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Microhabitat use by southern brook trout (*Salvelinus fontinalis*) in a headwater North Carolina stream

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Abstract – Brook trout are the one of the only *Salvelinus* species native to eastern North America and range from Canada to Georgia. Very little is known, however, about the ecology of the southern form of this species. We quantified microhabitat use of southern brook trout in Ball Creek NC, a third-order stream, during six seasonal samples (summer 2010, autumn 2010, spring 2011, summer 2011, autumn 2011 and spring 2012). In general, trout preferentially occupied deeper microhabitats with lower mean velocities and higher amounts of erosional substrata than were randomly available. Older trout (1+ and 2+) occupied deeper microhabitats with lower mean velocities than yearling trout. These microhabitats typically represent 'plunge pools'. Southern brook trout also occupied focal point velocities that were statistically indistinguishable from optimal velocities calculated for rainbow trout in the same system and thus may chose microhabitats that maximise net energy gain. Southern brook trout are found in isolated populations, and management strategies should focus on the preservation of plunge pool habitat for conservation of this subspecies.

Key words: salmonidae; habitat selection; stream fish; appalachian mountains; char; charr

Introduction

Brook trout (*Salvelinus fontinalis*) occur over nearly the entire length of the Appalachian Mountains and are one of the few, and most widespread, *Salvelinus* species native to eastern North America (Behnke 2002). From Canada to Georgia, brook trout inhabit headwater streams with cool, fast-flowing waters (Cunjak & Power 1986; Johnson & Dropkin 1996; Grossman et al. 2010). Over the past three decades, the natural distribution of southern brook trout has decreased, mostly in the southern portion of its range (Hudy et al. 2008). This decrease is a function of several factors including habitat degradation and displacement by invasive brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) (Habera & Moore 2005). Several distinct forms of brook trout exist; the southern brook trout, which possesses fixed genetic differences, likely warrants reclassification (Stoneking et al. 1981; Habera & Moore 2005). Unlike most salmonids, relatively little is known about the ecological characteristics and habitat requirements of southern brook trout (Habera & Moore 2005; Grossman et al. 2010) which restricts our abilities to scientifically manage this declining and genetically unique salmonid.

Large-scale factors such as global climate change are likely to have major impacts on the distribution and abundance of southern brook trout. Flebbe et al. (2006) modelled the effects of climate change on trout distribution within the southern Appalachians and predicted either a 53 or a 97% reduction in southern brook trout distribution depending on whether the Hadley Centre Global Circulation or the Canadian Centre Global Circulation Model was used. Similar reductions in salmonid distribution in the south-eastern United States were obtained by Meisner (1990) using the Goddard Institute for Space Studies model. Because most southern brook trout populations already are physically isolated above barriers with presumably low interpopulation exchange among streams, global climate change clearly will

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result in greater isolation by increasing stream temperatures and may even produce local or regional extirpation of this species (Flebbe et al. 2006)

Given the paucity of information on southern brook trout and the vulnerability of this species to climate change and invasive species, we quantified microhabitat use of a pure population of southern brook trout (T. King, United States Geological Survey unpublished data; Grossman et al. 2010) between summer 2010 and spring 2012 in upper Ball Creek, North Carolina. Specifically, we compared microhabitat use by southern brook trout to microhabitat availability to test the hypothesis that microhabitat use did not differ significantly from a random expectation (Skyfield & Grossman 2008). In addition, we tested for significant differences in microhabitat use by young-of-the-year (YOY), 1+ and 2+ southern brook trout within a season, as well as for seasonal differences within an age class.

Methods and materials

Study site

Our study site consisted of a 130 m section of stream located within a third-order portion of Ball Creek, NC, USA, located on the USDA Forest Service Coweeta Hydrologic Laboratory in Otto, North Carolina (35°11′N; 83°23′W). The study site and stream are typical of many small streams occupied by southern brook trout in the southern Appalachian Mountains and representative of relatively undisturbed streams in the region (personal observations). In general, these streams have barriers that prevent the upstream movement of other species of invasive trout. Consequently, the habitat that we report on, and the habitat occupied by most southern brook trout today, represents a subset of what was occupied historically by southern brook trout prior to the stocking of invasive trout (Habera & Moore 2005).

The study site was bisected by a small natural waterfall that was considered a possible barrier to fish movement. All microhabitat use and microhabitat availability observations were conducted in the two 50 m sections immediately above and below the waterfall. The study site consisted of riffle-pool morphology with a mean wetted width of 5.2 m s (±0.3 m; 95% C.I. summer 2010–spring 2012). The surrounding mixed hardwood-conifer forest provided dense canopy cover, shading the stream during the growing season. Riparian vegetation was dominated by rhododendron (*Rhododendron maximum*). The fish assemblage was composed of only three species: southern brook trout, mottled sculpin (*Cottus bairdi*) and an occasional rainbow trout (*O. mykiss,* less than 10 seen throughout the entire study).

Microhabitat availability measurements

We quantified microhabitat availability and microhabitat use for southern brook trout on June 28–July 16, 2010 (SU10); September 12–September 25, 2010 (AU10); April 23–May 10, 2011 (SP11); July 9–July 20, 2011(SU11); September 24–October 8, 2011 (AU11) and April 27–May 5, 2012 (SP12). Cross-stream transects were placed every 2 m yielding a total of 50 transects. We used a random number generator to select a random point on each transect and took the following measurements using the methods of Grossman & Skyfield (2009): water depth (metre stick), mean water column velocity (Marsh–McBirney model 201 velocity metre ±0.01 $m \cdot s^{-1}$) and substratum composition (visually estimated within a 400 cm^2 quadrant; % bedrock, boulder, large cobble, small cobble, gravel, sand, silt, debris). Wetted width was measured at 10 m intervals along the stream bank. We collected microhabitat availability data on the first and last days of each sampling period (100 points per seasonal sample).

