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Microhabitat estimation of an imperiled headwater fish, the Yazoo darter (*Etheostoma raneyi*), in coastal plain streams

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Abstract Headwater fishes in the southeastern United States make up much of the fish biodiversity of the region yet many are imperiled. Despite this, the specific habitat requirements of imperiled headwater fishes in lowland Coastal Plain streams have rarely been quantified. Using data collected over three years of seasonal sampling we provide estimates of the microhabitat requirements of the imperiled Yazoo darter (*Etheostoma raneyi* Suttkus and Bart), a small benthic insectivore. Our results indicate that the species is a microhabitat specialist and that optimum microhabitat within degraded contemporary streams consists of a narrow range of water depths (about 20–30 cm), current velocity $\geq 0.25\ \mathrm{m \cdot s^{-1}}$, complex stable debris piles, rooted macrophytes, and likely coarse substrate. No pronounced or generalized seasonal shifts in microhabitat use occurs, and no evidence exists for intraspecific partitioning of microhabitat. Though stable and complex instream cover is one of the most important variables explaining variation in microhabitat use by Yazoo darters, such cover is rare in the degraded streams within the range of the species. Current conservation classifications of the Yazoo darter by governmental agencies and nongovernmental organizations as well as associated management plans that are based on the assumption that Yazoo darters are habitat generalists should be reviewed in recognition of the increased risk of decline because Yazoo darters are microhabitat specialists. These considerations should also be extended to other closely related imperiled species of snubnose darters.

Keywords *Etheostoma* · Microhabitat · Grinnellian niche · Warmwater stream · Instream wood · Coastal plain

Introduction

Headwater stream fishes make up a considerable portion of biodiversity within river drainages (Paller 1994; Myer et al. 2007). Many of these fishes in the southeastern United States are also imperiled (Jelks et al. 2008). For small, benthic species especially, their particular suite of life history characteristics (Turner and Trexler 1998; Radinger and Wolter 2014) can compound the negative effects of habitat fragmentation leading to increased isolation of populations among scattered headwater tributaries (Sterling et al. 2012). Increased isolation results in smaller population sizes, reduction or elimination of gene flow, reduced available habitat, and can prevent dispersal to refugia during disturbance, all of which increases the risk of extirpation (Reed 2008).

Management efforts aimed at conservation of headwater fishes are hampered by a lack of specific information on the optimal habitat requirements of many species of concern, particularly for headwater fishes in lowland Coastal Plain streams of the southeastern United States

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(Warren et al. 2000; Jelks et al. 2008). Though an extensive set of literature is available on the habitat requirements of coldwater and upland warmwater fishes in headwater streams, the results of these studies cannot be assumed to apply to fishes of the Coastal Plain because the streams of this region are fundamentally different (e.g., geology, hydrology, land use history, and available habitat) from streams in other parts of the country (Meffe and Sheldon 1988; Shields et al. 1998).

The Yazoo darter (*Etheostoma raneyi*) is a small (<65 mm SL), benthic, insectivore endemic to small Upper Gulf Coastal Plain streams in the Yazoo River basin of north-central Mississippi (Suttkus et al. 1994; Johnston and Haag 1996; Sterling et al. 2013). Due to limited distribution and widespread and ongoing habitat degradation within its range, the species is categorized as a Tier 1 species of greatest conservation need by the Mississippi State Wildlife Action Plan (Mississippi Museum of Natural Science 2015), as Near Threatened by the IUCN (NatureServe 2014), and Vulnerable by the Southeastern Fishes Council and the American Fisheries Society (Warren et al. 2000; Jelks et al. 2008). Phylogenetic data indicate that the species is most closely related to other Coastal Plain snubnose darters (clade *Adonia*, Near et al. 2011) at least two of which (*Etheostoma cervus* and *E. pyrrhogaster*) are species of concern with limited ranges and are also at risk due to ongoing alteration and fragmentation of habitat. The habitat needs of these species are unquantified.

A study that examined the mesohabitat affinities of the Yazoo darter for a single stream population concluded the Yazoo darter was a habitat generalist among riffle, run, pool, and undercut-bank habitats (Johnston and Haag 1996). No relationships were found between Yazoo darter abundance and depth, velocity, instream cover, substrate, or canopy cover using ordination methods (Johnston and Haag 1996). Suttkus et al. (1994) described reach-scale Yazoo darter habitat as spring-fed streams with sandy substrate, often with burr-reed (*Sparganium* sp.) present but noted that within the range of the species channelized sites with unstable substrate and defoliated banks that were distant from spring sources did not yield Yazoo darters.

Our experience in the field and the species' occurrence among local streams indicated that Yazoo darters were not habitat generalists, and we hypothesized that cover, particularly instream wood, was closely associated with the occurrence of the species at the microhabitat scale. We also hypothesized that Yazoo darters may shift microhabitat use in response to seasonal changes in stream flow or water temperatures (Schlosser and Toth 1984; Schlosser 1991) and that Yazoo darters would shift microhabitat use in early spring when they spawn. We implemented a study to answer the following questions: 1) does the Yazoo darter use available microhabitat non-randomly; 2) what microhabitat variables best explain variation in habitat use; 3) are there seasonal shifts in microhabitat use; 4) is microhabitat use related to size and sex; 5) how could our results inform management efforts for imperiled Coastal Plain headwater fishes?

