



Habitat niche dynamics of the sicklefin redhorse: a southern Appalachian Mountain habitat specialist

Scott D. Favrot · Thomas J. Kwak

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Abstract Historically, suckers (Catostomidae) have been largely neglected in conservation efforts. Due to pervasive lotic habitat degradation and loss throughout North America, sucker habitat knowledge is urgently needed for conservation. The sicklefin redhorse (*Moxostoma* sp.) is an undescribed, imperiled sucker, endemic to a small geographic range in the southern Appalachian Mountains (USA). We described adult sicklefin redhorse seasonal and spawning microhabitat suitability, quantified spawning substrate composition, identified seasonal and spawning habitat niches (i.e., macrohabitats), and characterized foraging habitat. We combined radio-telemetry and visual observations of Hiwassee River basin adult sicklefin redhorses during March–January

(2006–2008) to address our objectives. Sicklefin redhorses occupied seasonal and spawning microhabitats non-randomly, and we developed season- and spawning-specific habitat suitability criteria (HSC) using a Bayesian approach. Adult sicklefin redhorses occupied habitats with swift midchannel currents, moderate depths, and coarse substrates supporting hornleaf riverweed (*Podostemum ceratophyllum*). In contrast, suitable spawning sites were located in near-bank shallow depths, slow currents, over intermediate-sized substrates near cover, but free of riverweed. Annually, principal component analyses indicated that sheet and run macrohabitats were predominantly occupied, while pocket-water riffles near depositional, edgewater zones provided spawning sites. Spawning substrate composition was predominantly small cobble (40.9%) and very coarse gravel (21.3%), but fines (3.0%) were also prevalent within interstitial spaces. Mean Fredle index was 28.2, indicating spawning substrate permeability at half potential. Annually, bedrock covered with hornleaf riverweed was the dominant foraging substrate. Our adult sicklefin redhorse annual, seasonal, and spawning HSCs, multivariate habitat niche characterizations, spawning substrate analyses, and foraging habitat descriptions can guide habitat conservation and restoration throughout the species' geographic range.

In memoriam: Thomas J. Kwak.

S. D. Favrot (✉)
Department of Applied Ecology, North Carolina
Cooperative Fish and Wildlife Research Unit, North
Carolina State University, Campus Box 7617, Raleigh,
NC 27695, USA
e-mail: sdfavrot@yahoo.com

Present Address:
S. D. Favrot
8 Tree Top Pl., Black Mountain, NC, USA

T. J. Kwak
Department of Applied Ecology, U.S. Geological Survey,
North Carolina Cooperative Fish and Wildlife Research
Unit, North Carolina State University, Campus Box 7617,
Raleigh, NC 27695, USA

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Thomas J. Kwak (8 August 1958–19 November 2021)—The impact of Tom’s remarkable career is immeasurable; only a moment in Tom’s presence was needed to witness his exceptionality. From Tom’s early years as a Master’s student working with black and golden redhorses in Illinois, to studying salmonids in Ozark tailwaters as an Arkansas Assistant Coop Unit Leader, to researching sicklefin redhorse reproductive ecology in the southern Appalachian Mountains, to studying native freshwater fishes of Puerto Rico as the North Carolina Coop Unit Leader, Tom continually exhibited an unrivaled desire to quantitatively describe the aquatic natural world around him. His insatiable desire to advance fisheries knowledge was only rivaled by his desire to recruit and foster the growth of young fisheries professionals. Tom was a high-energy, captivating professor and advisor that molded generations of fish biologists; Tom continually strived to “fill the cup” of those around him through advice, praise, encouragement, and camaraderie, especially his students. Tom was an extremely accomplished researcher and writer having authored 150+ peer-reviewed papers, numerous book chapters, and books. He was an active member of the American Fisheries Society and most recently served as President of its Southern Division (2020–2021). Perhaps Tom’s most endearing and admirable quality was his efforts advocating for diversity and inclusiveness in fisheries vocations; Tom was always quick to stand up for what was good and right. Those fortunate enough to work alongside Tom inevitably benefited from his fisheries science knowledge and strong analytical skill set; however, those that were truly lucky also acquired his overflowing kindness, warming inclusiveness, infectious laughter, and love for friends and family.

Robert E. Jenkins (9 February 1940–12 July 2023)—Bob’s contributions to fisheries science throughout his illustrious career are profound. From Bob’s early years as a doctoral student at Cornell University where he authored an 800+ page dissertation on the genus *Moxostoma*, to publishing his definitive work *Freshwater Fishes of Virginia*, to his recognition of the

sicklefin redhorse as a unique species in 1992 as a professor at Roanoke College, Bob consistently contributed grandiose contributions to the fisheries science community. Bob’s work ethic and thoroughness were on another level; Bob was often described as embodying the essence of “anything worth doing, is worth overdoing.” Bob was a professor at Roanoke College (Virginia) for over four decades where he inspired and mentored countless students, many of whom went on to have highly successful careers as fellow ichthyologists. Bob received numerous accolades during his career, which included the 1989 Thomas Jefferson Medal for Outstanding Contributions to Natural Science. Bob’s raw enthusiasm and love for the fishes of the southern Appalachian Mountains, especially the sicklefin redhorse, was palpable and contagious. Bob’s energy and exhilaration upon encountering a sicklefin redhorse was infectious, and to a degree, inspired this paper.

Introduction

Despite the remarkable species richness of southeastern US fish communities (Burr and Mayden 1992; Warren et al. 1997, 2000), only a small fraction of that fauna has commercial or recreational value; the majority are classified as nongame fishes, and many are imperiled (Jenkins and Burkhead 1994; Etnier and Starnes 1993; Jelks et al. 2008; Lauer and Pyron 2016). Nongame fishes typically become imperiled prior to receiving management or conservation efforts (Cooke et al. 2005). Currently, southeastern US fishes are disproportionately jeopardized compared to those in other regions of the country, primarily due to habitat degradation and loss (Wilcove et al. 1998; Jelks et al. 2008). Benthic habitats are especially sensitive to degradation, and thus, bottom-dwelling stream fishes (e.g., sculpins, darters, and suckers) exhibit disproportionately high levels of imperilment (Berkman and Rabeni 1987; Angermeier 1995; Warren et al. 1997, 2000; Sutherland et al. 2002). Moreover, isolated endemics are highly susceptible to extirpation due to habitat degradation and loss (Angermeier 1995; Warren et al. 2000).

Most suckers (Catostomidae) are classified as nongame species, benthic specialists, and isolated endemics

(Robison and Buchanan 1988; Jenkins and Burkhead 1994; Rohde et al. 1994; Etnier and Starnes 1993). The fish fauna of the southeastern USA includes 44 recognized catostomids, of which 17 species are of the genus *Moxostoma* (redhorses; Warren et al. 2000; Cooke et al. 2005). Redhorses face numerous threats associated with anthropogenic activities, such as environmental contaminants, nonindigenous species, migration barriers, water diversion, eutrophication, exploitation, hydro-power, and perhaps most prominently, habitat degradation and loss (Cooke et al. 2005).

A few redhorse species have recently been either rediscovered after being considered extinct (e.g., robust redhorse [*Moxostoma robustum*]) or remain undescribed (e.g., Carolina redhorse [*Moxostoma* sp.] and sicklefin redhorse [*Moxostoma* sp.]; Cooke et al. 2005). The sicklefin redhorse became known to science in 1992, but has long provided cultural value (Jenkins 1999; Altman 2006; USFWS 2015). Historically, sicklefin redhorses likely inhabited the majority of large streams and rivers in the Hiwassee and Little Tennessee river basins of the upper Tennessee River drainage (Ohio River Basin) in western North Carolina, eastern Tennessee, and northern Georgia, but currently inhabit less than 20% of that presumed historic distribution (Jenkins 1999; Favrot and Kwak 2018). Thus, the sicklefin redhorse is protected with state protective listings (GA and NC), a candidate for listing under the Endangered Species Act of 1973, and covered by a Candidate Conservation Agreement (GADNR 2015; NCWRC 2015; USFWS 2015, 2016).

The sicklefin redhorse is a potamodromous fish species (i.e., lifetime freshwater residency and migration; Favrot and Kwak 2018). For sicklefin redhorses, diminished geographic distribution is predominantly associated with habitat degradation and loss (Jenkins 1999; Warren et al. 2000; Cooke et al. 2005). During the late 1800s and early 1900s, prevalent agriculture, livestock grazing, and mining resulted in widespread sedimentation throughout western North Carolina and northern Georgia (Messer 1965; Jenkins 1999). Furthermore, extensive dam construction occurred within the Hiwassee and Little Tennessee systems between 1911 and 1957 (Etnier and Starnes 1993). To guide sicklefin redhorse management, conservation, and restoration in the Hiwassee and Little Tennessee river basins, knowledge of sicklefin redhorse habitat relationships are needed.

Knowledge of quantitative fish–habitat relations is crucial to effectively implement conservation,

management, and restoration strategies (Bovee 1986; Rosenfeld 2003). Habitat suitability criteria (HSC) translate structural and hydraulic characteristics of aquatic environments into indices of habitat quality (Bovee 1982; Thomas and Bovee 1993). In addition, HSCs are a species' "characteristic behavioral traits," which are established as standards to guide decision-making processes (Bovee 1986). Overwhelmingly, HSCs have been established for salmonids and incorporated into instream flow analyses (Degraaf and Bain 1986; Waite and Barnhart 1992; Beecher et al. 2002); however, recently, HSCs have been developed for nongame species to guide management of flow-regulated systems (Hewitt et al. 2009; Hightower et al. 2012; Fisk et al. 2014, 2015). Following historic habitat restoration challenges, ranging from restoration tactics exacerbating habitat degradation to displacing native biota (Fuller and Lind 1991; Frisell and Nawa 1992; Bernhardt et al. 2005), formal aquatic habitat restoration frameworks have been recommended (Hobbs and Norton 1996; Ebersole et al. 1997). A key aspect associated with these conceptual habitat restoration frameworks is that species- and season-specific critical habitat knowledge (e.g., HSCs) is an instrumental tool to achieve meaningful habitat protection and restoration.