Microhabitat use observations

We quantified southern brook trout microhabitat use using the methods of Grossman & Freeman (1987) and Grossman & Skyfield (2009). This method has been used to quantify microhabitat selection in salmonid and nonsalmonid stream fishes in both North America and Europe (Grossman & de Sostoa 1994; Grossman & Ratajzcak 1998). We began observations at the lower end of the site and carefully snorkelled upstream observing undisturbed fish (i.e., those that did not display characteristic disturbance responses, Grossman & Ratajzcak 1998). When we encountered an undisturbed fish, we collected the following measurements: standard length (visual estimate, nearest cm), average water column velocity (Marsh–McBirney model 201 velocity metre ±0.01 $m \cdot s^{-1}$, taken at 60% of the water column depth), focal point water velocity (Marsh–McBirney model 201 velocity metre ±0.01 $m \cdot s^{-1}$), water column depth (metre stick), distance from the substratum (metre stick), distance from shelter (metre stick), shelter type and substratum composition (visually estimated within a 400 cm^2 quadrant directly below the fish; % bedrock, boulder, large cobble, small cobble, gravel, sand, silt, debris). We defined shelter as any object capable of concealing at least 50% of a fish's body (Skyfield & Grossman 2008). All data were relayed to a recorder stationed downstream, and for consistency, all observations were made under base flow conditions. The latter parts of this study (2011–2012) were conducted coincidentally with a movement study of southern brook trout within the same site (Anglin Z.W. & Grossman G.D. 2013, unpublished data) which included four, single-pass electrofishing samples made on March 25, 2011; May 19, 2011; October 25, 2011; and May 25, 2012. The lack of differences between early and late microhabitat samples and low movement distances observed suggests that this sampling had little effect on microhabitat use by specimens (personal observations).

Statistical analysis

We quantified both seasonal changes in microhabitat availability and nonrandom microhabitat use by southern brook trout with the methods of Grossman & de Sostoa (1994) and Skyfield & Grossman (2008). To test for seasonal and annual differences in microhabitat availability, we ran a principal component analysis (PCA), on all seasonal microhabitat availability samples. We only interpreted principal components with eigenvalues greater than one, that also were ecologically interpretable and nonduplicative of components with higher eigenvalues. To test for nonrandom microhabitat use by fish within a season, we conducted a PCA on both microhabitat availability and fish microhabitat use data and then calculated centroid means and 95% confidence ellipses on pairs of components, for both data sets. We concluded that southern brook trout displayed nonrandom microhabitat use if the 95% confidence ellipses for microhabitat use and microhabitat availability centroids did not overlap (Skyfield & Grossman 2008). This method is analogous to a *t*-test with alpha of 0.05. Similar PCAs were conducted to test for differences in seasonal and age-related microhabitat use, and significance also was determined by a lack of overlap of 95% confidence ellipses on the groups being compared. An additional criterion was employed when examining data centroids for statistical interpretation. In some cases, centroids were so different on one component that even though there was overlap in their component scores on a second component, there was no overlap of confidence ellipses (compare SP11 and SU11 scores on PC2 in Fig. 1). In these cases, we only reported significant results for the component on which there was no overlap in absolute values of confidence ellipses. To test for age-related differences in microhabitat use, we also ran PCAs on microhabitat use data for YOY, 1+ and 2+ fish (based on standard length: SU10 & AU10: 4–8 cm young of the year, 10–11 cm 1+ year old and 12–13 cm 2+ years old; SP11: 4–8 cm young of the year, 9–11 cm 1+ year old and 12–13 cm 2+ years old; SU11: 4–9 cm young of the year, 10–12 cm 1+ year old and 13–15 cm 2+ years old; AU11: 4–9 cm young of the year, 10–13 cm 1+ year old and 14–16 cm 2+ years old; SP12:

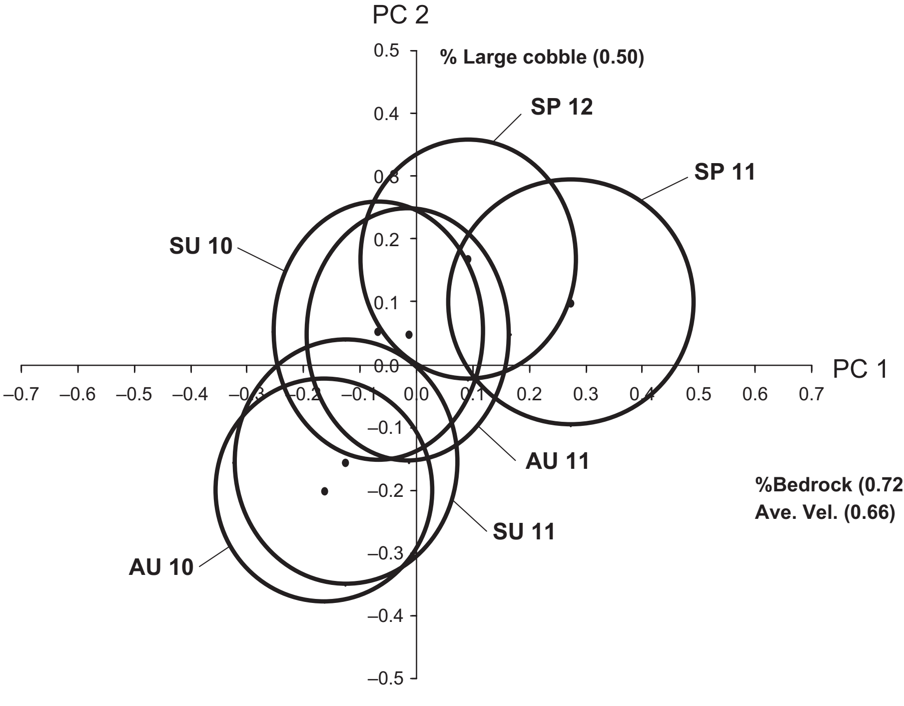

Fig. 1. Principal component analysis of seasonal microhabitat availability data in the study site. We only present PCA variables that had loadings greater than 0.40, and loadings are listed in parentheses after the variable name. Centroids represent sample means for each seasonal sample, and ellipses are 95% confidence intervals. Sample abbreviations for this and following figures are SU10 – summer 2010; AU10 – autumn 2010; SP11 – spring 2011; SU11 – summer 2011; AU11 – autumn 2011; SP12 – spring 2012. Ellipses that do not overlap represent samples that differ significantly at the 0.05 level using a *t*-test.