Methods

Site description and field methods

Yazoo darters are distributed within the Northern Hilly Gulf Coastal Plain Ecoregion (Chapman et al. 2004; Sterling et al. 2013). The area consists of low, rolling hills with elevations of about 80–180 m. We chose three perennial streams (Table S1) for our study sites based on previous sampling efforts indicating that these streams had higher catch rates for Yazoo darters compared with most other streams (Sterling et al. 2013) and also encompassed the two major drainages within their distribution. All three streams were typical of Gulf Coastal Plain streams where the species occurs (i.e., low gradient, flowing, predominantly sandy substrate, and moderately incised) (Shields et al. 1998; Warren et al. 2002) with similar water quality (see Supplemental text, Table S2).

Because stream widths and the amount of available habitat within a stream varied over time, we followed a standardized procedure to predetermine the length of our study reach. We fixed the location of the downstream edge of the reach and then measured the stream wetted width at five, 50-m intervals upstream. We calculated average width and multiplied the average by 30 m to obtain reach length (minimum reach length, 120 m). Due to the intermittent presence of beaver dams and impounded water, we moved study reaches up- or downstream as needed through time. We used a Hydrolab Quanta sonde to measure water quality parameters (temperature, conductivity, dissolved oxygen, and pH) before commencing stream sampling, but because of high similarity among streams and samples, we summarized but did not analyze those variables (Table S2).

For each sample, we first captured Yazoo darters and measured habitat use variables, then measured available habitat variables. We usually measured both sets of variables on the same day. For data collected on separate days (habitat used vs available habitat) the maximum number of days between paired samples used for analyses was five days and measurable rain did not occur. Samples were collected from 2 June 2009 to 6 March 2012. We grouped data into three seasons: Summer (May 15–October 31), Winter (Nov. 1-Feb. 15), and Spawn (February 16–May 14). The Summer season corresponds to the average annual low flow period for our study streams as well as the highest seasonal water temperatures. The Winter and Spawn seasons correspond with the average annual high flow period and lower water temperatures (United States Geological Survey 2016). Spawning in Yazoo darters occurs from the end of February to the first half of May, depending on water temperatures (Johnston and Haag 1996).

Starting at the downstream end of the study reach, we used single-pass backpack electroshocking and dip nets to sample Yazoo darters. We allocated fishing effort among all habitats within the study reach. Immediately upon capture of a Yazoo darter, we marked the capture location with a small anchored float. For each individual we recorded standard length (SL) and sex for adults (males retain orange pigment and color bands in the median fins year round) and juveniles when possible (>6–7 months of age when orange pigment in males develops). Juveniles that could not be sexed were not used for analyses. After releasing Yazoo darters at their point of capture we then immediately began to sample the next segment of the stream. Because darters in general are not highly vagile (Adams and Warren 2005; Radinger and Wolter 2014), and were recovering from capture after release, we are confident that we did not recapture the same individuals on any given day.

After Yazoo darter sampling was completed, we measured a suite of habitat variables within a 50 cm diameter circular quadrat centered on the point of capture of each darter. We measured water depth (Depth, cm), water velocity (Velocity, $m \cdot s^{-1}$), distance to the nearest instream cover (e.g., wood, rock, detritus, etc.) (DistNOC, cm), and the distance to the bank (DistBank, cm) from the point of capture. We recorded the relative abundance (primary, secondary, and tertiary) of cover and substrate types. For example, if small wood was the predominant cover but there was some detritus present we recorded small wood as the primary cover, detritus as the secondary cover, and no cover as the tertiary cover. We also recorded the number of cover (CovTypes) and substrate types (SubTypes) within the quadrat.

We defined cover types as Detritus (organic debris), LW (large wood, >10 cm diameter and >1.5 m long), SW (small wood, <LW), Plant (aquatic macrophytes and algae), Bank (rootwads, undercut banks, overhanging terrestrial macrophytes), Rock (substrate >16 mm, primarily rip rap), No Cover (no cover types within the quadrat), and Anthro (e.g., appliances, tires, bridge pilings).

We defined substrate types as Clay (particles <0.004 mm), Silt (0.004–0.063 mm), Sand (0.063–2 mm), Gravel (2–256 mm), and Hard Clay (>256 mm). Although we followed a modified Wentworth scale (Wentworth 1922) for substrate classification for Clay, Silt, and Sand, substrates larger than Sand are rare within the range of the Yazoo darter (Warren et al. 2002) so we combined fine gravel, coarse gravel, and cobble into one category (Gravel). Substrates larger than cobble are even more uncommon and were present in <1% of samples so were dropped from analyses.

After sampling for Yazoo darters, we surveyed random points within the study reach to characterize available habitat. We used the same procedures as described for Yazoo darter samples. To mark random points we used a random number generator to create paired points. Starting at the downstream edge of the study reach, the first number of a random pair indicated how many meters upstream to advance, and the second number indicated how far from the left bank to locate our sample. Each random point was marked with a weighted float and subsequently characterized. We located and measured random samples throughout the reach. Differences in stream sizes caused some variation in the number of random samples needed to fully sample the reach, but we sampled a minimum of 50 random sample points on each visit to a study site.

Tests of nonrandom habitat use

We used Multi-Response Permutation Procedures (MRPP) and SumF as implemented in PC-ORD ver. 6.21 (McCune and Mefford 2011) to test for nonrandom habitat use by comparing multivariate available habitat data to habitat use data. MRPP is a nonparametric multivariate method that tests for differences among groups and allows for unbalanced designs such as ours.

Output includes the test statistic *T*, which indicates separation among groups, and an effect size (*A*), which is a measure of within-group similarity. *P*-values are produced using permutation. We used Sorensen distances and rank-transformed all variables (McCune and Grace 2002). Sum F is similar to MRPP in that it is a multivariate permutation test; however, the test statistic (SumF) is the sum of univariate F-statistics calculated for each response variable included in the overall multivariate test. Samples are then randomly assigned to groups over many permutations and the resulting SumF values are compared with the observed value to obtain a *p*-value (Edgington 1995; Warton and Hudson 2004). One advantage of the SumF method is the output includes the F-statistic for each variable, which indicates the relative importance of each variable in distinguishing groups.

