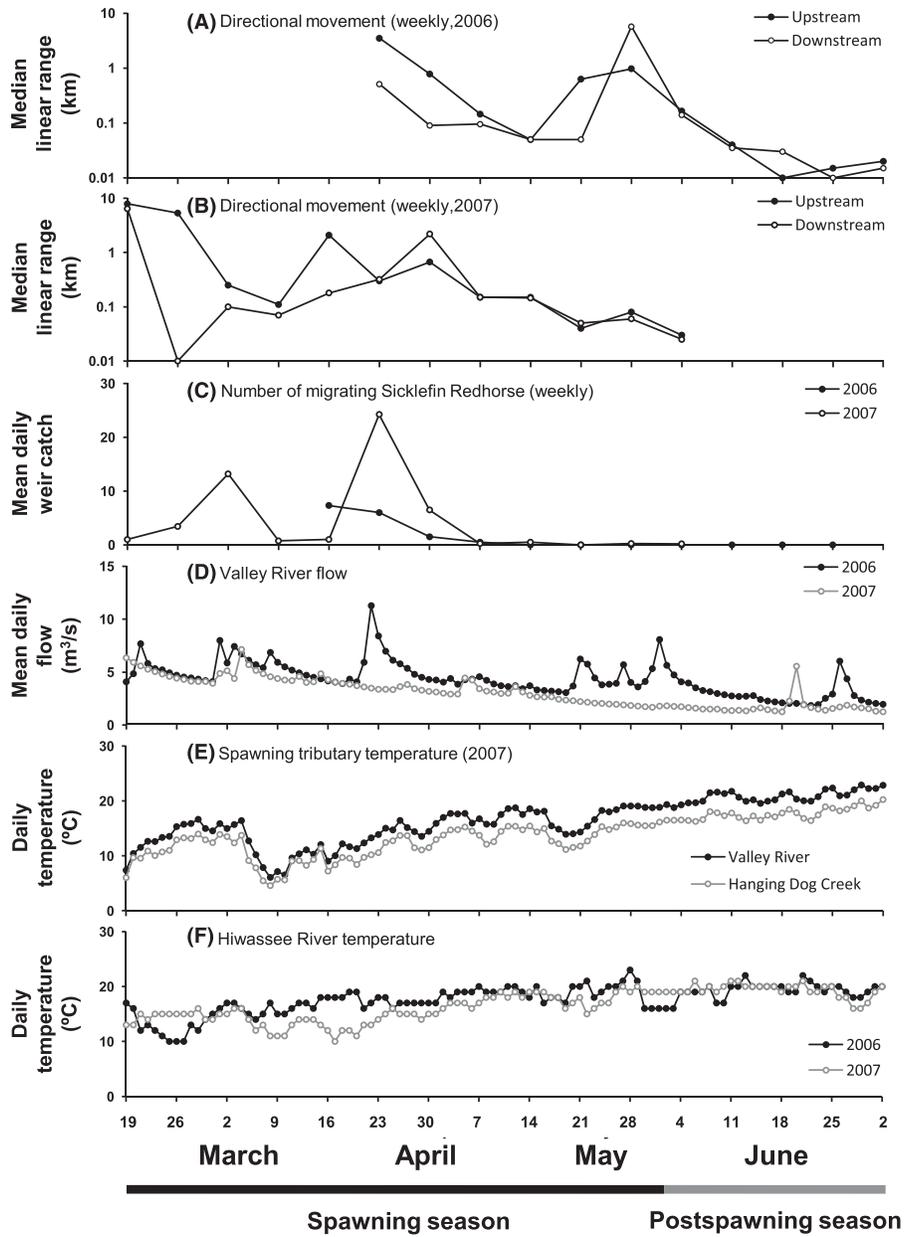


FIGURE 4. (A, B) Spawning-season median weekly linear range and (C) mean daily trapped migratory Sicklefins Redhorses per week in the Hiwassee River basin during 2006 and 2007. (D) Discharges and (E, F) water temperatures are provided for comparison.

spawning-tributary occupancy time. Generally, adults occupied spawning tributaries considerably longer during 2006 than in 2007 (Figure 4). Emigration during low-flow conditions in 2007 was not associated with discharge peaks (Figures 4 and 5). Low spawning-tributary discharge was associated with reduced migration occurrence during the spawning season. During relatively high discharge in 2006, 1 of 20 (5%) radio-tagged adults did not ascend a spawning tributary, but 5 of 27 (18.5%) adults did not ascend a spawning tributary during relatively low discharge in 2007.