Some fish taxa have approached extinction before they were even discovered or described, and their life history information and critical habitat knowledge are usually lacking (Warren et al. 2000). Under such circumstances, managing habitat may default to educated guesswork, which may fail and result in negative unforeseen consequences, or a "conserve-everything" approach is implemented, which can yield societal consequences that are difficult to justify (Rosenfeld 2003). Similarly, mostly anecdotal habitat use and foraging data exist for adult sicklefin redhorses (Jenkins 1999), while quantitative seasonal and spawning microhabitat HSCs and foraging microhabitats are lacking for adult sicklefin redhorses. Furthermore, hornleaf riverweed (*Podostemum ceratophyllum*, henceforth referred to as riverweed) is a foundation species (i.e., most influential species in an ecosystem), vitally important to the food web of co-occurring benthic macroinvertebrates and fish (Grubaugh et al. 1997; Hutchens et al. 2004; Argentina et al. 2010; Wood and Freeman 2017); however, knowledge of any interspecies relationships between the sicklefin redhorse and riverweed are lacking. Thus, sicklefin redhorse seasonal and spawning

HSCs, foraging microhabitats, and riverweed relationship knowledge may be critical toward developing future conservation, management, and restoration initiatives throughout the species' geographic range. Toward filling these knowledge gaps, our objectives were to (1) characterize Hiwassee River basin adult sicklefin redhorse annual, seasonal, and spawning microhabitat use and availability, (2) quantitatively characterize spawning substrate composition, and (3) identify seasonal foraging substrates and riverweed relationships.

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 one of only two known sicklefin redhorse populations (Fig. 1). Hiwassee River, in the upper Tennessee River drainage, is a highly regulated system that originates on the northwestern slopes of the Blue Ridge Mountains in northern Georgia. The majority of Hiwassee River's substratum is composed of rugose bedrock runs and sheets (i.e., shallow water flowing over smooth bedrock). Valley River, an unregulated spawning stream, is a moderate-gradient tributary of the upper Hiwassee River (Fig. 1).

Valley River has a maximum headwater elevation of 1,339 m and drains 303 km². Valley River's watershed is composed primarily of deciduous forest, while the lower floodplain is largely devoted to agriculture. At the Valley River and Hiwassee River confluence, Hiwassee River drains 1092 km², is 79 km long, and has a maximum headwater elevation of

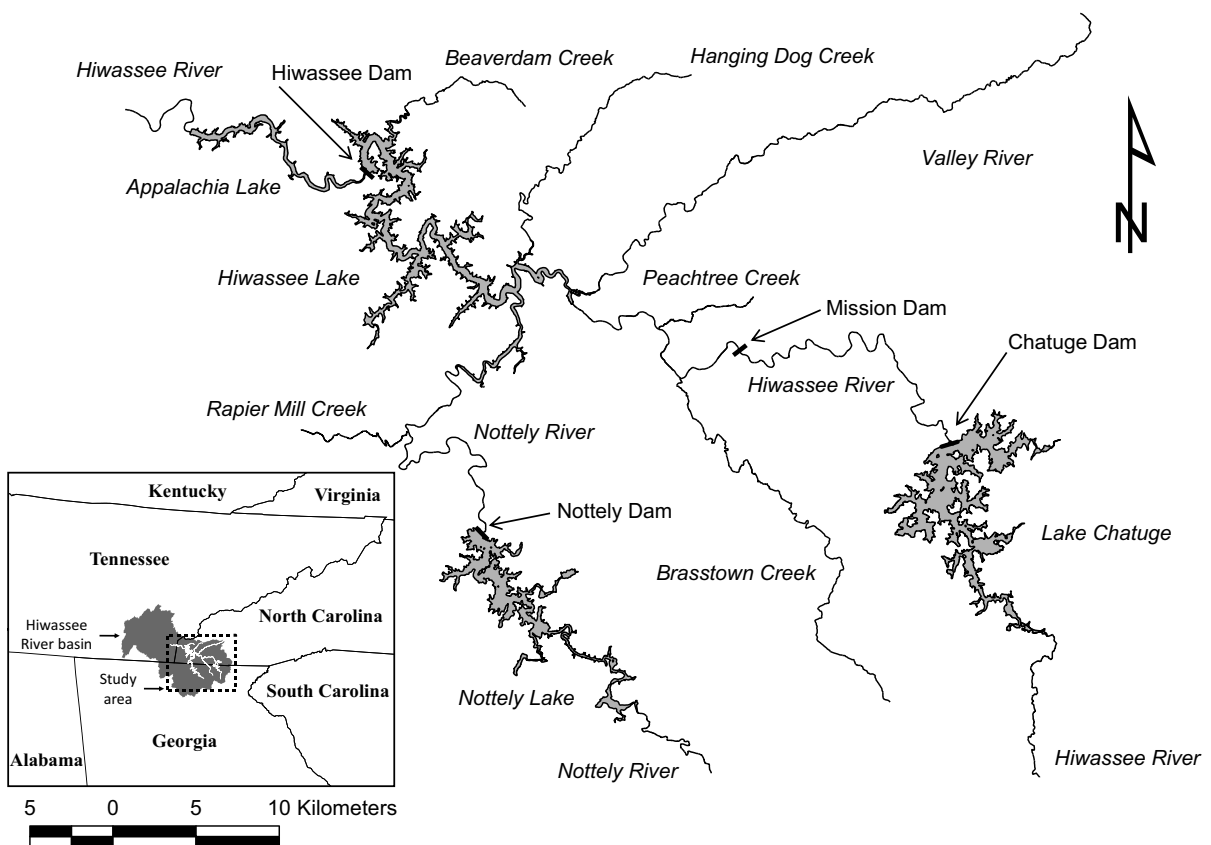


Fig. 1 Map of the upper Hiwassee River basin with the study area bounded downstream by Hiwassee Dam and upstream by Mission and Nottely dams

1422 m. Valley River converges with Hiwassee River 47 km from its origin in the Snowbird Mountains, and Valley River's mouth is periodically inundated by Hiwassee Lake (Fig. 1). In addition to Valley River, Hiwassee Lake and Hiwassee River receive numerous additional sicklefin redhorse spawning tributaries including Brasstown Creek, Hanging Dog Creek, and Nottely River (Fig. 1; Favrot 2009; Favrot and Kwak 2018).

Radiotelemetry

During March–April 2006 and 2007, 34 adult sicklefin redhorses, from lower Valley and Hiwassee rivers (i.e., prespawn staging areas; Favrot and Kwak 2018), were implanted with Advanced Telemetry Systems radio transmitters (48–49 MHz, Model F1820) programmed with a 12 h/d duty cycle. Adult fish to be tagged were captured by boat electrofishing, using a Smith-Root 2.5 GPP electrofishing unit with pulsed-DC current (60 Hz) at 3.0–5.0 A. Following capture, total length (TL, mm), weight (g), and water temperature (°C) were measured. Determination of sex was accomplished by gamete expression and tubercle development. Fish maturity was established using criteria found in Jenkins (1999).

Adult sicklefin redhorse weighing greater than 425 g were selected for tag implantation to ensure radio transmitters weighed less than 2% of the fish's total body weight (Table 1; Winter 1996). Implanted radio transmitters exhibited a mean weight of 8.19 g (SE 0.05) in air. All radio transmitters operated between 48.0 and 49.0 MHz and emitted a signal at a rate of 34 pulses per minute, guaranteeing a battery life of 287 days and an expected battery life of 575 days.

Sicklefin redhorse transmitter implantation surgeries were conducted on the stream bank promptly following capture. Immediately following capture, adult sicklefin redhorse were individually placed in an aerated 40 L container containing a 35–40 mg/L Benzocaine solution until a loss of equilibrium and reduced opercular rate was achieved. Following sicklefin redhorse displaying symptoms of stage 4 anesthesia (mean 4.5 min, SE 0.17; Summerfelt and Smith 1990), anesthetized adults were moved to a 4 L container to continuously expose each fish's gills to freshwater during surgery. A transmitter sterilized with a cold sterilant (Cidex, Johnson & Johnson

Company, USA) was inserted intraperitoneally through a 1.5 cm incision anterior to the pelvic girdle and offset 1.5 cm left of ventral midline. Transmitters with a trailing antenna were employed to maximize field range. The trailing antenna was coiled up and inserted into the body cavity to minimize mortality as external wire antennas may be associated with mortality and infection of tissues around the exit of the antenna (Matheney and Rabeni 1995). The tip of each trailing antenna included a 3-mm Scotchcast resin bead to prevent peritoneal irritation. All incisions were closed with three interrupted sutures that were made using sterile, non-absorbable, monofilament suture material (Monosof 3–0) with a 24-mm, 3/8 circle reverse cutting needle (Wagner and Cooke 2005). Mean total surgery time for all radio-tagged sicklefin redhorse was 7.9 min (SE 0.35). Once the incision was closed, fish were placed into an aerated, covered tank and monitored until normal equilibrium and opercular rate were regained (mean 2.6 min, SE 0.27). Following initial recovery, implanted fish were transferred to a 2.12-m³ coated wire mesh instream cage to ensure immediate post-surgery survival prior to release (mean 3.2 h, SE 0.16).

Seasonal microhabitat use and availability

Following a 14-day post-release recovery period (Stasko and Pincock 1977), radio-tagged fish were tracked weekly during spring and summer (April–June) to identify and characterize diurnal critical spawning and foraging habitats, respectively. In addition, to document fall and winter diurnal critical habitats, additional tracking occurred during October 2006 and January 2007–2008, respectively. During the study period, Brasstown Creek (23.8 km), Hanging Dog Creek (14.4 km), Hiwassee Lake, Hiwassee River (17.1 km), Nottely River (24.0 km), and Valley River (32.2 km) were tracked weekly to bi-weekly (Fig. 1). In addition, 18 Hiwassee River basin tributaries were opportunistically tracked by foot during the study period (Favrot 2009).