We compiled data from a single paired sample (use and availability) at each site (three replicates) for each season and had enough paired samples to create two tests per season comparing habitat availability and habitat use (i.e., non-random use of habitat). Though we sampled for three years, weather, logistics, and low sample sizes of Yazoo darters prevented three seasonal tests each year. We adjusted alpha for six tests ($\alpha = 0.0204$) using a false discovery rate method (Bender and Lange 2001; Benjamini and Yekutieli 2001; Narum 2006). We also used MRPP to test for differences in available habitat (six tests) and habitat use (six tests) among seasons (adjusted $\alpha = 0.0204$). Because tertiary Silt and primary, secondary, and tertiary Anthro were present in <1% of samples, they were dropped from all MRPP and SumF tests. All other variables defined in the Field Methods section were used (Table S3). To avoid pseudoreplication, we did not pool data from multiple samples at the same site within test groups. For all analyses measurement data (Depth, DistNOC, and DistBank) were log10 transformed, and count data (CovTypes, SubTypes, Velocity) were square root transformed (McDonald 2014).

Modeling and PCA ordinations

To estimate which variables were most influential in describing Yazoo darter habitat use, we used Nonparametric Multiplicative Regression (NPMR) as implemented in the program HyperNiche v.2.3 (McCune and Mefford 2004; McCune 2006). NPMR produces results comparable or superior to other commonly used niche modeling approaches (e.g., Random Forests, CART, MAXENT, MARS) (McCune 2006; Lintz et al. 2011; Tarkesh and Jetschke 2012). The primary advantage of the method is that model forms are not predetermined and reflect the multiple nonlinear responses of target species to their environment as well as complex interactions that are inherent to ecological data sets (for details see McCune 2006). To evaluate and compare model fit, HyperNiche output includes Area Under the Curve (AUC) from Receiver Operating Characteristic curves (Fielding 1999). This metric (range 0.5–1) is independent of sample size, and an AUC value of 0.5 indicates that model fit is no better than random. Variables included in final models are not in order of importance and interactions may be stronger than any single variable alone.

Because we were using NPMR as a descriptive tool, we pooled data from each of the two seasonal samples used for MRPP and SumF tests (i.e., instead of producing six models, two for each season, we created one model for each season). We also created one Overall model pooling all data from the six samples. We used a local mean Gaussian kernel model with the default moderate overfitting controls in HyperNiche.

We used Pc-ORD ver. 6.21 (McCune and Mefford 2011) to produce PCA ordinations as another visual interpretation of our data. We used the same data as detailed for NPMR models and produced ordinations for each season and overall. We used the built-in randomization feature to estimate the number of valid axes. Variables dropped from MRPP and SumF testing (present in <1% of samples) were not used for NPMR and PCA. All other variables defined in the Field Methods section were used (Table S3).

Availability versus use of cover and substrate

Though we had tested for non-random habitat use (MRPP and SumF), and estimated which variables were most influential in describing variation in habitat use by Yazoo Darters (NPMR, SumF, and PCA), we also investigated which primary cover and substrate variables showed differences between use and availability. We calculated relative proportions of all primary cover and substrate types for available habitat and habitat use samples for each season using the same data as for MRPP and SumF tests. To test for differences in seasonal proportions of cover and substrate types between available habitat and habitat use samples, we used resampling methods to produce the equivalent of Chi-square tests for small sample sizes (Statistics.com LLC 2009). Alpha was adjusted for four tests for substrate variables ($\alpha = 0.024$) and seven tests for cover variables ($\alpha = 0.0193$). Due to weather and logistics, we had sample data that were not used in hypothesis testing (too much time or measurable rain between paired samples). However, to summarize our proportional data using histograms we used all our data.

Because we believed that Yazoo darters were selecting for habitat with more complex cover and substrate, we used resampling methods (Statistics.com LLC 2009) to test for differences between the number of available and used cover types (CovTypes) and substrate types (SubTypes) for each season. We used the same data as for the MRPP and SumF analyses. The test statistic was the sum of the absolute deviations between the group means for available habitat and habitat use samples and the overall mean. Data was shuffled between available habitat and habitat use samples, and the test statistic was calculated from 10,000 iterations. To calculate a *p*-value, we compared the observed value for the test statistic to the number of randomizations with an equal or greater value for the test statistic.

Depth, velocity, DistNOC, and DistBank

We were interested in assessing the breadth of use of depth and velocity by the Yazoo darter versus that of available habitat. To do so, we used resampling methods to test whether the standard deviation for Depth and Velocity was different between available habitat and habitat use data (Statistics.com LLC 2009). Our null hypothesis was that the standard deviation was the same for available habitat and habitat used by the Yazoo darter. We shuffled the data for available habitat and Yazoo darter habitat and calculated the difference in standard deviations between the two treatments over 10,000 iterations. We calculated a *p*-value as described for number of cover types. We used data from a single sample at each site taken over one week (Summer 2010). The test requires a balanced design, but sample sizes for available habitat ($n = 160$) were higher than for Yazoo darter habitat ($n = 99$). To achieve a balanced design, we randomly eliminated available habitat points so that each site had an equal number of available and Yazoo darter habitat data points. To determine if this biased results, we created three balanced data sets and ran the randomization test for each; results were essentially identical.