Low discharge was associated with adults spawning in lower portions of tributaries. The Valley River spawning migration distance was shorter during 2007 low discharges, which were associated with severe and extreme drought conditions. In 2007, downstream weir catch was considerably greater compared with temporally similar upstream weir catch (Figure 5). Moreover, both weirs (upstream and downstream) collected identical numbers of immigrating adults during 2006; however, during low discharges in 2007, the upstream weir caught 86.1% fewer

immigrating adults than did the downstream weir (Figure 5).

During late March and early April 2006, Sicklefin Redhorses were staging or beginning upstream spawning migrations coinciding with water temperatures of 14.0–15.0°C. Average daily water temperatures during the spawning season ranged from 14.0°C to 17.0°C, while instantaneous water temperatures ranged from 9.0°C to 20.2°C. During 2007, the spawning migration commenced during late March when the water temperature was 12.5°C (Figure 5). During 2006 and 2007, the spawning migration concluded during early May and coincided with water temperatures ranging from 16.1°C to 17.5°C (Figure 5). Most adults emigrated from spawning tributaries considerably earlier during 2007 (late April) than in 2006 (early June); however, emigration-period mean weekly water temperatures were similar between years (18.4°C in 2006, 18.7°C in 2007; Figure 4). Mean weekly water temperatures in the postspawning season were similar between years (19.8°C in 2006, 21.5°C in 2007). During winter, emigration to the lower Hiwassee River was associated with decreasing water temperatures. Mean weekly water temperatures during mid-January were 8.6°C in 2006 and 5.5°C in 2007.

For all ( $N = 43$ ) observed spawning and courting acts, mean water temperature was 17.4°C (range = 11.0–21.1°C), and mean time of day was 15:44 hours (range = 11:13–21:30 hours). During the spawning season, unseasonably cold water appeared to interrupt Sicklefin Redhorse spawning migrations. In early April 2007, a cold front passed through the study area and revealed a possible water temperature threshold (>10°C) for Sicklefin Redhorse spawning immigration. Prior to unseasonably cold water temperatures (March 25 to April 5), mean hourly water temperature was 16.1°C when adults were ascending spawning tributaries; however, during the cold front, mean water temperature decreased to 9.3°C, temporarily terminating immigration (Figures 4 and 5). During the cold front, numerous (>50) Sicklefin Redhorses were observed motionless in the downstream margin of calm deep pools with numerous congenics (>200; Black Redhorse *M. duquesnei*, Golden Redhorse *M. erythrurum*, River Redhorse *M. carinatum*, Silver Redhorse *M. anisurum*, and Smallmouth Redhorse *M. breviceps*). Moreover, two (14.3%) radio-tagged fish that had previously commenced an upstream spawning migration in the Valley River reoccupied the Hiwassee River following declining water temperatures. During 2007, weir catch also demonstrated a spawning immigration delay associated with unseasonably cold water. Before the cold front (March 25 to April 5), 85 (42.3%) adults were captured. During the cold front, three (1.5%) adults were captured, and after the cold front (April 13 to May 4) when mean water temperature was 15.0°C, 113 (56.2%) adults were captured (Figures 4 and 5).

Similarly, spatially disproportional occupancy was observed in the Nottely River, where a cold hypolimnetic discharge occurred downstream of Nottely Dam. Water temperature directly below Nottely Dam was 13.0°C on June 22, 2006, and 11.1°C on April 29, 2007. During June 2006, numerous (>100) adult Sicklefin Redhorses were observed 22 rkm downstream from Nottely Dam (water temperature, 15.3°C), whereas adults were not observed in colder upstream hypolimnetic releases. During April 2007, several (<25) Sicklefin Redhorses (including one radio-tagged adult) were observed 8 rkm downstream of Nottely Dam (water temperature, 14.4°C), but none were observed farther upstream in unseasonably cold water.