Table 1. Means (standard deviations) of microhabitat availability, pooled microhabitat use and age-specific microhabitat use data for each season by southern brook trout in Ball Creek, N.C.

Season	Data type	n	Ave. Vel. ($m \cdot s^{-1}$)	Depth (cm)	% Bedrock	% Boulder	% Lg. Cob.	% Sm. Cob.	% Gravel	% Sand	% Silt	% Debris
Summer 2010	Available	100	0.30 (0.26)	14 (10)	16 (36)	9 (26)	23 (36)	12 (27)	11 (23)	11 (25)	16 (34)	1 (5)
	Use	88	0.19 (0.16)	38 (15)	11 (27)	10 (22)	6 (13)	7 (17)	18 (27)	28 (34)	11 (27)	8 (23)
	YOY	60	0.21 (0.17)	33 (9)	13 (28)	8 (19)	7 (18)	6 (14)	16 (25)	33 (38)	10 (25)	7 (21)
	1+	17	0.19 (0.12)	46 (20)	8 (21)	22 (30)	8 (17)	5 (8)	12 (18)	16 (23)	13 (28)	17 (34)
	2+	11	0.09 (0.05)	51 (17)	7 (24)	8 (19)	6 (15)	4 (10)	38 (37)	19 (27)	17 (37)	1 (3)
Autumn 2010	Available	100	0.24 (0.26)	14 (13)	11 (31)	18 (32)	19 (30)	10 (25)	16 (27)	3 (11)	19 (32)	4 (12)
	Use	79	0.15 (0.42)	34 (12)	10 (22)	13 (28)	9 (21)	7 (15)	16 (26)	20 (29)	24 (35)	3 (14)
	YOY	43	0.10 (0.07)	30 (11)	9 (21)	7 (19)	9 (13)	9 (19)	12 (17)	24 (30)	27 (35)	5 (17)
	1+	21	0.11 (0.07)	42 (13)	13 (22)	24 (37)	2 (7)	2 (6)	20 (33)	25 (34)	14 (31)	3 (11)
	2+	15	0.35 (0.96)	34 (11)	9 (26)	14 (31)	9 (26)	16 (34)	22 (36)	2 (5)	29 (41)	0 (0)
Spring 2011	Available	100	0.46 (0.42)	17 (14)	17 (35)	21 (38)	23 (36)	10 (25)	12 (25)	3 (12)	12 (27)	2 (11)
	Use	22	0.18 (0.25)	50 (21)	5 (21)	4 (11)	22 (24)	26 (29)	20 (21)	18 (27)	3 (8)	1 (4)
	YOY	–	–	–	–	–	–	–	–	–	–	–
	1+	10	0.11 (0.10)	46 (23)	10 (32)	0 (0)	20 (23)	34 (34)	14 (18)	15 (30)	6 (11)	0 (1)
	2+	12	0.24 (0.31)	53 (20)	0 (0)	8 (14)	24 (25)	20 (22)	26 (21)	20 (26)	1 (2)	2 (5)
Summer 2011	Available	100	0.22 (0.28)	13 (13)	13 (34)	16 (35)	21 (31)	7 (22)	19 (31)	5 (21)	16 (33)	1 (10)
	Use	64	0.20 (0.11)	39 (11)	14 (27)	16 (25)	14 (16)	7 (14)	11 (17)	18 (24)	16 (27)	4 (12)
	YOY	20	0.19 (0.08)	37 (12)	6 (17)	18 (25)	14 (18)	9 (14)	8 (12)	29 (29)	14 (21)	3 (11)
	1+	35	0.21 (0.11)	40 (12)	22 (32)	15 (24)	14 (14)	5 (13)	14 (21)	12 (19)	16 (29)	2 (8)
	2+	9	0.16 (0.14)	39 (11)	2 (7)	14	15 (18)	7 (13)	6 (6)	15 (22)	26 (33)	14 (22)
Autumn 2011	Available	100	0.28 (0.29)	12 (10)	15 (34)	13 (31)	23 (34)	11 (27)	16 (27)	10 (25)	7 (21)	5 (19)
	Use	39	0.17 (0.06)	38 (12)	6 (19)	17 (29)	15 (22)	6 (16)	24 (29)	20 (25)	7 (20)	4 (13)
	YOY	14	0.19 (0.06)	35 (11)	7 (15)	7 (7)	25 (24)	3 (7)	26 (29)	31 (24)	1 (3)	2 (5)
	1+	19	0.16 (0.07)	37 (13)	5 (23)	28 (39)	12 (21)	9 (21)	19 (27)	9 (21)	9 (24)	7 (17)
	2+	6	0.14 (0.05)	51 (5)	7 (10)	7 (11)	3 (6)	6 (7)	35 (33)	31 (27)	12 (28)	1 (2)
Spring 2012	Available	100	0.36 (0.30)	15 (11)	11 (31)	21 (39)	19 (30)	11 (26)	19 (31)	6 (15)	11 (27)	2 (10)
	Use	76	0.15 (0.10)	28 (13)	4 (17)	8 (25)	11 (21)	3 (11)	24 (35)	11 (22)	29 (41)	10 (27)
	YOY	49	0.12 (0.06)	23 (11)	0 (0)	0 (0)	8 (18)	0 (0)	22 (33)	12 (25)	44 (45)	15 (33)
	1+	14	0.20 (0.13)	35 (12)	3 (13)	4 (13)	29 (32)	10 (20)	34 (38)	15 (16)	4 (7)	1 (2)
	2+	13	0.23 (0.10)	41 (12)	17 (37)	43 (44)	5 (9)	6 (16)	22 (37)	3 (6)	2 (5)	2 (3)

6–12 cm young of the year, 13–14 cm 1+ year old and 16–17 cm 2+ years old, Grossman et al. unpublished data). Comparisons of microhabitat use were made among age classes within a season and across seasons (test for seasonal/annual variation) within age classes. Seasonal/annual comparisons were evaluated against seasonal variation in microhabitat availability to discern true seasonal differences from those produced by seasonal/annual changes in microhabitat availability.