To identify and characterize adult sicklefin redhorse seasonal microhabitat use and suitability, fish were relocated using an ATS Model R2100 receiver and loop antenna assembly from a two-person canoe. Radio-tagged fish locations were identified using triangulation techniques (Cooke et al. 2012). Tracking

Table 1 Summarized adult sicklefin redhorse microhabitat use and availability for occupied Hiwassee River basin streams during 2006 and 2007. Substrate abbreviations are CL (clay), SI (silt), SA (sand), FG (fine gravel), MG (medium gravel), CG (coarse gravel), VCG (very coarse gravel), SC (small cobble), SB (small boulder), and BR (bedrock)

Variable and statistic	Reproductive behavior		Period			Available
	Courting	Spawning	Spawning	Postspawning	Winter	
Total depth (m)						
<i>N</i>	17	43	353	260	20	1,815
Mean	0.34	0.28	0.53	0.45	0.75	0.37
SE	0.02	0.01	0.01	0.01	0.07	0.01
Range	0.18–0.46	0.15–0.46	0.09–1.88	0.08–1.66	0.40–1.50	0.00–2.00
Bottom velocity (m/s)						
<i>N</i>	17	43	353	260	20	1,815
Mean	0.16	0.20	0.17	0.14	0.21	0.10
SE	0.04	0.02	0.01	0.01	0.03	0.00
Range	0.00–0.42	0.02–0.55	0.00–0.75	0.00–0.90	0.03–0.58	0.00–1.23
Mean velocity (m/s)						
<i>N</i>	17	43	353	260	20	1,815
Mean	0.42	0.51	0.44	0.42	0.51	0.22
SE	0.06	0.02	0.01	0.01	0.05	0.01
Range	0.03–0.84	0.16–0.90	0.00–1.50	0.00–1.46	0.16–1.02	0.00–1.50
Dominant substrate						
<i>N</i>	17	43	357	266	20	1,815
Mode	SC	SC	BR	BR	BR	BR
SE	0.41	0.13	0.16	0.11	0.73	0.10
Range	FG–SB	MG–SB	SI–BR	SA–BR	SA–BR	CL–BR
Subdominant substrate						
<i>N</i>	17	43	357	266	20	1,815
Mode	VCG	VCG	BR	BR	BR	SA
SE	0.40	0.15	0.19	0.21	0.85	0.09
Range	SA–SB	CG–SB	SI–BR	SI–BR	SI–BR	CL–BR
Cover						
<i>N</i>	17	43	356	260	20	1,815
Mode	Boulder	Boulder	Boulder	No cover	No cover	No cover
Distance from cover (m)						
<i>N</i>	14	40	136	83	2	969
Mean	0.84	0.36	1.15	0.99	0.75	1.02
SE	0.19	0.07	0.05	0.07	0.25	0.02
Range	0.10–2.00	0.10–2.00	0.10–2.00	0.01–2.00	0.50–1.00	0.10–2.00
Distance from bank (m)						
<i>N</i>	17	43	347	260	20	1,815
Mean	4.00	2.85	7.50	13.53	21.15	13.43
SE	0.44	0.24	0.38	0.48	3.41	0.30
Range	1.00–6.00	0.75–8.00	0.50–45.00	1.00–30.00	4.00–60.00	0.00–83.00
Riverweed						
<i>N</i>	17	43	357	269	20	1,815
Present (%)	0	0	55	92	55	29
SE			0.03	0.02	0.11	0.01

via a canoe permitted trackers to closely approach (5–10 m) radio-tagged sicklefin redhorse prior to triangulating each fish's occupied location. Triangulation accuracy is higher when the distance between the transmitter and receiver is small (Simpkins and Hubert 1998), and triangulation techniques can produce accuracies ranging from 0.5 to 1.0 m² (David and Closs 2001, 2003). Caution was practiced during triangulation efforts not to disturb adult sicklefin redhorse and introduce fright bias (Cooke et al. 2012). During canoe tracking sessions, in addition to triangulated fish, microhabitat use data were collected from co-occurring undisturbed non-tagged conspecifics to minimize individual fish-level dependence. Co-occurring conspecifics were identified based on coloration and morphological features described in Jenkins (1999) as well as pre-study personalized *Moxostoma* identification training sessions with Dr. Robert E. Jenkins, the ichthyologist that recognized the sicklefin redhorse as a unique *Moxostoma* species in 1992 (Favrot and Kwak 2018). At each fish location (Favrot and Kwak 2018), microhabitat use variables were measured and included total depth (m), bottom velocity (m/s), mean column velocity (m/s), dominant substrate, subdominant substrate, cover type, distance from cover (m), distance from bank (m), and occurrence of riverweed (present or absent).

Microhabitat availability data were collected from occupied reaches (mean=2.6 sites per stream) of Hiwassee River, Nottely River, Valley River, Hanging Dog Creek, and Brasstown Creek during base flow conditions using line-transect surveys (McMahon et al. 1996; Stanfield and Jones 1998; Favrot 2009). Transects were spaced two mean stream widths apart (mean=49.8 m; range=14–150 m), and microhabitat variables were measured at evenly-spaced points across each transect (mean=2.2 m; range=0.7–5.0 m; Simonson et al. 1994). A total of 142 transects were surveyed and 1,815 survey points were assessed. A total of 7.6 km (6.8%) of the 112 km regularly radio-tracked were surveyed. Morphological stream characteristics obtained during microhabitat availability surveys included bank angle (°), undercut bank distance (m), and 30-m riparian land use (% agriculture, developed, or forested; McMahon et al. 1996; Bain and Stevenson 1999).

At microhabitat use and availability locations, a top-set wading rod was used to measure depth to the nearest centimeter. A Marsh-McBirney digital

flow meter (Model 2000) was used to measure bottom and mean column velocity (m/s). Mean column velocity was measured at depths 60% from the surface when total depth was ≤ 0.75 m; however, if total depth exceeded 0.75 m, velocities were measured at depths 20% and 80% from the surface and averaged (McMahon et al. 1996). Dominant substrate was visually determined using a modified Wentworth particle size classification (Bovee 1986).

Visual estimates of surface substrates may be subject to observer bias (Platts et al. 1983). Thus, following microhabitat variable measurements at visually confirmed spawning sites (i.e., quivering observed), 31 substrate samples were collected to describe spawning substrates from Valley River ($N=28$), Brasstown Creek ($N=2$), and Hanging Dog Creek ($N=1$). All substrate samples were collected from the exact location spawning occurred (i.e., pit). The majority ($N=22$) of substrate samples were collected immediately following spawning (i.e., quivering), while the remainder ($N=9$) were collected within 24 h. Sample depths were 10 cm, as depth of egg deposition by the river redhorse (*Moxostoma carinatum*, sister species to the sicklefin redhorse; Harris et al. 2002) is < 10 cm (Byron J. Freeman, University of Georgia, unpublished data). Due to high substrate coarseness, a round-point shovel was used to collect each sample (Young et al. 1991). Following decantation, all samples were visually inspected for eggs to determine presence or absence.

In the lab, substrate samples were oven dried at 60 °C for 24 h. Following hand-measuring the intermediate axis (b-axis, nearest 1.0 mm), cobble and very coarse gravel components were weighed separately (nearest 0.01 g). The remaining portion of each sample was sorted through five Tyler USA standard testing sieves (mesh sizes: 31.5, 16.0, 9.5, 2.0, and 0.074 mm) placed in geometric progression on a mechanical shaker (Tyler Ro-Tap Sieve Shaker) for 10 min. Sorted sieve contents were then weighed separately (nearest 0.01 g). Next, fine substrate particles (fines < 2.0 mm) were transferred to a muffle furnace and heated to 420 °C for 2 h (i.e., ashed). Finally, ashed samples were removed and weighed (nearest 0.01 g) to determine organic fines (%).

At each fish location, nearest dominant cover type within 2 m was visually determined and categorized as no cover, large wood (LW), small wood (SW), root wad, emersed aquatic vegetation (EAV), submersed

aquatic vegetation (SAV), terrestrial vegetation, undercut bank, and boulder. Similarly, presence or absence of riverweed was determined for each fish location and was considered present if it occurred ≤ 2 m from the fish location, but not considered physical cover due to its substrate-conforming nature.

Foraging and spawning habitat use

Foraging behavior occurrence (presence/absence) and microhabitat use (see above for details) were documented for visually observed sicklefin redhorses. Foraging behavior was confirmed if gulping or “sucking” behavior was observed (Jenkins 1999).

During the spawning season, observers used radio-tagged sicklefin redhorses as sentinels, polarized glasses, and binoculars to locate sicklefin redhorse exhibiting reproductive behaviors. Upon observation of reproductive behaviors, observers differentiated courting and spawning behaviors (Jenkins 1999; Favrot and Kwak 2018). For courting and spawning observations, effort was made to identify a spawning site via direct visual spawning observation (i.e., quivering) or inferred from evidence of spawning (e.g., silt-free depression). Spawning sites were categorized as “quivering” if spawning was observed and “courting” if not. At each spawning site, microhabitat measurements were collected from the center (pit) of the oviposition site and immediately upstream (flat; Jenkins 1999).

Statistical analyses

Based on sicklefin redhorse seasonal movement patterns, tubercle development, and maturation stage results from associated studies (Favrot and Kwak 2018), we stratified microhabitat use into three discrete functional periods (i.e., seasons) for analyses. Spawning season ranged from March 1 to May 31; postspawning season was June 1 to November 15; and the winter season spanned November 16 to February 29.

Microhabitat availability and use

Among occupied streams, morphology and riparian land use data were compared using the Kruskal–Wallis nonparametric ANOVA with a post hoc Dunn’s test for multiple comparisons (Zar 1996; Furlong et al. 2000). Sicklefin redhorse microhabitat use data

were stratified by reproductive behavior (courting and spawning) and season (spawning, postspawning, and winter). Annual, seasonal, and spawning microhabitat use data were compared to spatially corresponding availability data. We applied Bayesian statistical methods to construct annual-, season-, and spawning-specific microhabitat suitability models using resource selection functions (RSF; Thomas et al. 2004; Johnson et al. 2006; Hightower et al. 2012). Adult sicklefin redhorses exhibit spawning and post-spawning site fidelity (Favrot and Kwak 2018); thus, among streams and between years, microhabitat use data (i.e., radiotelemetry and observational) were pooled and compared with spatially analogous microhabitat availability data to generate type III univariate HSCs (Bovee 1986; Newcomb et al. 2007). Pooling of multi-technique and multi-year microhabitat use data can be statistically problematic as this approach does not account for possible fish- and year-level dependence; however, we justified pooling microhabitat use data because traditional HSC-type analyses will enable comparisons with previous catostomid HSC studies (Twomey et al. 1984; Kwak and Skelly 1992; Kwak et al. 1992; Bunt et al. 2013; Fisk et al. 2015; Nemeč et al. 2021). Seasonal microhabitat use was modeled with a multinomial distribution, following the approach developed by Thomas et al. (2004). We used Sturges (1926) equation to establish bin widths for continuous variables (Newcomb et al. 2007), with the exception of distance from cover, as our methods dictated a maximum distance of 2 m. Values at the high end of the suitability spectrum were grouped to increase sample sizes and decrease bin quantity (Harris and Hightower 2011). Similarly, cover types EAV and SAV were grouped due to low sample sizes.