Other than during spawning migrations, tagged adults avoided the lentic waters of Hiwassee Lake. During 2006, the lower 1.6 km of the Valley River and lower 2.3 km of the Hiwassee River were inundated by Hiwassee Lake, and tagged fish were not observed occupying these reaches. Following the 2006 spawning season, six adults remained in the lower Valley River and occupied lotic reaches just upstream (50–100 m) from Hiwassee Lake. Due to low flow, the confluence of the Valley and Hiwassee rivers was not inundated in 2007. Adults were not relocated within the extreme lower reaches of the Valley River during the postspawning season in 2007, suggesting that an elevated Hiwassee Lake may have isolated adult Sicklefin Redhorses and prevented them from returning to the Hiwassee River in 2006.

## Behavior

Visually documented behaviors during spawning and nonspawning periods were significantly different ( $\chi^2 = 94.7985$ ,  $df = 4$ ,  $P < 0.0001$ ), but foraging behavior was prevalent during both periods. During the spawning season (March 1 to May 31), 47.1% of our observations were of foraging, while 22.1% and 17.2% were of courting and spawning acts, respectively. Resting behavior was ascribed to 12.3% of spawning-season observations, but migration behavior was rarely observed. During the nonspawning period (June 1 to February 29), 87.0% of observations were of foraging behavior. Similar to the spawning season, 12.2% of observations in the nonspawning period were of resting behavior.

Of 31 spawning acts (i.e., quivering) from which behavior could be quantified, 29 were in the Valley River, one in Brasstown Creek, and one in Hanging Dog Creek. Of eight courting acts quantified, six occurred in the Valley River, one in Hanging Dog Creek, and one in Beaverdam Creek. The mean number of individuals engaged in courting was 11.8 (SE = 2.43, range = 2–20), and a mean of 3.8 individuals (SE = 0.43, range = 2–15) were engaged in spawning acts. Mean duration of quivering was 6.4 s (SE = 0.66, range = 3–15 s). No agonistic behavior was