Results

Seasonal and annual variation in microhabitat availability

The PCA of seasonal microhabitat availability data from 2010 to 2012 extracted six components with eigenvalues greater than 1.0 that explained 75% of the variance in the microhabitat availability data. Principal components one (PC1) and two (PC2) were ecologically interpretable, nonredundant and explained 16% and 14% of the variation, respectively (Fig. 1). To aid in interpretation of PCs, univariate means for microhabitat availability data for each season are presented in Table 1. Seasonal comparisons indicated that SP11 and SP12 had higher mean water velocities and greater amounts of bedrock than summer and autumn samples; however, only SP11 differed from AU10 (Fig. 1). No other seasons differed significantly on PC1. We observed no significant differences in microhabitat availability between the same seasons in different years.

Seasonal and annual variation in southern brook trout microhabitat use

Principal component analyses of microhabitat availability and southern brook trout microhabitat use data for the six individual seasons extracted a minimum of two significant components that explained between 69 and 79% of the variance present in the data sets. The strongest evidence for nonrandom microhabitat use always was observed on PC1, which typically represented a gradient of shallow, high-velocity areas with erosional substrata versus deeper areas with lower water velocities dominated by depositional substrata (Fig. 2). Principal component two (PC2) depicted a gradient of high amounts of erosional substratum versus high amounts of depositional

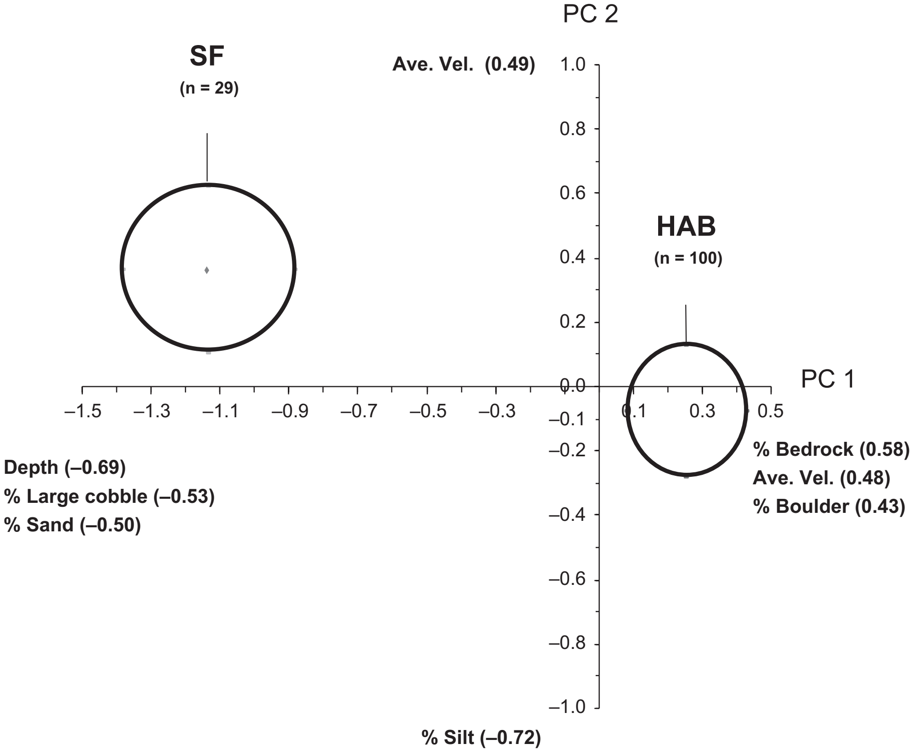

Fig. 2. A representative example of nonrandom microhabitat use during spring 2012 by southern brook trout in the Ball Creek, N.C. study site. See Fig. 1 for further details. Abbreviations SF and HAB represents southern brook trout data and microhabitat availability data, respectively (*N* = sample size). Ellipses that do not overlap represent samples that are significantly different at the 0.05 level using a *t*-test.

substrata. Depth always was negatively correlated with water velocity and positively correlated with increasing depositional substrata. In general, southern brook trout were over-represented in deeper areas with higher amounts of depositional substrata (Table 1), and a representative result (SP12) is presented in Fig. 2. In SP12, PC1 and PC2 explained 18% and 14% of the variation, respectively and represented a gradient (PC1) of high mean velocities with lower quantities of depositional substrata versus microhabitats with low mean velocities and greater quantities of depositional substrata (Fig. 2). PC2 portrayed a gradient of deeper areas with greater amounts of boulder and less gravel as opposed to shallower areas with greater amounts gravel and less boulder. Nonetheless, there was some minor variation among seasons.

Most seasonal changes in microhabitat use by southern brook trout could be related to seasonal shifts in microhabitat availability (e.g., trout utilised faster water velocities in SP11 than other seasons because microhabitat availability data showed that, on average, microhabitats in SP11 had higher mean water velocities than other seasons, that is, compare Figs 1 and 3, Table 1). Nonetheless, there were several significant shifts in microhabitat use among years, with SP12 exhibiting the largest shift (Fig. 3, Table 1). Book trout in SP12 utilised microhabitats with slower mean velocities and larger amounts of depositional substrata than southern brook trout in SP11, even though microhabitat availability for SP11 and SP12 did not differ significantly (Fig. 1). This difference may have been caused by a lack of data for YOY during SP11, which typically occupy slower microhabitats than adults. By summer, however, YOY were present in typical numbers; hence, the lack of SP11 YOY measurements did not represent year class failure. Southern brook trout in AU11 utilised microhabitats with higher mean water velocities and lower amounts of depositional substrata than fish in AU10, even though autumn microhabitat availability was not significantly different between years.