We calculated means and 95% confidence intervals (CIs) for Depth, Velocity, DistNOC, and DistBank for available habitat and Yazoo darter habitat for each season. We used resampling methods (Statistics.com LLC 2009) and 10,000 iterations to calculate CIs.

Niche breadth and overlap

To examine possible seasonal shifts in use of substrate and cover we calculated niche breadth and niche overlap for each season using all primary cover and substrate variables. We used niche metrics (De Cáceres et al. 2011) that account for availability of resources as well as use (Hurlbert 1978) and also similarity among resources (Colwell and Futuyma 1971). Niche values range from 0 to 1 with low values indicating narrow niche breadth and less niche overlap and the reverse for high values. Bootstrapping was used to estimate 95% confidence intervals (CIs) around point estimates for niche breadth and niche overlap among seasons. Calculations were carried out using the ‘indicspecies’ v.1.7.3 package in the R environment v.3.1.1 (De Cáceres et al. 2011; R Core Team 2014).

Size and male versus female habitat use

We were interested in comparing habitat use by adults of different sizes and sex. We used regression analysis to investigate possible relationships between SL of Yazoo darters and Velocity, Depth, DistNOC, and DistBank because we hypothesized that smaller Yazoo darters would use habitat that was shallower, closer to the bank and cover, and with lower flow than larger individuals. We used logistic regression to estimate relationships between SL and the number of substrate types and number of cover types because we thought that smaller individuals would be sampled in more complex habitat over less complex substrates (i.e., slower currents, depositional areas). To test for possible differences in habitat use between females and males, we used Pearson’s exact chi-square test (Cytel Inc. 2007) on relative proportions of primary cover types used by each sex. Because we hypothesized that female-skewed sex ratios (Johnston and Haag 1996) might be related to males using deeper habitats further from cover, we compared Depth, Velocity, and DistNOC between sexes using resampling methods to test for differences in means for each variable between sexes (Statistics.com LLC 2009). Because we believed that any differential intraspecific use of habitat would be influenced by density dependent processes, we only used data for these analyses from Big Spring Creek, which had the highest abundance of Yazoo darters among our study streams.

Results

Tests of nonrandom habitat use

Yazoo darters showed nonrandom use of habitat across time as indicated by MRPP (Table 1) and SumF (Table 2) results. Effect sizes (*A*) and the group differentiation statistic (*T*) from MRPP tests are similar for all tests. Results from SumF indicate that primary, secondary, and tertiary No Cover as well as CovTypes were most influential. However, secondary Detritus and Depth were also influential for some seasons (Tables 3 and S4). Use of habitat by Yazoo darters and available habitat differed significantly across seasons (MRPP; Table 4). Group differentiation (*T*) and effect size (A) are similar among seasons for habitat use and availability.

Modeling and PCA ordinations

Modeling consistently yielded Depth, primary No Cover, secondary No Cover, and CovTypes as the most influential variables describing Yazoo darter microhabitat use (NPMR; Table 5). Velocity and primary Plant, however, were included in final models for Spawn, and primary Detritus was included in the final overall model. Tertiary Detritus was included in the final model for Winter. Two dimensional response surfaces show a hump shape response for Depth and a positive linear response for Velocity and CovTypes (Fig. 1). Overall shapes of species response surfaces for all quantitative variables were consistent across all models (Fig. S1-S3). Response surfaces for categorical variables such as No Cover are not generated by HyperNiche, however, it is clear that Yazoo darters show a strong negative association with areas with no cover (Table 6 and Figs. S16-S19).

Table 1 MRPP analysis of non-random use of habitat across seasons

Test	n (Use)	n (Available)	*T*	*A*	p
Summer1	89	160	−15.86	0.041	<0.0001
Summer2	26	163	−11.79	0.041	<0.0001
Winter1	80	150	−37.52	0.094	<0.0001
Winter2	48	152	−13.57	0.042	<0.0001
Spawn1	58	150	−22.81	0.065	<0.0001
Spawn2	53	160	−21.25	0.062	<0.0001

T = group differentiation, *A* = within group similarity, adjusted $\alpha = 0.0204$

Table 2 SumF analysis of non-random use of habitat across seasons

Test	Obs. SumF	SumF Randomization				p
		Mean	Maximum	S.Dev	SumF*	
Summer1	221.4	37.98	98.79	11.83	0	0.0002
Summer2	141.5	38.53	201.75	12.93	1	0.0004
Winter1	464.6	37.29	108.51	11.54	0	0.0002
Winter2	160.7	38.34	97.87	11.4	0	0.0002
Spawn1	242.1	37.23	132.19	11.82	0	0.0002
Spawn2	266.8	38.17	100.82	11.75	0	0.0002

Obs. SumF = SumF from actual data, *Mean* = mean SumF from all randomizations, *Maximum* = largest SumF from randomizations, *S.Dev* = standard deviation from randomizations, *SumF** = number of randomizations with a SumF ≥ than the observed value of SumF

Model evaluations (Table 5) indicated that model fits are moderately well supported (AUC: 0.74–0.84). For the overall model about 3% of Yazoo darter use samples were classified by the model as absent (error of omission) and about 23% of habitat availability samples (random samples) were classified as present (error of commission).