Microhabitat suitability values range from 0 to 1, with 0 and 1 representing unsuitable and optimal microhabitat, respectively (Waters 1976; Bovee 1986). To convert our probability estimates to suitability estimates, we rescaled our relative use probabilities to a maximum value of 1 (Harris and Hightower 2011; Hightower et al. 2012). Bayesian statistics combine prior information with new data to generate refined estimates (McCarthy 2007); however, because no informative data exist, we used uninformative prior distributions to generate HSCs based entirely on our data. We employed a 95% credible interval (CI) to characterize uncertainty associated with each HSC. For each variable, we estimated a Bayesian P

value (i.e., probability of no preference) by comparing observed and simulated data sets produced under the null hypothesis of no preference (Thomas et al. 2004; Hightower et al. 2012). Markov chain Monte Carlo methods were used to sample posterior distributions, including three mixing chains with $\leq 400,000$ iterations each, and a $\leq 200,000$ -iteration burn-in period with no thinning. The r^* statistic was calculated to assess model convergence (Gelman and Hill 2007). All Bayesian statistical analyses were performed using OpenBUGS open-source software (Spiegelhalter et al. 2010), which was integrated into program RStudio using package R2OpenBUGS (Sturtz et al. 2005; R Core Team 2015).

Continuous microhabitat use variables from quivering and courting spawning sites were compared using the Mann–Whitney rank-sum test. Due to sample size limitations, a 2×3 Freeman–Halton extension of Fisher’s exact test was used to compare categorical variables. Riverweed occurrence was not compared due to complete absence at spawning sites.

Microhabitat variables depth, bottom velocity, mean column velocity, and dominant substrate were compared between pit and flat locations using the Student’s t test to ascertain if selected spawning microhabitats (i.e., pit) varied from theoretically undisturbed pre-spawning microhabitats (i.e., flat). Microhabitat variables distance from bank, cover type, and distance from cover were not compared because these variable measurements were identical between locations.

Continuous microhabitat variables were analyzed with a principal component analysis (PCA) to produce a visual representation of occupied habitat niches. Due to spatiotemporal differences in microhabitat use, seasonal and spawning PCAs were performed separately. Principal component analysis enables the cumulative interaction among several microhabitat variables to be examined and prioritized (Kwak and Peterson 2007). Principal components (PCs) with eigenvalues greater than 1.0 were retained (Kaiser 1960; Stevens 1996; Kwak and Peterson 2007). Habitat availability scoring coefficients were used to calculate microhabitat use PC scores. All PCs were broadly described based on a macrohabitat classification system (Arend 1999).

Spawning substrate composition

We described sicklefin redhorse spawning substrate composition by examining percent fines (< 2.0 mm)

and measures of central tendency (Chapman 1988; Young et al. 1991; Magee et al. 1996). Spawning particle size distribution was characterized by calculating the geometric mean diameter (D_g ; Shirazi and Seim 1981) and median diameter (D_{50}). Spawning substrate relative quality was determined by calculating the Fredle index (F_i ; Young et al. 1991). Bounds of central tendency (i.e., spread) were determined by plotting particle size diameter for each particle size class against cumulative percent mass on a log-probability graph. For each cumulative plot, D_{25} and D_{75} were calculated and defined as the substrate diameters below which 25% and 75% reside, respectively.

Foraging substrate and riverweed

To determine seasonal dominant foraging substrate, spawning and nonspawning period (i.e., postspawning season and winter) foraging behavior was examined. Foraging acts were distributed among bins according to foraging substrate particle size (e.g., clay, silt, sand, gravel, cobble, boulder, bedrock). A K-S test was performed on spawning period and nonspawning period foraging substrate use to assess if a seasonal shift occurred in dominant foraging substrates. To ascertain if sicklefin redhorse dominant substrate use was influenced by the presence of riverweed, excluding brief occupancy of spawning sites, a likelihood-ratio chi-square test was performed comparing annual dominant substrate use to availability based on the presence or absence of riverweed. Statistical software packages SAS/STAT 9.1 (SAS Institute Inc. 2003) and SigmaPlot version 12.5 (SYSTAT Software 2008) were used to conduct all non-Bayesian statistical analyses. A significance level (α) of 0.05 was applied for all statistical tests.

Results

Radiotelemetry

In 2006 and 2007, 34 adult sicklefin redhorses were radio-tagged from Valley and Hiwassee rivers. In 2006, water temperatures were 14.0–15.0 °C during surgery and 10.0 °C in 2007. In total, males ($N=18$) had a mean TL of 487 mm (SE, range; 7.8, 434–553 mm) and a mean weight of 1032 g (SE,

range; 50.3, 768–1588 g). Females ($N=16$) had a mean TL of 513 mm (SE, range; 6.5, 472–560 mm) and a mean weight of 1244 g (SE, range; 37.6, 993–1564 g). In aggregate, mean tag burden was 0.7% (SE=0.03%). In 2006, one male fish expressed milt, while no females were ripe. No fish expressed gametes during 2007. Of the 34 tagged fish, 7 (20.6%) mortalities or tag expulsions occurred during the study period. Tracking necessitated 7920 person-hours, spanned 3086 river-km, yielded 692 total fish locations, and 16.9 relocations per radio-tagged fish. All radio-tagged fish were accounted for during this study.

Stream morphology

Stream morphology characteristics revealed significant differences among occupied rivers (Kruskal–Wallis test: $H \geq 14.97$, $df=4$, $P \leq 0.005$), with the exception of undercut bank distance (Kruskal–Wallis test: $H=7.46$, $df=4$, $P=0.113$). Spawning tributaries had median stream widths ranging from 12.3 m (Hanging Dog Creek) to 25.0 m (Nottely River), while Hiwassee River was considerably wider at 45.9 m. All streams were entrenched with median bank angles ranging from 97.5° (Nottely River) to 140.0° (Hanging Dog Creek). Undercut bank distances revealed minimal lateral bank erosion at base flow levels with a median undercut bank distance of 0 m for all streams.

Riparian land uses were significantly different (Kruskal–Wallis test: $H \geq 21.74$, $df=4$, $P < 0.001$) among occupied streams and rivers. On average, 42.5% of Valley River's riparian zone was devoted to agriculture, while 40.3% was forested. The proportion of Valley River's riparian zone in agriculture was significantly greater compared to those of Brasstown Creek and Nottely River (Dunn's test: $Q \geq 2.82$, $P < 0.05$). Brasstown Creek and Hiwassee River exhibited a significantly greater degree of developed riparian zone compared to other streams (Dunn's test: $Q \geq 3.06$, $P < 0.05$). Brasstown Creek's riparian zone was 38.6% developed and 51.7% forested. Hanging Dog Creek's riparian zone was 69.0% forested, while 20.8% was in agriculture. Nottely River's riparian zone was predominantly forested (94.5%) and significantly more so compared to other streams (Dunn's test: $Q \geq 2.87$, $P < 0.05$). Agriculture, developed, and

forested land cover each constituted a third of Hiwassee River's riparian zone.

Spawning and seasonal microhabitat use and availability

For all variables, microhabitat use was not significantly different between quivering and courting spawning sites (Mann–Whitney test: $U \geq 128.5$; $N_1=12$, $N_2=31$; $P \geq 0.119$; Fisher–Freeman–Halton test: $P=0.1952$), with the exception of total depth and distance from cover ($U \leq 107.0$; $N_1 \geq 10$, $N_2 \geq 30$; $P \leq 0.033$). Pit and flat spawning microhabitats were not significantly different (Student's t -test: $t \leq 1.86$, $df=84$, $P \geq 0.0662$) for depth, bottom velocity, mean column velocity, and dominant substrate. Thus, quivering and courting spawning sites were pooled for analyses ($N=43$), and pit microhabitat use data were used to characterize all spawning sites.

Seasonally, occupied mean total depths were deeper than those available; however, spawning sites exhibited an opposite relationship (Table 1). Seasonally and at spawning sites, mean occupied velocities were swifter than those available (Table 1). Seasonally, modal occupied and available dominant substrates were bedrock, while the spawning site dominant substrate mode was small cobble (Table 1). Annually, adult sicklefin redhorses occupied locations lacking cover, except during the spawning season and at spawning sites (Table 1). Of 43 spawning sites, 34 (79%) were associated with boulders, 6 (14%) were associated with LW, and three (7%) lacked cover. Seasonally, mean distance from cover of occupied and available sites were similar; however, mean distance from cover at spawning sites was comparatively small (Table 1). Of 43 spawning sites, 27 (63%) were situated ≤ 0.25 m from cover. Seasonally, occupied sites distance from bank means were large compared to availability (Table 1). In contrast, the spawning site mean distance from bank value revealed near-bank spawning (Table 1). Occupied locations exhibited high riverweed presence, especially during the postspawning season (92%), but riverweed was not present at any spawning site, despite its low to moderate availability (Table 1). Specifically, riverweed availability was low in spawning tributaries, ranging from 18% (Valley River) to 27% (Brasstown Creek) occurrence, but was more abundant in Hiwassee River (56%).

Bayesian suitability models

Our Bayesian HSCs indicated that adult sicklefin redhorses do not select seasonal and spawning site microhabitats randomly. Annually, including the spawning and postspawning seasons, the probability of HSCs exhibiting these patterns under the null hypothesis of no preference was ≤ 0.001 for all variables. Similarly, during winter, most HSCs indicated nonrandom habitat preference ($P < 0.05$), except for cover ($P = 0.122$) and riverweed occurrence ($P = 0.503$). Likewise, at spawning sites, all HSCs indicated nonrandom habitat preference ($P < 0.05$), except that for distance from bank ($P = 0.104$). Despite pooled microhabitat use data exhibiting year- and fish-specific dependence, our HSCs exhibited wide 95% CIs, suggesting minimal dependence (Figs. 2 and 3).