Age-related variation in southern brook trout microhabitat use

Age-related differences in microhabitat use varied within seasons, among seasons, and annually. Principal component analyses of within-season age-specific microhabitat use extracted at least two significant components that explained between 67 and 80% of the variance in the data sets, and a representative example of seasonal results is presented in Fig. 4. Principal component one typically represented a gradient of shallow, high-velocity locations with erosional substrata versus deep, low-velocity areas

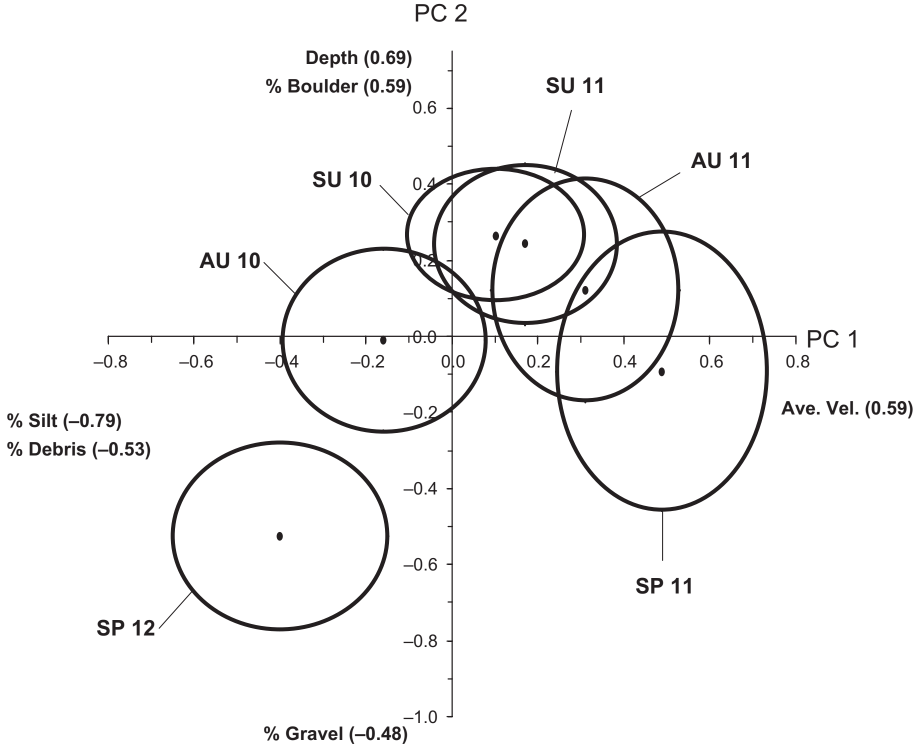

Fig. 3. Interseasonal differences for pooled southern brook trout microhabitat use data in Ball Creek, N.C. See Figs 1 and 2 for further details. Sample abbreviations are as follows: SU10 – summer 2010; AU10 – autumn 2010; SP11 – spring 2011; SU11 – summer 2011; AU11 – autumn 2011; SP12 – spring 2012. Ellipses that do not overlap represent samples that are significantly different at the 0.05 level using a *t*-test.

and depositional substrata. Principal component two generally depicted a similar gradient, with fewer variables.

Age-related differences in microhabitat generally involved differences in velocity, depth and always involved substratum, and a representative example is provided in Fig. 4. Young of the year southern brook trout utilised microhabitats that differed significantly from age 1+ and age 2+ of brook in SU10, AU11 and SP12 (Fig. 4, Table 1). In SU10, YOY occupied microhabitats with greater amounts of sand and bedrock than 1+ and 2+ trout. In AU11, YOY utilised deeper areas with greater amounts of small cobble and sand and less debris than 1+ and 2+ trout. During SP12, YOY used shallower areas with more silt, lower mean velocities and less small cobble and gravel than 1+ and 2+ trout. When YOY occupied microhabitats that differed from older southern brook trout, they generally were found over greater amounts of depositional substrata. Age 1+ southern brook trout utilised microhabitats that were significantly different from YOY and age 2+ southern brook trout for two of six seasons (AU10 and SP12). In AU10, 1+ southern brook trout occupied deeper areas with more erosional substrata and less silt than YOY and 2+ trout (Table 1). Similarly, in SP12, 1+ southern brook trout utilised deeper areas with higher mean velocities, greater amounts of small cobble and gravel and less silt than YOY southern brook trout (Fig. 4). By contrast, in SP12, 1+ fish occupied shallower areas with less boulder than 2+ southern brook trout (Fig. 4).

We observed seasonal differences in microhabitat use by YOY southern brook trout but not by 1+ fish (compare Figs 1 and 6). YOY microhabitat use data produced five components with eigenvalues greater than 1.0 and explained 69% of the variance in the microhabitat use data. Two components, PC1 and PC2 were ecologically interpretable and nonredundant and explained 20% and 15% of the variation, respectively (Fig. 5). Principal component one described a microhabitat gradient contrasting locations with high mean velocities and high amounts of sand and boulder versus those with low mean velocities with greater amounts of silt. PC2 portrayed a gradient of deeper areas with less small erosional substrata versus shallower areas with greater amounts of small erosional substrata. Microhabitat use by YOY in 2010 differed significantly among seasons, although microhabitat availability did not. In SU10, YOY utilised areas with higher mean velocities, less silt and more sand and boulder than YOY in AU10 (Table 1). Microhabitat use in 2011 did not differ among seasons. Over all years, YOY southern brook