In overall support of the modeling results, PCA revealed Yazoo darters are decidedly associated with cover in all ordinations. Ordinations show slight changes between Summer and Spawn, but apparently larger differences between Winter and the other two seasons (Figs. S4-S15). A cover gradient from no cover (primary, secondary No Cover) to complex cover (CovTypes) and wood (primary, secondary SW) was consistent on Axes 1 and 2 for all ordinations. For Summer and Spawn a gradient on Axis 3 is apparent from flowing water associated with Yazoo darters (primary Sand and Velocity) to backwater or deep pool environments (primary Silt and secondary Sand). This pattern is consistent, but weaker, for Winter. Another consistent gradient (Axis 1) is from complex substrate (SubTypes), gravel (primary, secondary Gravel), and rock (primary,

Table 3 Results from SumF showing variables ranked by F-value for each test

Test	Variable 1	Variable 2	Variable 3	Variable 4	Variable 5
Summer1	1NoCover	CovTypes	2NoCover	Depth	1SW
Summer2	2NoCover	2Detritus	CovTypes	1NoCover	Depth
Winter1	2NoCover	CovTypes	1NoCover	3NoCover	Depth
Winter2	2NoCover	CovTypes	2Detritus	1NoCover	3Rock
Spawn1	2NoCover	CovTypes	1NoCover	2Detritus	3NoCover
Spawn2	2NoCover	CovTypes	3NoCover	1NoCover	DistNOC

See Table S4 for complete results; numerical prefixes refer to primary, secondary, and tertiary substrate and cover types

secondary Rock) that is associated with Yazoo darters to less complex substrates dominated by sand (primary Sand). In Winter Depth, primary SW, and secondary LW are associated with Yazoo darters on Axis 2.

Availability versus use of cover and substrate

Across seasons, univariate analyses indicate Yazoo darters completely avoid microhabitats without cover (No Cover), occupy areas with diverse cover types, and show some differences in use of available cover, but no differences in use versus availability of number of substrates. Proportional differences between available cover and use of cover indicated that Yazoo darters use instream wood (SW and LW) in higher proportion than is available during Summer and SW during Spawn (Table 6). They also show a proportional increase in use of SW and Rock during Winter. Yazoo darters also occur significantly more often in areas with a greater number of cover types (i.e., more complex cover) in all seasons (Table 7, see also Figs. 1 and S16-S19). Proportional differences between available substrate and Yazoo darter use of substrate show no statistically significant differences; likewise for differences in the number of substrate types used (see Table S5, Figs. S20-S23).

Depth, Velocity, and DistNOC

Standard deviation for Depth ($p < 0.0002$) was significantly lower for habitat used by Yazoo darters than for available habitat. No significant difference was detected for standard deviation of Velocity in used versus available habitat ($p = 0.91$).

Means and confidence intervals of variables between available habitat and use indicate Yazoo darters consistently occupy habitats nearer to other cover (DistNOC) than is available, but patterns for availability versus use of Velocity and Depth vary among seasons (Fig. 2). Relative to available habitat, Yazoo darters showed a pattern of occurring in deeper, faster water in Summer, faster water in Winter, and deeper water during Spawn. Comparisons show less overlap of CIs among available habitat variables than for habitat use variables.

Niche breadth and overlap

Yazoo darters exhibited narrow niche breadth for habitat and virtually complete seasonal niche overlap in habitat. Estimates for niche breadth are low for cover and substrate variables and are similar among seasonal comparisons (Table 8). Upper 95% CIs are all <0.2 for substrate and <0.03 for cover variables. The niche overlap estimates are all near 1 and lower 95% CIs are all >0.6 for substrate and >0.98 for cover variables.

Size and male versus female habitat use

No relationships were detected between size or sex and habitat use. Regression analysis indicates no relationship between SL and Velocity ($R^2 < 0.01$, $p = 0.26$),

Table 4 Results from MRPP testing for differences in available habitat and habitat use by season

	Summer vs. Winter			Summer vs. Spawn			Winter vs. Spawn		
	T	*A*	p	*T*	*A*	p	*T*	*A*	p
Available	−19.71	0.037	0	−11.54	0.022	<0.0001	−6.05	0.011	0.0003
Use	−4.27	0.017	0.003	−5.33	0.023	0.0005	−3.05	0.014	0.02

T = group differentiation, *A* = within group similarity, adjusted α = 0.0204

Table 5 Results from NPMR models (HyperNiche) for each season and an Overall model

	AUC	Omission	Commission	Variable a	Variable b	Variable c	Variable d
Overall	0.81	0.032	0.23	Depth	1NoCover	2NoCover	1Detritus
Summer	0.74	0.014	0.32	Depth	1NoCover	CovTypes	
Winter	0.78	0.005	0.29	Depth	2NoCover	CovTypes	3Detritus
Spawn	0.84	0.012	0.22	1NoCover	2NoCover	Velocity	1Plant

Numerical prefixes refer to primary, secondary, and tertiary substrate and cover types; variables are not ranked

See Figs. 1 and S1–3 for response surfaces and polarity of effects of variables

AUC = area under the curve, *Omission* = error of omission, *Commission* = error of commission

Depth ($R^2 < 0.01$, $p = 0.31$), DistNOC ($R^2 < 0.01$, $p = 0.98$) or DistBank respectively ($R^2 < 0.01$, $p = 078$). Logistic regression of SL and CovTypes ($\chi^2 = 2.61$, $p = 0.63$) and SubTypes ($\chi^2 = 2.85$, $p = 0.42$) indicated no relationships. Standard length of Yazoo darters at Big Spring Creek ranged from 30 to 52 mm. Microhabitat use between sexes does not show differences for Depth (resampling methods; $p = 0.57$), Velocity ($p = 0.82$), or DistNOC ($p = 0.23$). Likewise, there are no significant differences in cover or substrate use between sexes (Pearson's Chi-square exact test) (all $p > 0.07$). The male to female sex ratio at Big Spring Creek was 1:4.7.