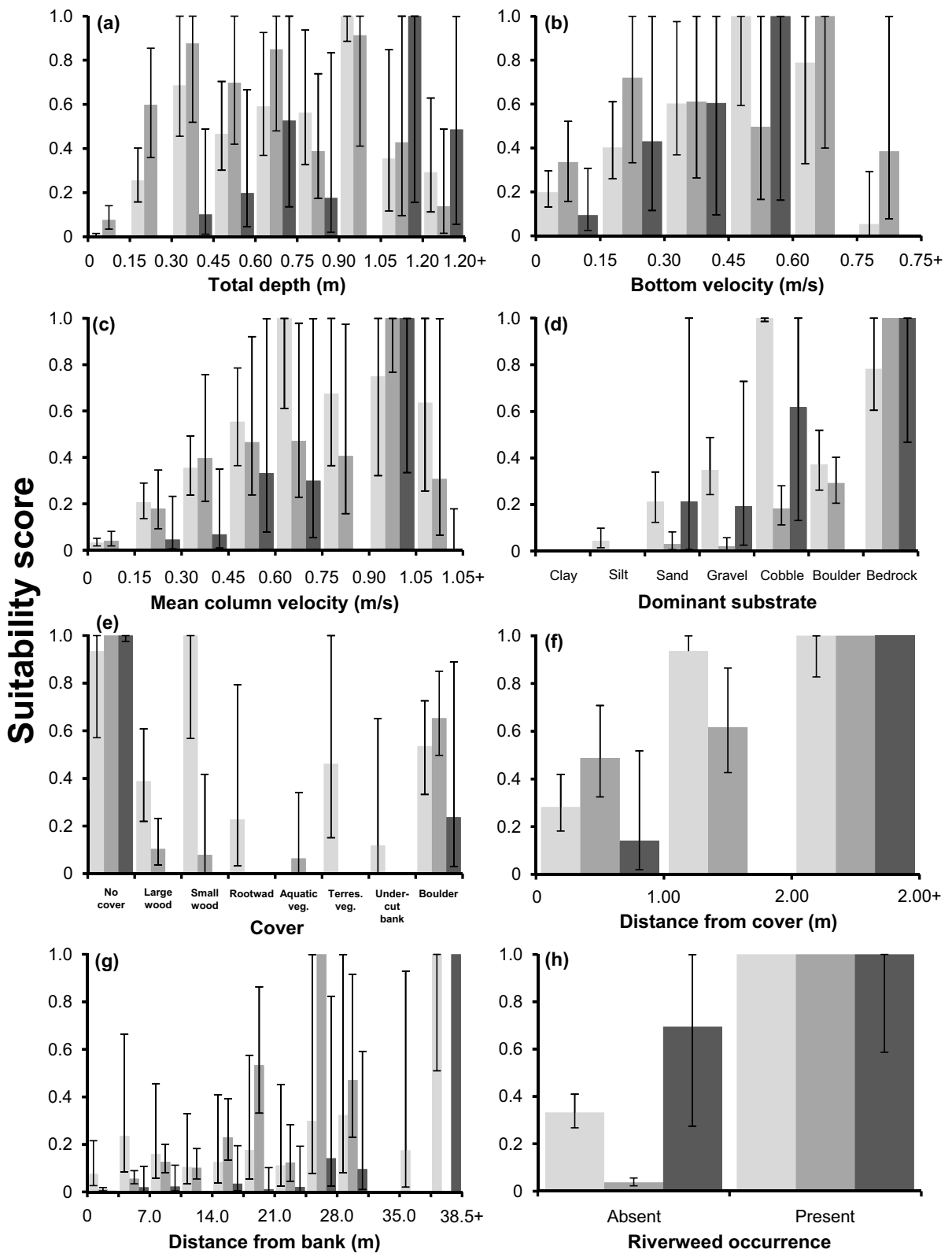
Annually, including spawning and postspawning seasons, moderately deep habitats (0.90–1.05 m) were most suitable; however, shallow spawning sites were most suitable (0.15–0.30 m), and deep winter habitats were most suitable (1.05–1.20 m; Figs. 2 and 3). Annually and at spawning sites, moderate bottom velocities (0.45–0.60 m/s) were most suitable; however, during the postspawning season, swifter bottom velocities (0.60–0.75 m/s) were most suitable (Figs. 2 and 3). Annually, including the postspawning and winter seasons, swift mean column velocities (0.90–1.05 m/s) were most suitable (Figs. 2 and 3). At spawning sites and during the spawning season, slow (0.45–0.60 m/s) and moderate (0.60–0.75 m/s) mean column velocities were most suitable, respectively (Figs. 2 and 3). Annually, including the postspawning and winter seasons, bedrock was most suitable, while cobble was most suitable during the spawning season (Figs. 2 and 3). At spawning sites, small cobble was most suitable (Fig. 3). Annually, including the postspawning and winter seasons, habitats with no cover were most suitable (Figs. 2 and 3). During the spawning season, small wood and no cover were most suitable (Fig. 2). In contrast, at spawning sites, habitats with no cover exhibited low suitability, while boulders and large wood were most suitable (Fig. 3). Annually and seasonally, distances ≥ 2 m from cover were most suitable; however, distances < 0.5 m from cover were most suitable at spawning sites (Fig. 3). Annually, including spawning and winter seasons, distances ≥ 38.5 m from the bank were most suitable (Figs. 2 and 3). During the

postspawning season, more moderate distances from the bank (24.5–28.0 m) were most suitable; however, at spawning sites, distances < 3.5 m from the bank were most suitable (Figs. 2 and 3). Annually and seasonally, substrates supporting riverweed were most suitable; however, clean substrates (i.e., no riverweed) also exhibited high suitability during winter (Figs. 2 and 3). In contrast, at spawning sites, clean substrates were most suitable, while substrates with riverweed were unsuitable (Fig. 3).

Microhabitat multivariate analyses

Annually, seasonally, and for spawning sites, multivariate PCAs characterized two contrasting habitat gradients. Annually and seasonally, PC1 characterized a habitat gradient ranging from depositional edgewater (low scores) to chute (high scores; Table 2; Fig. 4). Generally, PC2 characterized a habitat gradient ranging from lateral rapid (low scores) to straight scour pool (high scores; Table 2; Fig. 4). For spawning sites, PC1 described a habitat gradient ranging from depositional edgewater (low scores) to sheet (high scores; Table 2; Fig. 5). The PC2 habitat gradient ranged from pocket-water riffle (low scores) to glide (high scores; Table 2; Fig. 5). Among all PCAs, PC1 explained a mean cumulative variance of 44.5%, while PC2 explained a mean cumulative variance of 60.0% (Table 2).

Annually, seasonally, and at spawning sites, adult sicklefin redhorses occupied habitat niches nonrandomly for PC1 and PC2 (K–S test: $D \geq 0.08$, $P \leq 0.0017$; Table 2), except for PC2 during spawning and winter seasons (K–S test: $D \leq 0.25$, $P \geq 0.0939$; Table 2). Annually and during the spawning and postspawning seasons, fish occupied runs and sheets (moderate PC1 scores), and rarely occupied depositional edgewater (low PC1 scores; Fig. 4). Occupied near-bank habitat niches exhibited shallow and swift currents (e.g., riffles and rapids; low PC2 scores), while midchannel habitat niches providing deep, slow currents were rarely used (straight scour pools; high PC2 scores; Fig. 4). During winter, fish occupied midchannel runs and sheets lacking cover (moderate PC1 scores) and avoided depositional edgewater cover (low PC1 scores; Fig. 4). Additionally, overwintering fish occupied moderate to deep pools exhibiting moderate currents (moderate PC2 scores); fish avoided shallow riffles and rapids (low PC2 scores; Fig. 4).



◀**Fig. 2** Seasonal Bayesian microhabitat suitability scores and 95% credible intervals for Hiwassee River basin adult sicklefin redhorses for variables (a) total depth, (b) bottom velocity, (c) mean column velocity, (d) dominant substrate, (e) cover, (f) distance from cover, and (g) distance from bank. Seasonal Bayesian suitability scores and 95% credible intervals for (h) riverweed occurrence are also provided. The light gray histograms represent the spawning season, the gray histograms represent the postspawning season, and the dark gray histograms represent the winter season

Spawning sicklefin redhorses selected runs and riffles with moderate currents flowing over medium to coarse substrates proximate to depositional edgewater (intermediate PC1 scores; Fig. 5). Additionally, spawners occupied pocket-water riffles with moderate to swift near-cover currents (low PC2 scores). Spawning sites never occurred in slow deep glides lacking cover (high PC2 scores; Fig. 5).

Spawning substrate composition

Thirty-one spawning substrate samples averaged 7.7 kg (range, 3.0–15.3 kg) each. On average, small cobble (40.9%), very coarse gravel (21.3%), and large cobble (13.2%) were most common at spawning sites. Large cobble was present in nearly half ($N=15$) of substrate samples. On average, spawning site substrate samples contained 3.0% fines (SE, range; 0.38%, 0.4–9.7%), which were 2.4% organic (Table 3). Measures of central tendency revealed an average geometric mean diameter (D_g) of 54.0 mm (i.e., very coarse gravel) and average median diameter (D_{50}) of 78.7 mm (i.e., small cobble; Table 3). Generally, average bounds of central tendency exhibited little to moderate deviation from average median diameter (D_{50}) estimates. Mean first quartile diameter (D_{25}) was 34.8 mm (i.e., very coarse gravel), while the mean third quartile diameter (D_{75}) was 127.4 mm (i.e., large cobble; Table 3). On average, spawning substrates exhibited a sorting coefficient (S_o) and Fredle index of 1.93 (SE, range; 0.02, 1.7–2.4) and 28.3 (SE, range; 1.6, 14.2–55.1), respectively (Table 3).

Of the excavated spawning sites, only 1 (3.2%) contained eggs or embryos. Eggs recovered from this location were adhered to sand and small gravel situated beneath cobble. Although spawning sites were spatially similar, only the most upstream spawning substrate sample contained eggs; postspawning digs were associated with this sample.

Substrate, riverweed, and foraging behavior

Adult sicklefin redhorses occupied microhabitats with coarse substrates (larger than very coarse gravel; 87.7%) more frequently compared to smaller substrates (12.3%). Among coarse substrates, bedrock and boulders were used more frequently (77.3%) than small and large cobble (22.7%). Of the coarsest dominant substrates, bedrock was used 80.0% of the time compared to boulders. Riverweed was absent more frequently than present among occupied dominant substrates finer than large boulder, and considerably so for available substrates smaller than large boulder. Bedrock was the only dominant substrate class that exhibited riverweed more frequently than not.