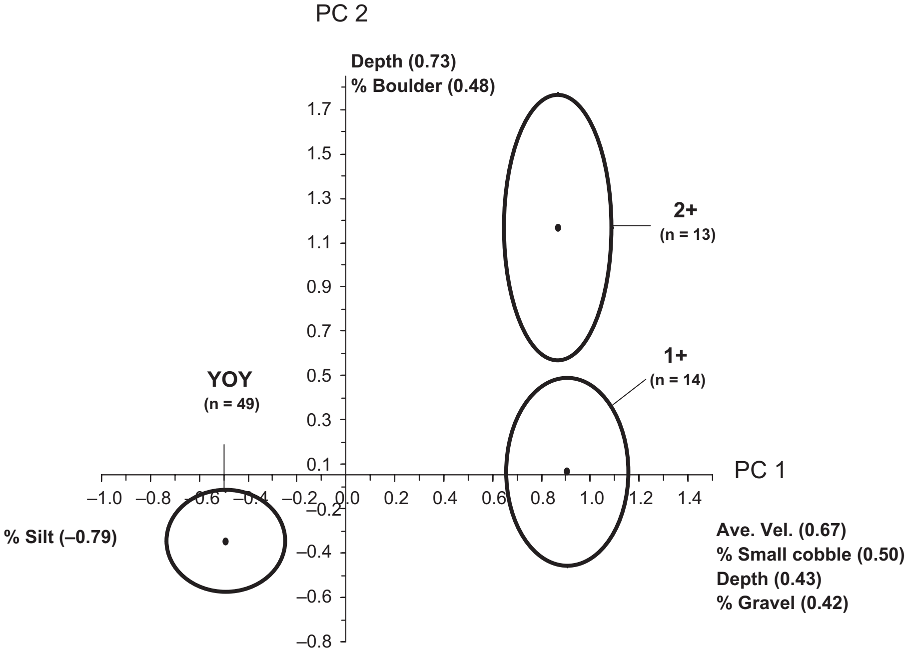

Fig. 4. Test for age-related differences in microhabitat use by southern brook trout during spring 2012. Results for this season are typical for seasons where significant differences were observed (i.e., SU10 and AU11). See Figs 1 and 2 for further details. Sample abbreviations are as follows: (i) YOY represents young of the year southern brook trout, (ii) 1+ represents age 1+ southern brook trout and (iii) 2+ represents age 2+ southern brook trout (*N* = sample size). Ellipses that do not overlap represent samples that are significantly different at the 0.05 level using a *t*-test.

trout utilised significantly lower mean velocities and more silt and less sand and boulder in SP12 than in any other season. In AU11, YOY occupied microhabitats with higher mean water velocities and greater amounts of sand and boulder than those used by YOY in AU10. Interannual seasonal comparisons did not reveal significant differences in microhabitat use by 1+ trout attributed other than those that mimicked seasonal changes in microhabitat availability (compare Figs 1 and 6, Table 1).

Analyses of seasonal microhabitat use among years by 2+ southern brook trout extracted five components with eigenvalues greater than 1.0 and explained 71% of the variance present in the data set. Principal components one and two were ecologically interpretable and explained 18% and 16% of the variation, respectively (Fig. 7). Microhabitat use by 2+ trout in 2010 differed significantly among seasons, with trout in SU10 occupying deeper microhabitats with lower mean velocities and greater amounts of sand and lower quantities of small cobble and silt than 2+ trout in AU10 (Fig. 7, Table 1). Microhabitat use in 2011 did not differ significantly among seasons. Interannual comparisons revealed that in SU11, age 2+ occupied shallower areas with higher mean velocities and more small cobble and silt and less sand than in SU10 and that these shifts were not associated with shifts in microhabitat availability (Figs 1, 2 and 7, Table 1).

Discussion

To our knowledge, this is the first study of habitat use by fish that have been genetically typed as pure southern brook trout. In general, this species occupied deeper areas with greater quantities of small erosional and depositional substrata and lower amounts of large erosional substrata. In Ball Creek, these areas corresponded to plunge pools. There were several clear seasonal/annual changes in microhabitat use that involved both velocity and substratum, but these differences likely were affected by differences in density and year class recruitment time (i.e., YOY in 2011 recruited after spring sampling). Both of these factors are known to affect habitat selection in salmonids (Hill & Grossman 1993). Age-related seasonal differences were more complex. Microhabitat use by age 1+ and 2+ southern brook trout was very similar with most older trout occupying lower velocity microhabitats with greater quantities of depositional substrata (i.e., more pool-like). By contrast, we observed differences in microhabitat use between YOY and older fish in three of five seasonal samples (YOY were absent in SP11).

Why do southern brook trout display nonrandom microhabitat use? Previous studies have shown that some stream fishes utilised a microhabitat selection strategy that maximises their net energy gain, and this behaviour should be favoured by natural selection