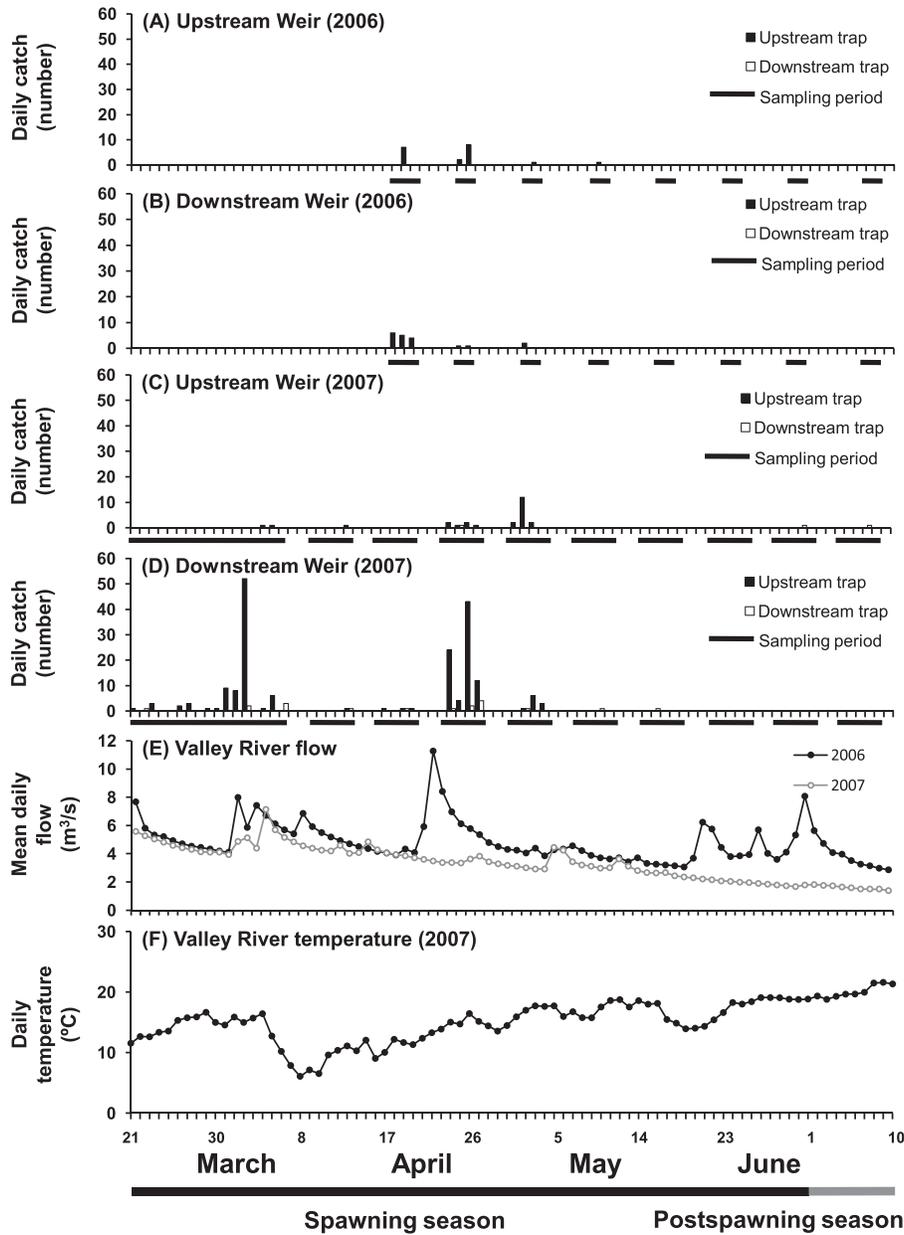


FIGURE 5. (A–D) Spawning-season two-way resistance board weir daily directional catch for Sicklefin Redhorses in 2006 and 2007. (E) Valley River discharges are provided for comparison. Sampling periods are denoted by darkened x-axis segments.

observed from males; however, on numerous occasions, a presumed smaller male was seen quickly swimming into and past a troupe of quivering adults, which terminated the spawning act. During the single (5.9%) courting act observed in Beaverdam Creek, two Sicklefin Redhorses were courting with a Black Redhorse troupe ( $N = 10$ ). On three (9.7%) occasions, a single Black Redhorse was observed spawning with a Sicklefin Redhorse troupe.

Site preparation by spawning Sicklefin Redhorses was not observed. Adults used several oviposition sites within a relatively small area (~9–12 m<sup>2</sup>). Before spawning

sessions, females typically held motionless on substratum directly downstream from an oviposition site. On five occasions, an adult Sicklefin Redhorse was observed breaking the surface water displaying behavior similar to surface foraging. This behavior was observed only during the spawning season and in spawning tributaries. Typically, a spawning trio (i.e., one centralized female and two flanking males) was observed spawning. However, on three (9.7%) occasions, only two fish (i.e., one male and one female) were observed during quivering, and on two (6.5%) occasions supernumerary males (>10) were

observed joining a spawning trio following quivering initiation.

We observed pod- or troupe-forming behavior at spawning areas between quivering sessions. Pods were usually roaming, as a collective unit, within slack and deeper water downstream from raised large boulders. Pods were tightly formed, exhibiting complex and organized movement behavior, and appeared to be composed of numerous (10–15) smaller males that were slowly swarming around and gently nudging a single larger female. Typically, male fish, but no females, were observed foraging immediately downstream from and within the oviposition site following spawning acts.

During all spawning acts, adults remained mostly parallel to flow; however, a substantial silt plume was present during all quivering acts. For 8 of 31 (25.8%) observed spawning acts, a secondary body undulation in females occurred (postspawning digging), which was distinctly different from quivering. Following quivering, the female promptly returned to the oviposition site and forcefully thrashed its caudal and anal fins against the substrate immediately upstream from the oviposition site while rapidly advancing upstream. This behavior started at the oviposition site and progressed upstream for approximately 0.5–2.0 m. Mean elapsed time between repeated postspawning digs, for which video recordings were obtained ( $N = 18$ ), was 101.1 s (SE = 20.8, range = 17–245 s). These postspawning digs occurred for 1–2 h after quivering.

## DISCUSSION

Through a combination of multiple field techniques, including radiotelemetry, two-way resistance board weirs, and direct visual observations, we were able to determine spatial and temporal bounds of the spawning migration, quantify seasonal weekly movement patterns, and characterize seasonal and spawning behavior of an undescribed, rare, imperiled, potamodromous sucker species, the Sicklefins Redhorse. Each technique provided complementary data and observations toward the first comprehensive and quantitative study of this species' reproductive ecology. This type of intensive study and associated findings substantially advance our understanding of these fish behaviors over previous qualitative and anecdotal observations and are critical to guide conservation and management of this and other fish species for which little is known.