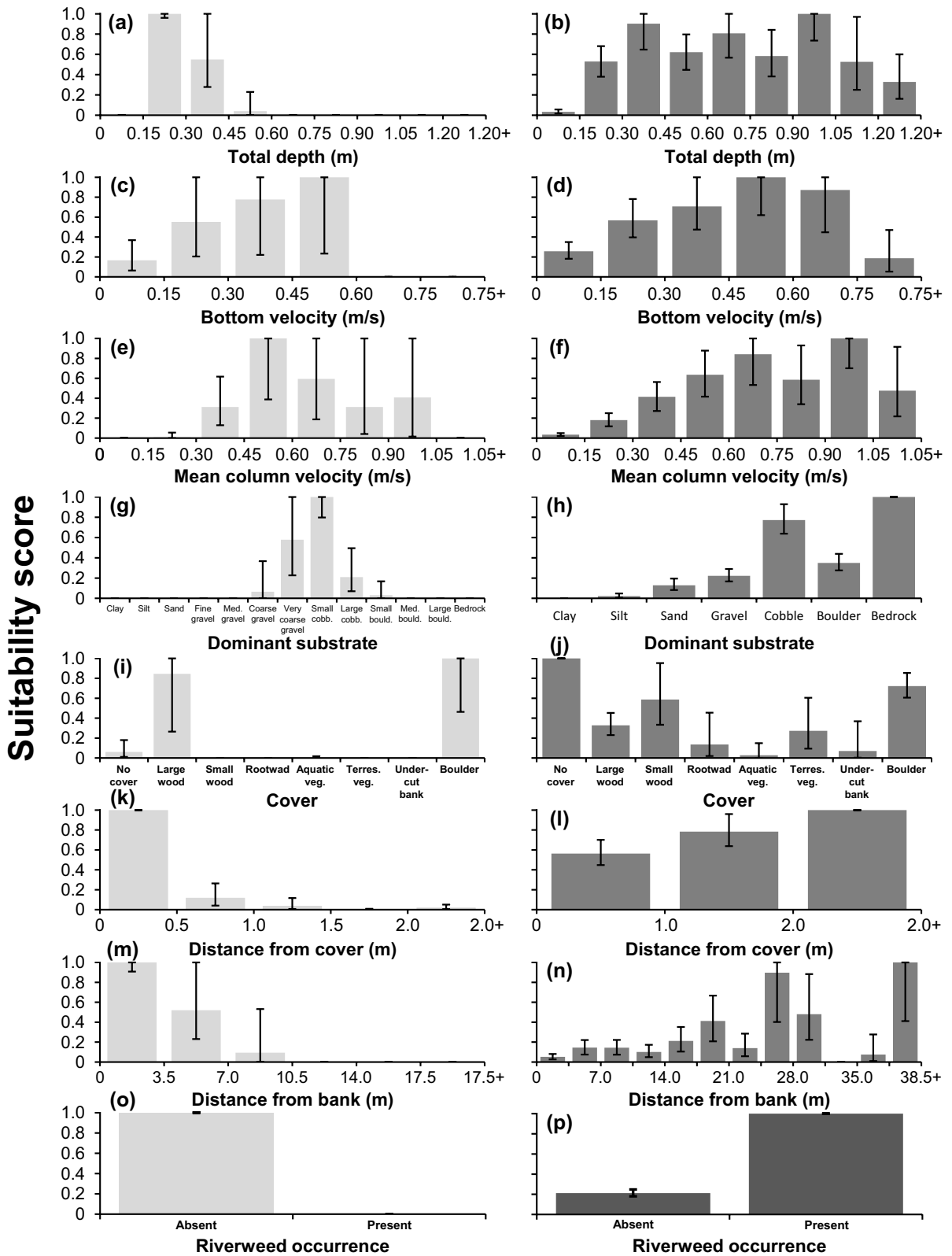
For occupied dominant substrates larger than gravel, presence of riverweed (%) was significantly greater than that for available dominant substrates ($\chi^2 \geq 5.29$, $df=1$, $P \leq 0.0214$), with the exception of small boulder ($\chi^2=0.44$, $df=1$, $P=0.5097$). Occupied large boulders and bedrock had riverweed presence estimates of 87.5% and 92.9%, respectively. Conversely, available dominant substrates boulder and bedrock had riverweed presence estimates of 40.3% and 54.4%, respectively. Such a large divergence indicates that adult sicklefin redhorses occupied substrates larger than gravel supporting riverweed beds significantly more frequently than such combinations are available, especially for large boulders and bedrock ($\chi^2 \geq 25.64$, $df=1$, $P < 0.0001$).

During the spawning season (1 March–31 May), 47.1% of fish observations confirmed foraging. During the nonspawning period (1 June–29 February), 87.0% of fish observations confirmed foraging. Annually, foraging was most frequently associated with coarse substrates. During the spawning season, bedrock (43.8%), cobble (37.5%), and boulder (12.5%) were used most frequently for foraging. During the nonspawning period, bedrock (85.1%) and boulder (12.2%) substrates were most frequently used for foraging.

Discussion

Microhabitat use and suitability

Specialist species exhibit unique morphological and behavioral characteristics to persist within a narrow



◀**Fig. 3** Spawning site and annual Bayesian microhabitat suitability scores and 95% credible intervals for Hiwassee River basin adult sicklefin redhorses for variables (a, b) total depth, (c, d) bottom velocity, (e, f) mean column velocity, (g, h) dominant substrate, (i, j) cover, (k, l) distance from cover, and (m, n) distance from bank. Spawning site and annual Bayesian suitability scores and 95% credible intervals for (o, p) riverweed occurrence are also provided. Spawning site and annual Bayesian suitability histograms are represented by light and dark gray histograms, respectively

ecological niche (Brown 1984; Futuyma and Moreno 1988; Ferry-Graham et al. 2002). In addition to the sicklefin redhorse's exceptionally falcate dorsal fin compared to other *Moxostoma* spp. (Jenkins 1999), our empirical fish–habitat relationships indicate the sicklefin redhorse is a habitat specialist, especially pertaining to spawning oviposition sites. Often, human modifications (e.g., hydrosystems) to stable lotic habitat templates decrease the value of life-history traits, which increases extirpation risk (e.g., hare-lip sucker (*Moxostoma lacerum*; Scarnecchia 1988; Miller et al. 1989; Jenkins and Burkhead 1994; Poff and Allan 1995). Throughout the sicklefin redhorse's geographic range, anthropogenic habitat degradation and loss have considerably altered the historic habitat template, creating a conservation concern (Messer and Ratledge 1963; Messer 1965; Jenkins 1999; Favrot and Kwak 2018).

Habitat complexity and heterogeneity are critical factors governing the spatiotemporal life history requirements of lotic potamodromous fish assemblages (Gorman and Karr 1978; Poff and Allan 1995; Fausch et al. 2002; Favrot and Kwak 2018). Hiwassee River basin adult sicklefin redhorses conduct extensive migrations into relatively shallow spawning tributaries during spring, while deep lower reaches of Hiwassee River are occupied in winter (Favrot and Kwak 2018). Numerous sucker species occupy shallow depths for spawning and deep waters during winter (Curry and Spacie 1984; Kwak and Skelly 1992; Matheney and Rabeni 1995; Grabowski and Isely 2006, 2007; Fisk et al. 2015). Human activities within the sicklefin redhorse's geographic range contribute to homogenized depths including reservoirs, agriculture, timber harvest, mining, channelization, and urbanization (Yeager 1993; Waters 1995; Jenkins 1999). Our finding that adult sicklefin redhorse exhibit distinctly different seasonal and spawning site HSCs indicates that basin-scale habitat complexity

and heterogeneity are vital to future management and restoration initiatives.

Occupancy of a wide range of current velocities is typical of North American suckers (Matheney and Rabeni 1995; Grabowski and Isely 2007). Suckers tolerate habitats ranging from calm reservoirs to swift rapids (Jenkins and Burkhead 1994); however, lentic reservoir habitats generally negatively affect redhorses (Miranda and Dembkowski 2016; Miranda et al. 2017). Adult sicklefin redhorses appear to exclusively occupy lotic portions of Hiwassee River basin, except during spawning migrations to partially impounded spawning tributaries (e.g., Nottely River; Jenkins 1999; Favrot and Kwak 2018). Other suckers, such as the torrent sucker (*Thoburnia rhothoeca*) and blue sucker (*Cycleptus elongates*), similarly occupy swift currents (Parker and McKee 1984; Sule and Skelly 1985; Jenkins and Burkhead 1994; Vokoun et al. 2003; Neely et al. 2010). The Hiwassee and Little Tennessee river basins host extensive hydrosystems, which have dramatically reduced the availability of diverse currents, both in impounded reservoirs and dam tailwaters (Jenkins 1999).

Suckers generally spawn over medium to coarse gravels (Page and Johnston 1990), including the northern hog sucker (*Hypentelium nigricans*), white sucker (*Catostomus commersoni*; Curry and Spacie 1984), flannelmouth sucker (*Catostomus latipinnis*; Weiss et al. 1998), black redhorse (*Moxostoma duquesnei*), golden redhorse (*Moxostoma erythrum*; Kwak and Skelly 1992), and robust redhorse (Fisk et al. 2015). In slight contrast, very coarse gravel and small cobble were most suitable at sicklefin redhorse spawning sites. Other suckers also spawn over cobble substrates, such as the bridgelip sucker (*Catostomus columbianus*; Murdoch et al. 2005) and the blue sucker (Etnier and Starnes 1993); yet, others exhibit spawning substrate plasticity ranging from sand to cobble [e.g., razorback sucker (*Xyrauchen texanus*); Tyus 1987; Tyus and Karp 1990]. In contrast, sicklefin redhorses exhibit extreme spawning substrate specificity. Anthropogenic activities contribute to degradation of lithophilic riverine substrates via sedimentation, substrate homogenization, and coarse substrate degradation, which are highly detrimental to benthic fishes such as the sicklefin redhorse (Berkman and Rabeni 1987; Waters 1995).

For many lithophils, clean permeable interstitial spaces are crucial to reproductive success (Balon 1975).