Discussion

The weight of evidence from all our analyses leads us to conclude that Yazoo darters are decided microhabitat specialists. Theory and the Yazoo darter's life history characteristics are consistent with this conclusion. The distribution of the Yazoo darter appears to be tightly linked to perennial flow and groundwater input (Suttkus et al. 1994), and the modifying influence of springs and groundwater input apparently prevented large variation in available habitat for our study streams (e.g., water velocities, depth, and temperatures). Theory indicates that if habitat is relatively stable during an individual's lifetime, adaptation to local conditions will favor Grinnellian specialization (Levins 1968). Yazoo darters seldom live beyond two years (Johnston and Haag 1996), and in the perennial streams they inhabit disturbance is likely minimized over that time. Yazoo darters show limited distribution (Sterling et al. 2013), low dispersal (Adams and Warren 2005; Sterling et al. 2012), and resultant genetic subdivision (Sterling et al. 2012) and lower genetic diversity (Sterling et al. 2012), factors that are also associated with specialization (Levins 1968; Turner and Trexler 1998; Devictor et al. 2010; Li et al. 2014). Though our data (MRPP and means with CIs) do show significant shifts in available habitat among seasons, those differences are relatively small. The only large change occurred in the winter with the annual input of leaves from deciduous plants.

Results show that Yazoo darters use all forms of cover (Figs. S16-S19), however their relatively greater use of in-stream wood combined with greater use of complex cover (CovTypes) suggest that cover stability is important. Within the unstable and flashy streams of our study area (Shields et al. 1998), more stable forms of cover such as rooted macrophytes, LW, or even anthropogenic objects such as tires or appliances (Adams 2014) may collect more diverse and structurally complex cover over time and form debris piles. This in turn may offer greater protection from predators (Everett and Ruiz 1993) and flashy flows (Crook and Robertson 1999), as well as provide habitat for aquatic insect larvae that compose much of the diet of the Yazoo darter (Pitt and Batzer 2011; Stewart et al. 2012), and spawning substrate for attaching eggs (Johnston and Haag 1996).

Substrate variables were not included in NPMR models explaining variation in microhabitat use by Yazoo darters. Comparisons of use and availability of primary substrate types did not show statistically significant differences except perhaps for decreased use of Sand and increased use of Gravel during Spawn (Table S5) when NPMR models indicated that Yazoo darters were selecting for erosional habitat (Table 5). However, PCA ordinations (Figs. S4-S15) did indicate that complex substrates and Gravel were generally associated with Yazoo darter habitat use and NPMR models did show a moderate positive response to more complex substrate (Fig. S3). Likewise, the F-statistics

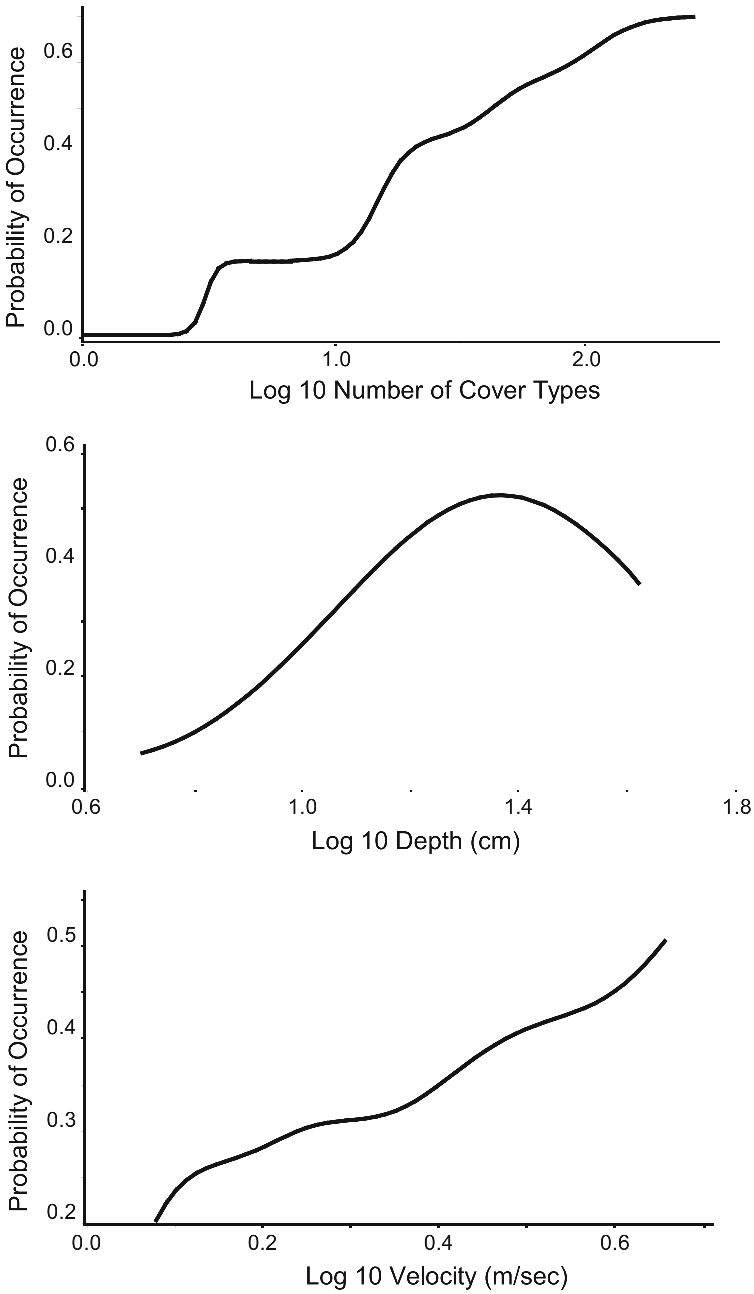

Fig. 1 Output from NPMR model using overall data showing: (*upper*) two dimensional response curve for the number of cover types (CovTypes; x-axis); the probability of occurrence (y-axis) increases as the number of cover types increases; (*middle*) two dimensional response curve for Depth (x-axis); the probability of occurrence (y-axis) shows a hump-shaped response to water depth; and (*lower*) two dimensional response curve for Velocity (x-axis); the probability of occurrence (y-axis) increases as stream velocity increases