### Spatiotemporal Occupancy and Movement

Using biotelemetry, we documented several spawning tributaries within the the Hiwassee River basin; however, with few exceptions, a small portion of the Hiwassee River (17.1 km) was occupied most of the year (summer,

fall, and winter). Other redhorse populations also occupy a small or rare critical habitat; the Robust Redhorse *M. robustum* population in the Savannah River, Georgia, is restricted to spawning at two main-channel shoals (Grabowski and Isely 2006). River basins with a high degree of habitat complementarity and interconnectivity support more robust populations (Kim and Lapointe 2011), while narrowly confined habitat use could increase population vulnerability to a catastrophic event (Copeland et al. 2014). High occupancy of the Hiwassee River during non-spawning periods, coupled with the isolation and small size of the Hiwassee River between Mission Dam and Hiwassee Lake, may function as an ecological bottleneck on the Sicklefins Redhorse population in the Hiwassee River basin.

Adult Sicklefins Redhorses were not detected in Hiwassee Lake; however, several adult Sicklefins Redhorses migrated through the lake to ascend spawning tributaries. In addition, a considerable proportion of the adult Sicklefins Redhorse population in the Hiwassee River basin conducted downstream winter migrations, but this migration appeared to be limited by the lentic habitat of Hiwassee Lake. Our inability to document an adult Sicklefins Redhorse occupying impounded reaches of Hiwassee Lake accords with the serial discontinuity concept (Ward and Stanford 1983), which suggests that dams have the potential to impose a longitudinal shift on physical parameters (e.g., stream velocity) or biological phenomena (e.g., species abundance). Similarly, Miranda and Dembkowski (2016) reported that numerous rheophilic species (including *Moxostoma* spp.) exhibited decreased abundance as several Tennessee River reservoirs transitioned from riverine to lacustrine habitat.

In addition to reducing the longitudinal distribution of rheophilic species, hydroelectric dams physically fragment habitat. In general, habitat fragmentation is detrimental to population persistence (Wilcox and Murphy 1985). Fish species with a limited physiographic range that display migratory behavior or are ecologically specialized are at an elevated risk for extirpation or extinction as a result of an exacerbated vulnerability to reduced numbers, fragmentation, and isolation (Angermeier 1995). Genetic, demographic, and environmental stochasticity have profound effects on species constrained to small and fragmented geographic ranges, resulting in an elevated probability of extinction and reduced species richness (Shaffer 1981; Lande 1988; Reid et al. 2008a).

Fragmented small populations tend to have fewer alleles in their gene pools, rendering such populations less adaptive to environmental change and more susceptible to extirpation (Primack 1993). Catostomid allelic richness decreases in highly fragmented river reaches compared with free-flowing rivers (Bessert and Ortí 2008; Reid et al. 2008b). Sicklefins Redhorse populations in both the

Hiwassee and Little Tennessee river basins have experienced reduced numbers, fragmentation, and isolation (Jenkins 1999). Thus, the Sicklefin Redhorse is currently a candidate for listing under the U.S. Endangered Species Act of 1973, is protected with state listings, and is covered by a Candidate Conservation Agreement (USFWS 2005, 2008, GADNR 2015; NCWRC 2015).

### Migration and Environmental Conditions

Despite considerably different water temperature and discharge patterns between 2006 and 2007, tubercle development and maturation stage similarities between years suggest that a uniform stimulus (e.g., photoperiod) is responsible for physiological changes that prepare Sicklefin Redhorses for spawning migration and reproduction (Huber and Bengtson 1999). Water temperature appeared to be an important proximate cue influencing the occurrence, timing, and function of the spawning migration. Water temperature has been associated with spawning migration of other sucker species, including White Sucker *Catostomus commersonii* (Curry and Spacie 1984), Robust Redhorse (Grabowski and Isely 2006; Straight et al. 2015), Northern Hog Sucker *Hypentelium nigricans* (Matheney and Rabeni 1995), and Razorback Sucker *Xyrauchen texanus* (Modde and Irving 1998). Unseasonably cold water, such as that associated with spring cold fronts or hypolimnetic dam releases, appeared to interrupt the Sicklefin Redhorse spawning migration and this phenomenon occurs in other potamodromous fishes (Straight et al. 2015). Yet, efforts to restore natural thermal regimes are rarely included in environmental flow assessments, which are primarily intended to reestablish natural discharge regimes (Olden and Naiman 2010).