Table 2 Annual, seasonal, and spawning site principal component (PC) loadings for adult sicklefin redbreast microhabitat use and availability, eigenvalues, cumulative variance explained (%), and Kolmogorov–Smirnov (KS) two-sample test results (significance level (α)=0.05). Principal components were calculated based on microhabitat availability data during base flow conditions; PC scores were calculated for both available microhabitat and corresponding microhabitat use. Loadings in bold italics were determined to have predominantly influenced the corresponding PC. Microhabitat use and availability loadings were compared using K-S tests to investigate for nonrandom habitat niche use

Variable or statistic	Annual				Spawning season				Postspawning season				Winter season				Spawning site			
	PC1		PC2		PC1		PC2		PC1		PC2		PC1		PC2		PC1		PC2	
	N		N		N		N		N		N		N		N		N		N	
Available	1815		1815		1704		1704		620		620		493		493		493		493	
Use	674		350		262		262		20		20		36		36		36		36	
Total depth (m)	0.21	0.68	0.21	0.68	0.24	0.48	0.24	0.66	0.27	0.42	0.27	0.65	0.30	0.48	0.30	0.64	0.30	0.47	0.30	0.33
Bottom velocity (m/s)	0.49	-0.47	0.49	-0.47	0.57	-0.26	0.35	-0.06	0.36	-0.06	0.36	0.09	0.34	-0.03	0.43	0.29	0.33	-0.03	0.43	0.29
Mean column velocity (m/s)	0.58	-0.26	0.58	-0.26	0.35	-0.07	0.35	-0.07	0.36	-0.07	0.35	0.27	0.34	-0.03	0.43	0.29	0.33	-0.03	0.43	0.29
Dominant substrate	0.31	0.33	0.31	0.33	0.30	0.33	0.30	0.33	0.36	0.36	0.36	0.27	0.21	0.21	0.21	0.29	0.21	0.21	0.21	0.29
Distance from cover (m)	0.41	0.38	0.41	0.38	0.42	0.35	0.42	0.35	0.42	0.35	0.42	0.25	0.47	0.29	0.47	0.29	0.47	0.29	0.47	0.29
Distance from bank (m)	2.26	1.32	2.26	1.32	2.26	1.32	2.26	1.32	2.35	2.35	2.35	1.23	2.42	1.24	2.42	1.24	2.42	1.24	2.42	1.24
Eigenvalue	37.7	59.8	37.7	59.8	37.6	59.7	37.6	59.7	39.1	59.7	39.1	59.7	40.3	61.1	40.3	61.1	40.3	61.1	40.3	61.1
Cumulative variance explained (%)	0.4421	0.0849	0.4055	0.0722	0.5237	0.1825	0.5237	0.1825	0.6645	0.2548	0.6645	0.2548	0.3191	0.8193	0.3191	0.8193	0.3191	0.8193	0.3191	0.8193
D-statistic	<0.0001	0.0017	<0.0001	0.0939	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0022	<0.0001	0.0022	<0.0001	0.0022	<0.0001	0.0022	<0.0001
P value	<0.0001	0.0017	<0.0001	0.0939	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0022	<0.0001	0.0022	<0.0001	0.0022	<0.0001	0.0022	<0.0001

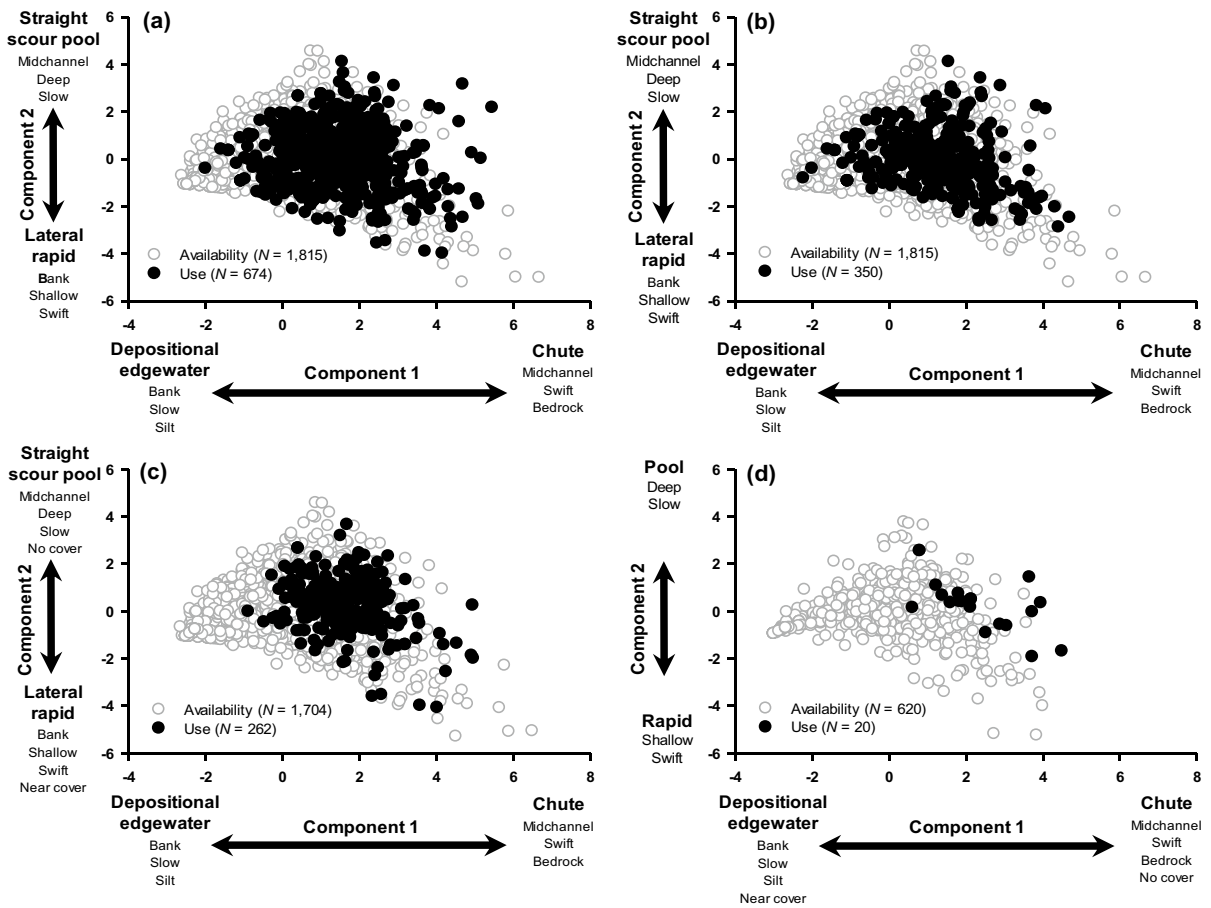


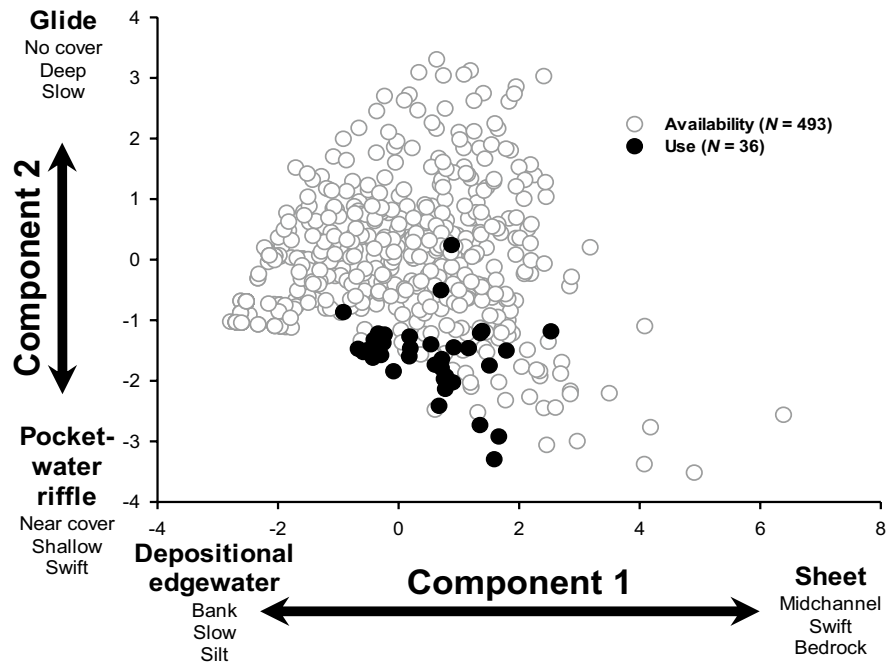
Fig. 4 Annual and seasonal plots of principal component scores for adult sicklefin redhorse microhabitat use and available microhabitat in Hiwassee River basin, western North Carolina and northern Georgia: **(a)** annual, **(b)** spawning season, **(c)**

postspawning season, and **(d)** winter season. Principal component loadings, eigenvalues, and percent cumulative variances are provided in Table 3

Anthropogenically-introduced sediment is the single greatest pollutant in freshwater systems of the U.S. and one of the greatest Hiwassee River basin water quality threats (Messer 1965; Ritchie 1972; Waters 1995; Jenkins 1999; NCDWR 2002, 2007, 2012). Cumulatively, our mean S_o , D_g , and F_i values revealed that Hiwassee River basin sicklefin redhorse spawning substrate pore size and permeability were at half potential. A S_o of 1 indicates perfectly sorted substrates or maximum permeability (i.e., unity: Krumbein and Pettijohn 1938; Lotspeich and Everest 1981). Permeability is maximized when F_i and D_g are equal (i.e., $S_o=1$); thus, relative to large D_g values, low F_i values are indicative of sedimented interstitial spaces (i.e., embeddedness: Platts et al. 1983), which are detrimental to catostomid egg and larvae survival (Jennings et al. 2010).

The vast majority (96.8%) of our sicklefin redhorse spawning substrate samples contained no eggs or embryos. Intraspecific post-spawn egg foraging may be indicative of low spawning substrate egg retention in the Hiwassee River basin (Favrot and Kwak 2018). Survival-to-emergence (STE) has been the primary concern for spawning sites of lithophilic-spawners, with a focus on postburial mechanisms (Muncy et al. 1979; Chapman 1988; Kondolf 2000; Jennings et al. 2010). However, spawning over embedded interstitial spaces can cause egg mortality via several mechanisms, such as suffocation, physical damage, predation, and deposition in poor habitat (Crane and Farrell 2013). Moreover, fines inhibit egg adhesion to spawning substrates, and coarse substrates exhibit relatively low egg retention (Crane and Farrell 2013);

Fig. 5 Plot of principal component scores for adult sicklefin redhorse spawning site microhabitat use and available microhabitat in Hiwassee River basin, western North Carolina and northern Georgia. Principal component loadings, eigenvalues, and percent cumulative variances are provided in Table 3



sicklefin redhorse spawning substrates exhibit both of these detrimental characteristics. Despite coarse spawning substrates, silt plumes are prevalent during sicklefin redhorse spawning acts (Favrot and Kwak 2018). Similarly, considerable disturbance of fines and low egg abundances have been reported for other redhorses in sedimented streams draining agriculture-dominated landscapes (Kwak and Skelly 1992; Jennings et al. 1996, 2010).