from our SumF results (Table S4) indicate that the number of substrate types became more important during Spawn. This is supported by the histograms of substrate use during Spawn (Fig. S23). If available substrate had been more diverse, our methods would have possibly produced a stronger indication of the relative importance of substrates like gravel (likely positively associated) and silt (likely negatively associated) in estimating Yazoo darter microhabitat use. Even so, our results strongly hint that coarse and complex substrate is potentially an important component of Yazoo darter microhabitat use at least during Spawn.

Our data do not indicate pronounced shifts in microhabitat use related to seasonal differences. This result was unexpected (Angermeier 1987; Schlosser 1991; Gillette et al. 2006; but see Grossman and Freeman 1987; Skyfield and Grossman 2008). We suspect that during droughts, unusually high flows following spates, or

Table 6 Results from resampling analyses of proportional use and availability of primary cover types for each season,

	Group	n	1Detritus	1LW	1SW	1Plant	1Bank	1Rock	1NoCover
Summer	Use	89	0.146	0.124	0.551	0	0.045	0.135	0
	Available	160	0.244	0.019	0.325	0.013	0.019	0.106	0.275
	p		0.046	0.0006*	0.0005*	0.41	0.21	0.31	<0.0001*
Winter	Use	80	0.45	0.05	0.3625	0	0	0.1375	0
	Available	150	0.507	0.007	0.08	0	0.007	0.007	0.393
	p		0.25	0.049	<0.0001*	—	0.65	0.0002*	<0.0001*
Spawn	Use	58	0.31	0.121	0.328	0.052	0.035	0.138	0
	Available	150	0.373	0.033	0.147	0.02	0	0.1	0.313
	p		0.25	0.023	0.004*	0.22	0.073	0.28	<0.0001*

n = sample size for each group across seasons; adjusted $\alpha = 0.0193$

*significant result

during periods of extreme cold or heat, Yazoo darters likely shift microhabitat use over short time periods. Even so, our results indicate that Yazoo darters mostly adhere to a narrow microhabitat niche across seasons and that generalized, seasonal shifts in microhabitat use do not occur.

Our results, however, are not entirely consistent. Significant differences occurred in seasonal habitat use (MRPP), though the effect sizes were small. Proportional use of substrate variables during the spawning season show increased use of Gravel and decreased use of Sand and Silt relative to other seasons (Figs. S20-S23) as discussed earlier. Likewise, NPMR models indicated that Velocity and Plant were important variables explaining variation in microhabitat use by Yazoo darters during Spawn. These results point to increased use of erosional habitats during the spawning season and perhaps use of aquatic vegetation as spawning substrate. However, gravel and rock substrates (and rocky riffles) are so uncommon within our study streams (< 4% of random samples overall) and small streams in general within the range of the Yazoo darter (Warren et al. 2002), any seasonal shift is likely small due to limiting suitable habitat.

Table 7 Results from resampling analyses of the number of cover and substrate types for habitat use and availability across seasons

		Available		Use		p
		n	Mean (± S.D.)	n	Mean (± S.D.)	
Cover	Summer	160	1.81 (1.14)	89	2.58 (0.85)	<0.0001
	Winter	150	1.54 (0.73)	80	2.39 (0.75)	<0.0001
	Spawn	150	1.41 (1)	58	2.33 (0.76)	<0.0001
Substrate	Summer	160	1.71 (0.82)	89	1.89 (0.97)	0.135
	Winter	150	1.61 (0.67)	80	1.69 (0.84)	0.456
	Spawn	150	1.73 (0.8)	58	1.95 (0.63)	0.065

n = sample size, *S.D.* = standard deviation

Our study results apparently conflict with the conclusion of Johnston and Haag (1996) that Yazoo darters were habitat generalists, a conflict likely due to factors related to study designs and spatial scales. Their main focus was to describe life history characteristics, not habitat relationships, and so the sampling approach and analytical methods are inherently different in the two studies. Most notably, our study focused on habitat use at a much smaller spatial scale (cm^2 vs. m^2). The comparison of microhabitat use of Yazoo darters via small quadrats against random points over a three year period at three streams allowed us to quantify patterns of habitat use that were undetectable by applying an ordination method to seine hauls pooled across seasons from a single study reach (Johnston and Haag 1996).

Instream cover, particularly in-stream wood, is important for fishes in many lowland streams (Schlosser 1987; Monzyk et al. 1997; Dolloff and Warren 2003; Warren 2012), and our results support the importance of in-stream wood to a headwater darter. Stable, complex cover in the channelized, incised, and flashy streams within the range of the Yazoo darter is likely limiting (Shields et al. 1998; Warren et al. 2002; Warren 2012), especially for streams running through lands that have been deforested and converted to agricultural and urban use. Because the Yazoo darter attaches eggs to instream wood (Johnston and Haag 1996; unpubl. data), the lack of LW may also limit recruitment of the species.