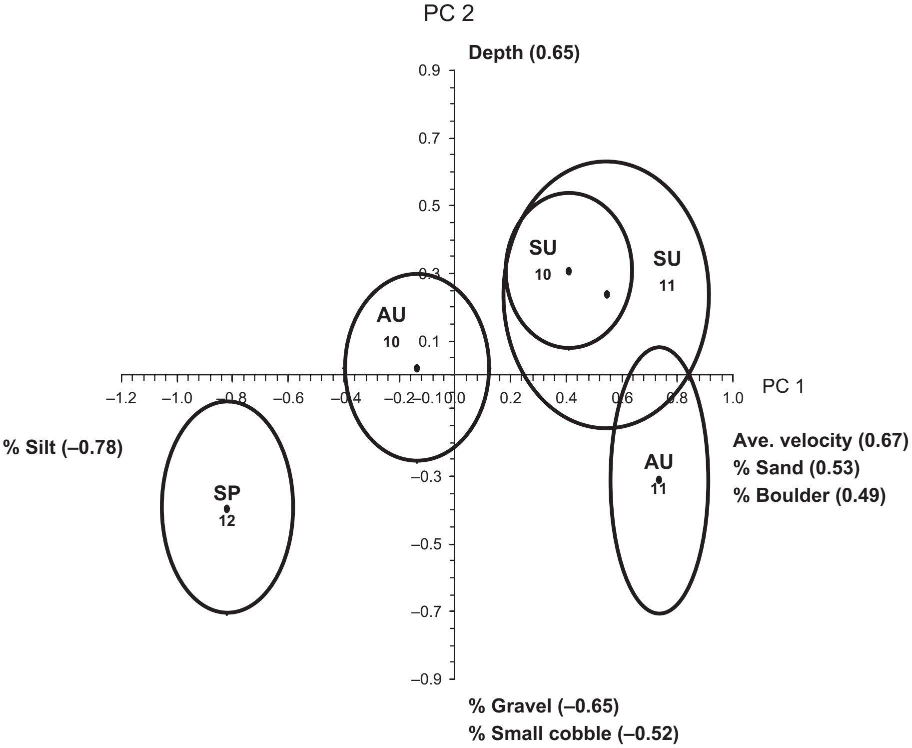

Fig. 5. Interseasonal differences in microhabitat use by YOY southern brook trout in Ball Creek, N.C. See Figs 1 and 2 for further details. Seasonal abbreviations are as follows: SU10 – summer 2010; AU10 – autumn 2010; SP11 – spring 2011; SU11 – summer 2011; AU11 – autumn 2011; SP12 – spring 2012. Ellipses that do not overlap represent samples that are significantly different at the 0.05 level using a *t*-test.

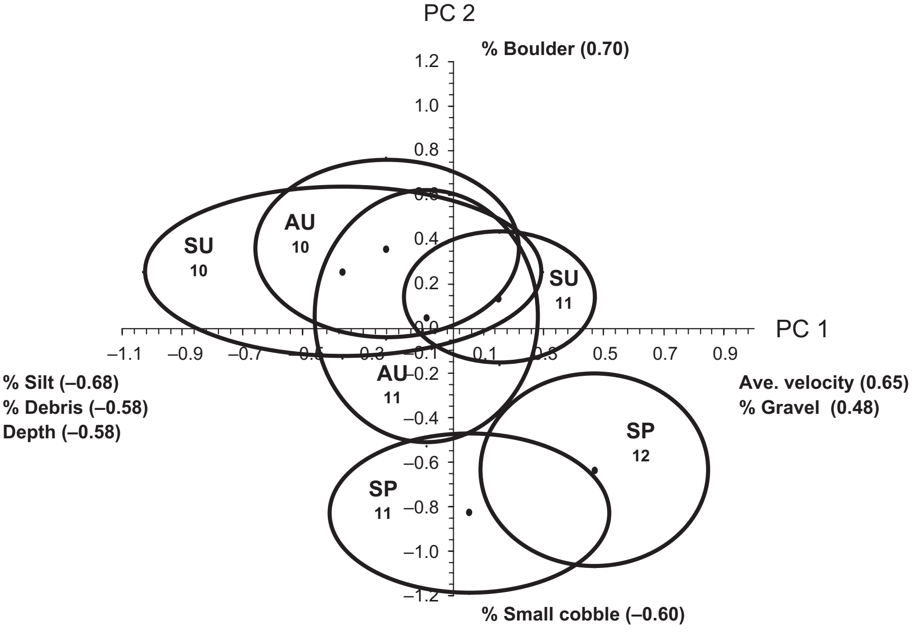

Fig. 6. Interseasonal differences in microhabitat use by age 1+ southern brook trout in Ball Creek, N.C. See Figs 1 and 2 for further details. Seasonal abbreviations are as follows: SU10 – summer 2010; AU10 – autumn 2010; SP11 – spring 2011; SU11 – summer 2011; AU11 autumn 2011; SP12 – spring 2012.

(Hill & Grossman 1993; Grossman et al. 2002). Linking net energy gain to microhabitat use is particularly appropriate for drift feeders like southern brook trout because stream microhabitats differ in their net profitability (Hill & Grossman 1993; Grossman et al. 2002). Southern brook trout must balance

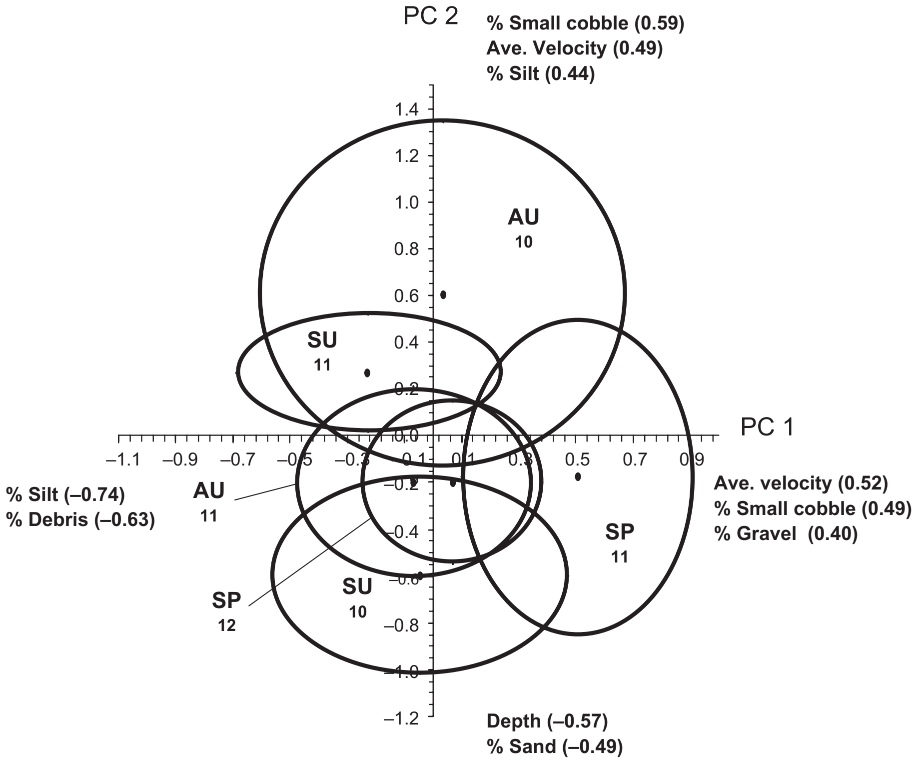

Fig. 7. Interseasonal differences in microhabitat use by age 2+ southern brook trout in Ball Creek, N.C. See Figs 1 and 2 for further details. Seasonal abbreviations are as follows: SU10 – summer 2010; AU10 – autumn 2010; SP11 – spring 2011; SU11 – summer 2011; AU11 – autumn 2011; SP12 – spring 2012.