For Sicklefin Redhorses, water temperature appeared to govern migration timing, while discharge served as a proximate cue for spawning migration magnitude, distance, and duration. Suppressed or discontinued spawning migration runs occur in numerous potamodromous and anadromous fishes following unseasonably low discharge (Purkett 1961; Paukert and Fisher 2001; Firehammer and Scarnecchia 2006, 2007). Studies focused on the imperiled Robust Redhorse have associated highly variable regulated discharge regimes with fine particulate deposition (Dilts 1999; Grabowski and Isely 2007), dewatering of oviposition sites (Grabowski and Isely 2007; Fisk et al. 2013), and decreased suitable spawning habitats (Fisk et al. 2015). Our findings and related research on other sucker species highlight the interactive nature of temperature and discharge on potamodromous fish reproductive ecology and the potential benefit of enhanced regulated flows (Barton 1980; Paragamian and Kruse 2001).

Linear home range estimates for Sicklefin Redhorses revealed behavior that was highly mobile during the spawning season and relatively sedentary during

postspawning and winter seasons. Spatiotemporal identification and characterization of potamodromous fish home ranges are critical for management. Gerking (1953) defined home range for fishes as “the area over which the animal normally travels,” leaving ample room for interpretation due to the ambiguity of the term “normal” (Mohr 1947; Funk 1957; Gowan et al. 1994; Gowan and Fausch 1996; Rodriguez 2002). We defined Sicklefin Redhorse home range as a stream reach occupied during a particular functional period (e.g., spawning season) to fulfill specific life history requirements (e.g., foraging and spawning). Tagged Sicklefin Redhorses displayed similar movement patterns to those of the Robust Redhorse; Robust Redhorse movement is highest during the spring spawning migration and minimal during winter (Grabowski and Isely 2006; Fisk et al. 2015). Conversely, Sicklefin Redhorses migrate shorter distances than do Robust Redhorses and occupy spawning tributaries rather than spawning within a main-stem large river. Use of spawning tributaries by other redhorse species has been reported for the Shorthead Redhorse *M. macrolepidotum* (Sule and Skelly 1985), Black Redhorse, Golden Redhorse (Curry and Spacie 1984; Kwak and Skelly 1992), and other sucker species (Bottcher et al. 2013; Cathcart et al. 2015).

Several radio-tagged Sicklefin Redhorses exhibited substantial movement between spawning areas. In addition to diadromous fishes (Pipal et al. 2012), use of multiple spawning areas or “wandering” has been documented for several potamodromous fishes such as the Robust Redhorse (Grabowski and Isely 2006), Razorback Sucker (Tyus and Karp 1990; Mueller et al. 2000), and Paddlefish *Polyodon spathula* (Paukert and Fisher 2001; Stancill et al. 2002). Wandering behavior may indicate habitat evaluation prior to oviposition site commitment (Grabowski and Isely 2006).

High site fidelity is common among numerous riverine suckers and other migratory fish species (e.g., Northcote 1997; Pearson and Healey 2003; Heise et al. 2004; Neely et al. 2009). Between years, Sicklefin Redhorses exhibited fidelity to spawning areas, postspawning reaches, and spawning tributaries, albeit to a degree not as rigid as that of the Robust Redhorse (Grabowski and Isely 2006). This behavioral difference between species may be related to habitat availability, as suitable Robust Redhorse spawning areas in the Savannah River are extremely scarce, but the spawning area fidelity of these two and other sucker species suggests a common pattern among potamodromous suckers.

Site fidelity and sedentary behavior align with the restricted movement paradigm (RMP; Gerking 1959; Gowan et al. 1994). The RMP, which states that adult riverine fishes not associated with spawning migrations are predominantly sedentary (e.g., Gerking 1953, 1959; Bachman 1984), is a widely supported phenomenon associated

with many riverine fishes. In accord with the RMP, Sicklefins Redhorses exhibited spawning tributary fidelity, postspawning-season site fidelity, downstream displacement during winter, straying movements, and high mobility associated with spawning migrations.