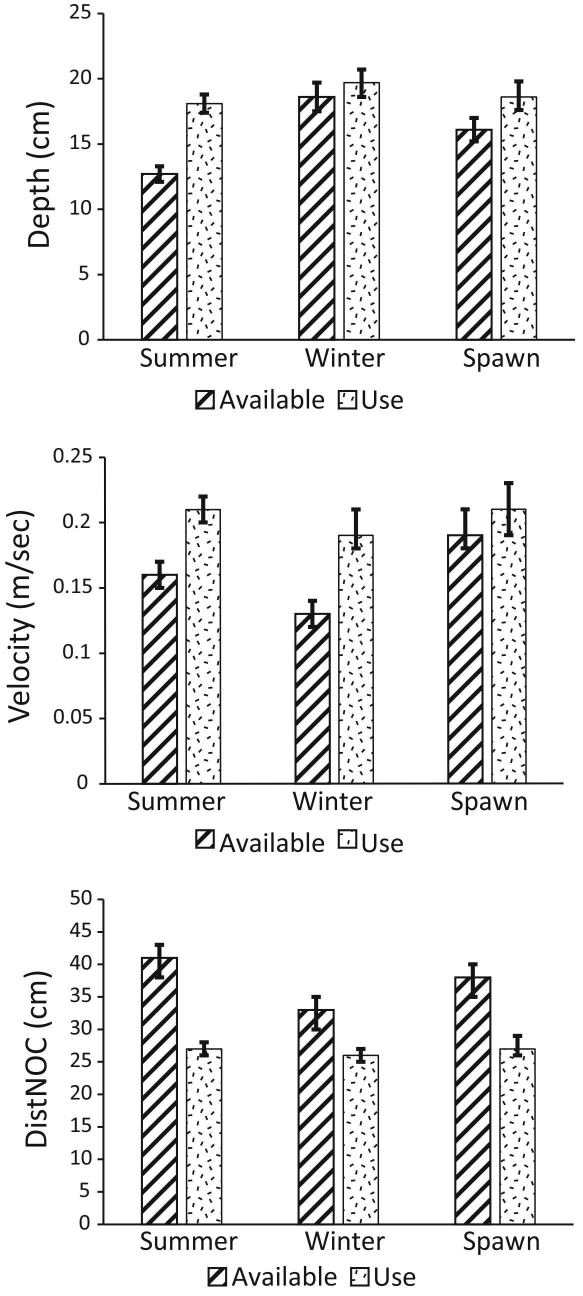

Fig. 2 Means and 95% CIs of available habitat (Available) and habitat use (Use) for each season for water depth (*upper*), stream current velocity (*middle*), and the distance to nearest other cover (DistNOC) (*lower*)

Table 8 Results from niche overlap and niche breadth estimates with 95% confidence intervals in parentheses for substrate and cover variables for each season

Niche Breadth	B (Substrate)	B (Cover)
Summer	0.101 (0.07–0.167)	0.017 (0.014–0.02)
Winter	0.126 (0.072–0.187)	0.007 (0.003–0.01)
Spawn	0.101 (0.046–0.165)	0.015 (0.012–0.021)
Niche Overlap	O (Substrate)	O (Cover)
Summer vs. Winter	0.946 (0.618–1)	0.99 (0.99–1)
Summer vs. Spawn	0.988 (0.824–1)	1 (0.99–1)
Spawn vs. Winter	0.989 (0.857–1)	0.99 (0.99–1)

B = niche breadth, *O* = niche overlap

We believe our results provide reasonably accurate estimates for Yazoo darter microhabitat use that can be generalized to the entire range of the species. These estimates could be used for small-scale habitat enhancement projects within streams inhabited by Yazoo darters. Such projects could be undertaken with relatively small effort and expense and would likely benefit not only Yazoo darters, but the headwater fish community as a whole (Monzyk et al. 1997; Warren et al. 2002, 2009). Similarly, management that encourages the recruitment and retention of LW within streams and conserves riparian buffers to decrease siltation and preserve what little gravel substrate is present would also likely have a positive impact on Yazoo darter populations.

From a conservation perspective, our finding that the Yazoo darter is a microhabitat specialist should result in recognition by management that there is increased risk of decline for the species relative to a recent conservation assessment (Sterling et al. 2013). The Yazoo darter (clade *Adonia*) is closely related to at least 10 other species of concern (Jelks et al. 2008; Near et al. 2011), at least two of which (*Etheostoma cervus, E. pyrrhogaster*) also inhabit small Upper Gulf Coastal Plain streams (Carney and Burr 1989; Powers and Mayden 2003) and have presumably experienced similar patterns of habitat degradation and loss (Jelks et al. 2008). It appears likely that many of these species could be microhabitat specialists due to apparent niche conservatism (Etnier and Starnes 1993; Boschung and Mayden 2004), and our results could inform conservation management efforts for these species.

Yazoo darters are microhabitat specialists, and the lack of their preferred habitat is likely limiting. Our results indicate optimum microhabitat within degraded contemporary streams consists of a narrow range of moderate water depths (about 20–30 cm) and current velocity ≥ 0.25 $m \cdot s^{-1}$ with complex stable debris piles, rooted macrophytes, and likely coarse substrates. No pronounced and generalized seasonal shifts in microhabitat use occurs, and no evidence exists for intraspecific partitioning of microhabitat. From our results we hypothesize that introduction of LW, rooted macrophytes, and rock rubble over small spatial scales within stream reaches with suitable water depths and velocity would result in greater occurrence of stable and complex debris piles which would have a positive influence on the long-term persistence of the Yazoo darter and closely related species. We suggest a series of experiments using this type of habitat modification be conducted to fully evaluate effects on Yazoo darters and associates.

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Compliance with ethical standards All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest The authors declare there is no conflict of interest.

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