the cost of maintaining position against the increased profitability obtained from occupying faster velocities (Grossman et al. 2002). In fact, previous studies have shown that velocity is a very important component of microhabitat use for multiple fish species in the Coweeta drainage (Grossman et al. 2002) including rainbow trout (Hill & Grossman 1993). The latter authors found that rainbow trout maximised net energy gain by occupying a mean focal point velocity of 17.0 ± 3.9 cm·sec^{-1} (95% C.I.) which does not differ significantly from the mean focal point velocity occupied by southern brook trout in Ball Creek (17.3 ± 4.3 cm·sec^{-1}). This suggests that southern brook trout also may be selecting microhabitats that maximise net energy gain, especially because the size ranges examined for the two species were similar (Hill & Grossman 1993). Energy maximisation is a microhabitat selection strategy utilised by other stream salmonids (Hughes & Dill 1990; Hughes et al. 2003).

Direct (i.e., underwater) observational studies of microhabitat use are not common for either native or invasive populations of northern brook trout (Griffith 1972), and this subspecies usually is found in larger streams than southern brook trout (personal observations). In most areas, southern brook trout are only found above barriers to fish movement (e.g., high waterfalls) and likely have been displaced from downstream habitats by invasive rainbow and brown trout (Moore et al. 1983; Grossman et al. 2010). Thus, although our observations are likely representative of southern brook trout microhabitat use in many streams in the southern Appalachians, in fact, there is much habitat that is unavailable to this species because it currently is utilised by rainbow trout in Ball Creek as well as other streams.

Northern brook trout generally occupy deep, slow flowing microhabitats dominated by cobbles and boulders, although these conclusions commonly are derived from limited seasonal (summer only) data or a single year (Johnson & Dropkin 1996; Sotiropoulos et al. 2006). Our results are similar to these authors with the exception of substratum use. Southern brook trout in Ball Creek generally were found over depositional substrata rather than cobble and boulder. Northern brook trout display age-linked shifts in microhabitat use that are similar to those observed in southern brook trout from Ball Creek. Specifically, older fish utilised deeper, slower flowing microhabitats with larger substrata and greater amounts of cover than YOY (Griffith 1972; Cunjak & Power 1986; Johnson et al. 1992; Johnson & Dropkin 1996; Johnson 2008). However, unlike northern populations, 1+ and 2+ southern brook trout occupied microhabitats with greater amounts of depositional substrata than YOY fish although this likely represented a depth response. Comparisons of microhabitat use by southern and northern YOY were less similar. Southern YOY displayed variable microhabitat use occupying low- to high-velocity locations, deep to shallow areas and a mixture of substrata. This variation may be a result of frequent antagonistic interactions with older southern brook trout (personal observations), and intraspecific competition has been identified as an important process in the regulation of density in this (Grossman et al. 2010) and other brook trout populations (Grossman et al. 2012).

Salmonids are one of the most well-studied groups of fishes, largely due to their popularity as sport fishes. Generally, salmonid microhabitat use can be characterised as consisting of deeper areas (Johnson & Dropkin 1996) dominated by cobbles, boulders or gravel, with nearby cover (Johnson & Dropkin 1996; Meyer & Griffith 1997; Grossman & Ratajzcak 1998; Huusko et al. 2007). Age-related differences in microhabitat selection are common in salmonid species with adult utilising deeper microhabitats with greater amounts of erosional substrata and substantial cover, whereas YOY salmonids occupying shallower waters with less available cover and greater amounts of depositional substrata (Griffith 1972; Cunjak & Power 1986; Baltz et al. 1991; Johnson et al. 1992). Southern brook trout differ from the general trend in age-related microhabitat use; in that, older individuals occupy microhabitats with greater amounts of depositional substrata, whereas young individuals utilise more erosional substrata. It is important to note that microhabitat use by salmonids frequently varies both seasonally and among systems (Johnson & Dropkin 1996; Gries & Juanes 1998; Rosenfeld et al. 2000).

Although our findings are relatively consistent, they may have been affected by several shortcomings. First, although our fish were of known genetic origin (Grossman et al. 2010), our data are from a single population from a single stream. Nonetheless, this drainage is representative of many in the region (Grossman et al. 2010) as is the habitat occupied by southern brook trout. Second, we were unable to measure microhabitat use for YOY in SP11 because these fish recruited after sampling. Third, our results for 2+ fish are based on low sample sizes (6–15 fish), because most southern brook trout typically do not live past their third year of life (Grossman et al. 2010). Although not uncommon for microhabitat studies, we did not sample during winter months because fish in this region typically are quiescent during winter (Grossman & Ratajzcak 1998). With respect to environmental conditions during our study, regional precipitation was normal for all seasons except for SP11 and AU11 which were wetter than average (USGS Tallulah River GA gage 02178400). In addition, although our focal point velocity measurements for southern brook trout were statistically indistinguishable from those of optimal microhabitats for rainbow trout in the same system (Hill & Grossman 1993), it would be beneficial if an energy maximisation model were developed specifically for southern brook trout. This might yield insights into why southern brook trout shifted microhabitat use between spring seasons and autumn seasons of different years while microhabitat availability remained relatively constant for those seasons.

Southern brook trout posses fixed genetic differences that distinguish it from northern populations (Stoneking et al. 1981; Habera & Moore 2005). Given the declines in this species both throughout its range and especially in the southern Appalachian region, our quantification of the microhabitats utilised by southern brook trout should aid in management and conservation of remaining populations. Specifically, if plunge pools are the preferred microhabitat of southern brook trout, management efforts should be directed towards preserving those habitats from siltation and other aspects of habitat degradation. It is likely that southern brook trout will continue to face future habitat degradation and fragmentation both via changes in land use and warming from global climate change (Flebbe et al. 2006). It is our hope that our data will aid managers in preserving this unique subspecies of trout.

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