The spawning substrate sample containing eggs was associated with female postspawning digs, bolstering the notion that postspawning digs may

Table 3 Summary statistics characterizing sicklefin redhorse spawning (i.e., quivering) subsurface substrate composition for observed spawning acts in Hiwassee River basin, North Carolina and Georgia

Statistic or index	Mean	SE	Min–max
Fredle index	28.2	1.59	14.2–55.10
Sorting coefficient (S_w)	1.9	0.02	1.7–2.4
Geometric mean diameter (mm)	54.0	2.97	30.5–107.7
Median diameter (D50, mm)	78.7	6.32	39.0–230.5
First quartile diameter (D25, mm)	34.8	2.80	15.8–99.00
Third quartile diameter (D75, mm)	128.2	10.35	66.2–377.9
Total fines (%)	3.0	0.38	0.4–9.70
Organic fines (%)	2.4	0.16	1.4–5.70

function as an egg burial mechanism (Favrot and Kwak 2018). In addition to male sicklefin redhorses foraging on unburied eggs following spawning (Jenkins 1999; Favrot and Kwak 2018), we anecdotally observed increased male egg foraging following post-spawning digs, suggesting this catostomid-unique behavior may winnow exposed eggs from embedded spawning substrates. Collectively, Hiwassee River basin’s high sedimentation and embeddedness levels coupled with the reproductive strategies of the sicklefin redhorse suggest spawning site egg retention (i.e., pre-burial survival) may be a primary sicklefin redhorse STE concern.

A common outcome of human activity in aquatic ecosystems is reduced instream structure, which negatively affects populations and assemblages (Smokorowski and Pratt 2007). Nevertheless, catostomid cover relationships have received relatively little attention (but see Grabowski and Isely 2006; Fisk et al. 2015). Although, catostomid spawning sites typically lack cover (Page and Johnston 1990), recent research indicates strong catostomid cover relationships during critical life history periods (winter and spawning periods: Grabowski and Isely 2006; Favrot and Kwak 2018). Similarly, our HSC and PCA results indicate that cover is an integral component of sicklefin redhorse spawning sites.

Suckers typically select spawning sites in midchannel riffles and near-bank areas during nonspawning periods (Curry and Spacie 1984; Kwak and Skelly 1992; Grabowski and Isely 2006; Fisk et al. 2015). In contrast, near-bank spawning locations were most suitable for sicklefin redhorses, while midchannel areas were most suitable annually. It is unclear why adult sicklefin redhorses exhibit divergent bank proximity preferences; however, explanations may be linked to fundamental lotic-specific hydrologic characteristics. In general, high to moderate gradient streams and rivers exhibit deeper depths, swifter currents, and coarser substrates at midstream, while marginal areas are shallower with slower currents and more abundant cover (Matthews 1998). An affinity for spawning adjacent to cover may explain why marginal areas were optimal for sicklefin redhorse spawning site selection. Likewise, thalweg areas may have been most suitable during nonspawning periods because associated coarse substrates and swift velocities are conducive to high riverweed abundance and subsequent adult Sicklefin Redhorse foraging opportunity.

Habitat suitability criteria and transferability

Habitat suitability models are widely considered the biological underpinning in professional conclusions pertaining to habitat quality (Newcomb et al. 2007). Commonly, highly transferable HSCs can be used across a species' geographic range (Bovee 1986; Newcomb et al. 2007); however, HSCs can demonstrate poor transferability (Sheppard and Johnson 1985; Kwak et al. 1992; Rosenfeld et al. 2005).

Unfortunately, establishing population-specific HSCs can be prohibitively expensive and time consuming, so transferable HSCs are valuable fisheries management resources (Newcomb et al. 2007). Generally, riffle specialist (e.g., sicklefin redhorse) HSCs exhibit a higher likelihood of appropriate across-stream transferability compared to pool generalist HSCs (Freeman et al. 1997); thus, the likelihood of appropriate transfer of our sicklefin redhorse HSCs to the Little Tennessee River basin may be high. However, conspecific HSCs can be drastically different due to between-basin body size differences (Witzel and MacCrimmon 1983; Moyle and Baltz 1985). Generally, Hiwassee River basin adult sicklefin redhorses are smaller than Little Tennessee River basin

conspecifics (North Carolina Wildlife Resources Commission, unpublished data), and thus, application of our Hiwassee River basin HSCs to Little Tennessee River basin conspecifics warrants caution (Bovee 1986; McHugh and Budy 2004; Newcomb et al. 2007).

Dominant substrate, riverweed, and foraging

Riverweed is a common swift-water macrophyte in Appalachian Mountain streams and is vital to benthic macroinvertebrates and fish (Grubaugh et al. 1997; Hutchens et al. 2004; Argentina et al. 2010). Despite individual- and population-level dependence on trophic resources (Ross 2013), foraging habitats are quantitatively undescribed for many suckers. Our findings revealed that foraging was strongly associated with bedrock hosting riverweed mats. Riverweed is rare in small tributaries, but abundant in large rivers (Grubaugh et al. 1997). Lower availability of riverweed in sicklefin redhorse spawning tributaries may influence post-spawn emigrations back to Hiwassee River (Favrot and Kwak 2018), where riverweed availability was considerably higher.

Conservation, research, and management implications

Riverweed is imperiled across much of its native geographic range in eastern North America (Philbrick and Crow 1983; Wood and Freeman 2017). Restoration strategies beneficial to riverweed include dam removal, elimination of aberrant hydrological conditions, reduced sedimentation, and pollution elimination (Wood and Freeman 2017). Restored riverweed biomass can increase benthic macroinvertebrate prey availability; thus, adult sicklefin redhorses may receive fitness, bioenergetic, and population demographic benefits (Argentina et al. 2010). Restored access to unoccupied, isolated reaches upstream from hydroelectric dams (e.g., Mission Dam on the Hiwassee River) can restore access to historically available macrohabitats, riverweed clusters, and macroinvertebrate communities via geographic range expansion (Favrot and Kwak 2018). In addition, minimizing seasonal variability in reservoir levels (e.g., ~3 km of Hiwassee River downstream from Valley River's mouth) may restore and maintain healthy riverweed

mats for adult sicklefin redhorses during winter and prespawn staging periods (Favrot and Kwak 2018).

Benthic-insectivores and lithophilic-spawners are particularly vulnerable to sedimentation in lotic systems, and the sicklefin redhorse belongs to both guilds (Berkman and Rabeni 1987; Jenkins 1999). We found high sedimentation in all Hiwassee River basin creeks and rivers occupied by adult sicklefin redhorses; however, adult sicklefin redhorse exhibited near-obligatory use of coarse substrates. Generally, lotic portions of the Hiwassee River occupy the historic channel; however, many sicklefin redhorse spawning tributaries have been channelized to the valley margins to facilitate agriculture and exhibit prolific fine sediments and substrate embeddedness (Messer 1965; Jenkins 1999). Floodplain reactivation, braided channels, increased sinuosity, increased riparian vegetation, increased sediment sinks, and restoration of beaver complexes are restoration tools that can reduce, immobilize, and remove spawning tributary sedimentation (Waters 1995; Pollock et al. 2007; Kemp et al. 2012); however, sediment reduction efforts will be contingent on curtailment of future sediment influxes (Waters 1995; Harding et al. 1998).

Egg and embryo stages have the most restrictive ecological niche of all fish life stages (Cunjak et al. 1998; Kemp et al. 2011). We observed low sicklefin redhorse egg occurrence in degraded spawning substrates, indicating high preburial egg mortality. Despite considerable sampling effort, sicklefin redhorse larvae and juvenile observations (age 1) are rare (Jenkins 1999; Favrot 2009; Favrot and Kwak 2016; Ivasauskas 2017), while larvae and juveniles of congeners are relatively common in spawning tributaries and downstream reservoirs (Jenkins 1999; Ivasauskas 2017). Larval sicklefin redhorses that have been collected from Valley River were predominantly documented in upstream reaches (Ivasauskas 2017), possibly indicating less degraded upstream reaches exhibit higher egg retention and STE rates. Adult sicklefin redhorses exhibit spawning tributary fidelity (Favrot and Kwak 2018); thus, reintroduction and supplementation efforts such as brood collection, instream egg outplanting, acclimation, and direct stream releases may be more effective if less degraded upstream reaches are targeted. Moreover, given the sicklefin redhorse's unique spawning habitat niche and reproductive ecology, future research quantifying preburial egg mortality may be particularly germane to

biologists managing the sicklefin redhorse and other lithophilic-spawning suckers.

All stressors contributing to the imperiled status of the sicklefin redhorse are attributed to anthropogenic activities (Jenkins 1999; GADNR 2015; NCWRC 2015). Since 2010, human population growth in North Carolina and Georgia is among the highest in the southeastern USA and is nearly double the national average (U.S. Census Bureau 2017). The riparian zones of Hiwassee River basin streams and rivers occupied by sicklefin redhorses were largely devoted to agriculture or developed. Intact riparian zones are crucial to lotic ecosystem integrity; however, riparian corridors are rarely sufficiently maintained (Peterjohn and Correll 1984; Jones et al. 1999). Riparian zone conservation initiatives are vital toward stemming future sediment inputs and maintaining quality instream habitat (Waters 1995; Diamond et al. 2002).

Habitat loss and degradation have been implicated as the largest threat to imperiled species in the U.S. and are a primary cause of extinction (Ehrlich and Ehrlich 1981; Richter et al. 1997; Wilcove et al. 1998). Habitat restoration decisions designed to benefit the sicklefin redhorse are most likely to succeed if employed approaches are informed, focused, structured, and adaptive (Conroy and Peterson 2013). Riverscape-wide habitat continuity and heterogeneity will be vital components of any sicklefin redhorse conservation initiative. Although instream habitat restoration can improve the quality of lotic system habitat (Gowan et al. 1994; Quinn and Kwak 2000), conserving currently accessible habitat while increasing the quantity of available suitable habitat niches via range reclamation may prove an optimal approach (Harding et al. 1998; Fausch et al. 2002). The results of this research can support decisions to manipulate aquatic habitat in an effort to protect and enhance the sicklefin redhorse, while attempting to address objectives of affected stakeholders. Implementation of freshwater protected areas, restored riverscape continuity, and establishment of flow regimes that mimic a natural hydrograph would likely benefit the sicklefin redhorse (Crivelli 2002; Cooke et al. 2005). Our seasonal and spawning HSCs, multivariate habitat niche descriptions, spawning substrate analysis, and foraging habitat findings provide fisheries managers and restoration ecologists conservation guidance to apply throughout the sicklefin redhorse geographic range.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval Capture and handling protocols were approved by the Institutional Animal Care and Use Committee at North Carolina State University, Raleigh, NC, USA.

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