Despite our linear range results indicating that adult Sicklefins Redhorses are sedentary during the postspawning season, we observed adult Sicklefins Redhorses to exhibit frequent localized foraging movements during the postspawning season. Similarly, other potamodromous suckers have exhibited considerable localized movement during sedentary periods (Bestgen et al. 1987; Booth et al. 2013). Occasionally, suckers conduct crepuscular foraging movements from daytime refuges to exploit high resource habitats owing to temporally depleted local benthic macroinvertebrates (Booth et al. 2013). During the current study, all detections were diurnal; thus, nocturnal movement behavior was not evaluated. Nevertheless, when not conducting migrations to spawning and overwintering reaches, adult Sicklefins Redhorses concurrently displayed extreme site fidelity and frequent localized foraging movements.

One male and five female adult Sicklefins Redhorses did not migrate during a spawning season, but all tagged fish conducted at least one spawning migration. A skipped spawning migration (i.e., spawning omission) is a widely occurring phenomenon for migratory fishes (Rideout et al. 2005; Secor 2008; Doherty et al. 2010). Skipped spawning likely occurs as a result of a compromise between present and potential reproduction (Bull and Shine 1979; Rideout et al. 2005). Our finding that skipped spawning migrations were uncommon and never for consecutive years for the same individual suggests that energetic shortcomings are an exception for adult Sicklefins Redhorse, especially males.

Our radiotelemetry results and weir catch revealed that males and females arrived at spawning tributaries and spawning areas simultaneously. A sexual dichotomy related to spawning migration chronology has been reported for numerous suckers such that male fish precede female fish up spawning tributaries and arrive at spawning areas before females (e.g., protandry: Hackney et al. 1967; Page and Johnston 1990; Vokoun et al. 2003). Sicklefins Redhorses exhibited no oviposition site preparation and were nonterritorial; thus, there is a possibility that males do not derive a reproductive advantage from arriving on spawning areas before females. However, adult male Sicklefins Redhorses occupy spawning areas longer than females, and many relocate to spawning tributary lower reaches, rather than to the Hiwassee River as females do, and remain there until winter when males join females in the lower Hiwassee River. The longer spawning tributary residence time for adult Sicklefins Redhorse males has been documented for numerous other diadromous fish species (Loesch and Lund 1977; Carmichael et al. 1998;

McCubbing et al. 1998). Despite several species exhibiting longer male residence times after spawning and immediate spawning tributary descent by females, explanations for this sexual dichotomy are lacking, but males and females are likely responding to varying physiological and environmental migration cues (Baker 1978; Carmichael et al. 1998).

### Reproductive Behavior

Sicklefin Redhorse spawning behavior was generally similar to that of other redhorse species, but we observed a female spawning behavior (postspawning digging) not yet described for any sucker species. Postspawning digging has been observed in Pacific salmon *Oncorhynchus* spp. (Healey et al. 2003; Tiffan et al. 2005), but despite detailed descriptions of spawning in *Moxostoma* (Page and Johnston 1990; Kwak and Skelly 1992), postspawning digging has not been observed among redhorses. We observed foraging on eggs by male Sicklefins Redhorses, but not by females. Jenkins (1999) also reported foraging behavior within oviposition sites by Sicklefins Redhorses, which we confirmed was by the smaller males. If Sicklefins Redhorse eggs are not completely buried during the act of quivering due to coarse spawning substrates or not protected against heterocannibalism (i.e., consumption of unrelated conspecifics) as a function of male agonistic behavior, then female postspawning digs may function to bury and protect embryos from predation, as well as enhance incubation.

### Conservation and Management Implications

Currently, the Sicklefins Redhorse is listed as a threatened and endangered species in the states of North Carolina and Georgia, respectively, and is a candidate for federal endangered status under the U.S. Endangered Species Act of 1973 (GADNR 2015; NCWRC 2015). In 2015, a Candidate Conservation Agreement was established for the Sicklefins Redhorse with the objective of cooperatively conserving, managing, and restoring the species to preclude the necessity of federal listing (USFWS 2015). Current threats to the species are many and include pollution, climate change, and natural system modifications such as hydroelectric dams and reservoirs (NCWRC 2015).

