Microhabitat use by blackbanded (*Percina nigrofasciata*), turquoise (*Etheostoma inscriptum*), and tessellated (*E. olmstedi*) darters during drought in a Georgia piedmont stream

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Abstract We used underwater observations to quantify microhabitat use for blackbanded, *Percina nigrofaciata*, turquoise, *Etheostoma inscriptum*, and tessellated, *E. olmsteadi*, darters in a 116 m reach of a Piedmont stream during 2001–2002. The sampling period and the previous 12 months were the first and second driest years on record, respectively. Spring 2002 had the greatest amount of available habitat, and principal component analysis indicated that only one of three species pairs displayed significant differences in microhabitat use during this season. Conversely, in fall 2001 (intermediate microhabitat availability), all three species used significantly different microhabitats. In general, turquoise darters used areas with greater amounts of erosional substrata, tessellated darters occurred over more depositional substrata, and blackbanded darters utilized intermediate microhabitats. During fall 2001, large blackbanded darters (≥55 mm SL) occupied faster microhabitats with more erosional substrata, and used a greater variety of depths than smaller conspecifics (40–55 mm). In fall 2001, large turquoise darters (≥40 mm) used deeper microhabitats with higher velocities and more erosional substrata than smaller individuals, whereas the opposite was true (≤50 mm in faster, more erosional, than >50 mm) in fall 2002. In general, darters did not occur in microhabitats with significantly higher invertebrate abundances, however both blackbanded and tessellated darters occupied microhabitats with higher percentages of Diptera in a single season. The inconsistent responses of darters to microhabitat prey abundance may have been influenced by extreme drought conditions.

Keywords Patchiness · Habitat selection · Fish · Fish habitat · Southeastern United States

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Introduction

The southeastern United States is the center of diversity for darters (subfamily Etheostominae) in North America (Matthews 1998), many of which are imperilled (Warren et al 2000). Although detailed ecological information is available for relatively few darter species, extant information suggests that most species are benthic insectivores that inhabit lotic systems (Page 1983; Folkerts 1997; Warren et al. 1997, 2000). Darter species commonly are sympatric and in some cases utilize resources differently from one another (diet – Greenberg 1991; Van Snik Gray et al. 1997; substratum – Kessler and Thorp 1993; Welsh and Perry 1998; Van Snik Gray and Stauffer 2001; depth – Kessler et al. 1995; Welsh and Perry 1998; current velocity – Kessler et al. 1995; distance

from the substratum – Greenberg 1991; Welsh and Perry 1998; and activity time – Greenberg 1991). However, the general relationship between differences in resource use and coexistence is unknown for most sympatric darters (but see Greenberg 1988; Van Snik Gray and Stauffer 2001). In addition, there is little information on the role that habitat heterogeneity and patchiness plays in habitat selection by lotic benthic fishes such as darters (Grossman et al. 1995; Petty and Grossman 2004).

Most stream fish habitat studies focus on physical habitat characteristics such as velocity, depth, and substratum composition (Grossman et al. 2002). Several recent studies, however, have shown that the prey abundance within a microhabitat (i.e., patch) may be a better predictor of microhabitat use than physical habitat characteristics alone (Petty and Grossman 1996, 2004; Thompson et al. 2001). Given the paucity of knowledge regarding both microhabitat use in darters and the relationship between prey patchiness and microhabitat use in stream fishes in general, we examined both of these factors in three darter species (blackbanded darter, *Percina nigrofasciata*, tessellated darter, *Etheostoma olmsteadi*, and turquoise darter, *E. inscriptum*) in a Georgia Piedmont stream. Specifically, we asked: 1 – Do physical habitat availability and invertebrate abundance vary seasonally? 2 – Do darters occupy microhabitats that differ from those available at random? and 3 – Do darters occupy microhabitats with greater invertebrate abundance than those randomly available?

Materials and methods

Study site

Our study site was a 116 m long section of Cloud's Creek, a third order tributary of the South Fork Broad River (SFBR), Madison and Oglethorpe Counties, Georgia, USA (83° 07′ 17″ W, 34° 00′ 21″ N). Mean bank-full width in the study site was 19.4 m (Henry 2006). The site was located in Watson Mill Bridge State Park, approximately 244 m upstream of the confluence of Cloud's Creek and the SFBR, at an elevation of 146 m above sea level (Henry 2006). The SFBR watershed land cover is deciduous, coniferous, and mixed forests interspersed with pasture, hay, and row crops.