Fish do not ascend spawning tributaries and select spawning areas randomly (Werner and Lannoo 1994). Spawning tributary philopatry results in reproductive isolation of spawning populations, which yields specialized adaptations for spawning tributary-specific habitats (Taylor 1991; Dittman and Quinn 1996) and promotes population life histories that are synchronized with specific environmental constraints (Brannon 1993). We documented spawning-tributary fidelity for Sicklefins Redhorses. A considerable proportion of overwintering adult Sicklefins

Redhorses descended the Hiwassee River before ascending the Valley River, while others continued downstream into Hiwassee Lake before ascending Hanging Dog Creek or the Nottely River to spawn. This phenomenon indicates that adult Sicklefin Redhorses in the Hiwassee River basin generally employ mechanisms other than olfactory imprinting to initially conduct spawning-tributary homing, which may hold implications for future reintroduction efforts. Selecting donor hatchery spawning stocks from spawning tributaries proximate to proposed reintroduction tributaries may improve the likelihood of hatchery-produced progeny successfully exhibiting spawning-tributary homing and fidelity.

Our observations of interbreeding between Black Redhorse and Sicklefin Redhorse indicate that reproductive isolating mechanisms can breakdown between *Moxostoma* species (Favrot 2009). Translocation initiatives applied as a management tool are best justified by the establishment of historical occupancy. Whether interbreeding between the Black Redhorse and Sicklefin Redhorse can produce viable progeny is unknown; however, this may be an important consideration for reintroduction planning. Identification of introgression using genetic markers has been principally applied to salmonids (e.g., Kanda et al. 2002; Kalinowski et al. 2011); however, the small geographic range of the Sicklefin Redhorse may warrant future genetic research designed to identify historical introgression between the Black Redhorse and Sicklefin Redhorse as a means to establish Sicklefin Redhorse historical occupancy and justify future reintroductions. Furthermore, historical stocking programs have unintentionally introduced genetically undesirable progeny ranging from those exhibiting reduced genetic diversity (e.g., Sicklefin Redhorse: Moyer et al. 2009) to hybrids (e.g., Greenback Cutthroat Trout *O. clarkii stomias*: Metcalf et al. 2012). Thus, we emphasize caution in future reintroduction initiatives to ensure that hatchery-produced Sicklefin Redhorses exhibit genetic diversity representative of wild fish.

Restoration approaches that may benefit the Sicklefin Redhorse via range expansion include dam removal, fish passage upstream and downstream of dams, and population reintroduction or augmentation. In 2010, a 15.3-km upstream reach was reconnected to the Tuckasegee River through the removal of Dillsboro Dam, North Carolina, which facilitated Sicklefin Redhorse colonization and range expansion (USFWS 2015). Fish passage designed for the Sicklefin Redhorse would provide benefits to other migratory species in the fish assemblage, but success would depend on a suitable flow management plan (Thiem et al. 2013; Favrot and Kwak 2016). Perhaps the quickest, most cost-effective approach to range expansion is the reintroduction of the Sicklefin Redhorse into suitable periphery streams and watersheds that were occupied historically. Our documentation of adult Sicklefin Redhorses

occupying the lower Nottely River, the longest tributary to the Hiwassee River (Hitch 1971), during the spawning season may justify reintroducing Sicklefin Redhorses into portions of the upper Nottely River. In addition, knowledge that adult Sicklefin Redhorses descend the Hiwassee River and enter lentic habitats to reach and ascend downstream spawning tributaries suggests that low-gradient portions of the Hiwassee River in eastern Tennessee may not have precluded the lower Hiwassee River tributaries (e.g., Ocoee–Toccoa river system) from being used as spawning tributaries. Suitable candidate rivers for geographic range expansion may be situated both upstream and downstream from the current Sicklefin Redhorse distribution.

Basinwide conservation and management initiatives that could benefit Sicklefin Redhorse populations in the Hiwassee River and Little Tennessee River basins include migration barrier removal, elimination or mitigation of hypolimnetic discharges from hydroelectric dams (e.g., Nottely Dam), and delayed inundation of the confluence of the Hiwassee and Valley rivers until after the spawning season. Past efforts have been successful at restoration on the watershed scale within the Hiwassee River basin. Future restoration objectives may be most effective if efforts are made to restore form and function to occupied streams to a pre-anthropogenic condition while providing ample consideration of the requirements of principal stakeholders to enhance the probability that voluntary resolutions will be broadly implemented (Bowling et al. 1997). The findings of our research on the behavior and reproductive ecology of this little-known, rare, and imperiled fish species may serve as a basis to guide such holistic efforts and maintain sustainable Sicklefin Redhorse populations.

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