A bedrock outcrop with cobble/boulder substratum interspersed with sand dominated the upstream half of the site, whereas sand, silt, and occasional cobbles dominated the lower half of the site. Exposed bedrock platforms and boulders delimited natural subsections throughout the site, and we sampled one subsection at a time. In Georgia, August 2001 to July 2002 was the driest 12 month period on record since 1895. The preceding year, September 2000 to August 2001 ranked second in dryness.[1] During our study, variation in wetted width within the site was substantial and in summer 2002 only the upper 28 m of the 116 m site were deep enough to sample.

Microhabitat availability

We quantified physical microhabitat availability in the site in three seasons: fall 2001 (13–15 November), spring (8–9 May), and summer (31 July) 2002. Heavy rains prevented collection of fall 2002 habitat availability data. We made microhabitat availability measurements using the methods of Thompson et al (2001). In brief, we established cross-sectional transects at 4 m intervals along the stream banks, and recorded measurements every 2 m for the entire cross-section. At each point we measured depth (±1 cm, meter stick), average and bottom current velocities ±0.01 cm s^{-1}, Marsh–McBirney Model 201 electronic velocity meter), and visually estimated the percent composition of eight substratum classes based on maximum linear dimension (bedrock [embedded to the surface]; boulders – unembedded particles >30 cm; large cobble – ≤30 and >15 cm; small cobble – ≤15 and >2.5 cm; gravel – ≤ 2.5 and >0.2 cm; sand – ≤0.2 cm; and silt – material suspendable in the water column; Grossman and Freeman 1987) in a 20×20 cm^2 quadrat. Debris and vegetation, *Podostemum* spp., were not categorized by size class (Grossman and Freeman 1987). All depths were less than 75 cm; hence we measured average velocity at 0.6 X stream depth (Bovee and Milhous 1978). The number of microhabitat availability quadrats ranged from 199 (fall 2001) to 227 (spring 2002), respectively.

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[1] National Climate Data Center (2006) http://www.ncdc.noaa.gov/oa/ncdc.html.

Fish microhabitat use

We quantified fish microhabitat using the methods of Grossman and Freeman (1987). We made fish measurements from 24 October–8 November, 2001 (fall 2001), 18 April–9 May, 2002 (spring 2002), 24 July–29 July, 2002 (summer 2002), and 3–10 October, 2002 (fall 2002). To minimize disturbance, we entered the site from downstream and slowly sampled upstream. Upon sighting an undisturbed specimen, we marked its exact position using a painted weight and recorded the following measurements: time, species, standard length (±1 cm, meter stick), depth (±1 cm meter stick), distance to substratum (±1 cm, meter stick), distance to shelter (±1 cm, meter stick, shelter was considered to be any object capable of concealing at least 50% of the fish's body), type of shelter, distance to nearest neighbor (±1 cm, meter stick), and species of nearest neighbor (fish within 20 cm). We also measured average, focal, and bottom current velocities (electronic velocity meter ± 0.1 cm s^{-1}) following Bovee and Milhous (1978), and visually estimated percent substratum composition as described previously. Focal-point velocity was measured at the nose of the fish. All fish observations were made between 11:00 and 17:00 h.

Macroinvertebrate abundance

We quantified macroinvertebrate abundance at both random locations and at the fish's position to determine the relationship between prey abundance and microhabitat use. We generated coordinates for random samples via a random number table, and stratified the site into five equal sections to ensure even coverage (i.e., equal number of random samples from each section). We collected benthic macroinvertebrate samples after fish measurements on 20 November–6 December 2001 (fall 2001). For spring and fall 2002 we collected fish microhabitat use and macroinvertebrate samples concurrently, although spring random samples were collected on 29 May 2002. Due to drought conditions, benthic samples were not collected in summer 2002.

We collected macroinvertebrate samples as follows. After completion of microhabitat measurements for a fish, we agitated a 20×20 cm area directly below the specimen to a depth of 10 cm, scraped rocks and debris, and collected all dislodged materials with a 27 cm^2 net (250 um), positioned downstream. Samples were kept in individual plastic jars and preserved with a 10% formalin solution. Using a 40X dissecting scope, we sorted and identified macroinvertebrates to family using the methods of Petty and Grossman (1996). To estimate biomass for each family we measured head capsule width (HCW) as per Petty and Grossman (1996). We then used published regressions to calculate macroinvertebrate HCW-biomass relationships, utilizing family-specific constants averaged over all families found in the site (Benke et al 1999; Gibson et al. 2004).

Statistical analyses

We used the methods of Grossman and de Sostoa (1994) to quantify non-random microhabitat use by fishes in Cloud Creek. We entered both microhabitat availability and fish microhabitat use data into a principal component analysis (correlation matrix solution) and then calculated means and 95% confidence ellipses for both microhabitat availability and use data on each pair of components. A lack of overlap of the 95% confidence ellipses demonstrated significance at the 0.05 level (Grossman and de Sostoa 1994). We analyzed data separately for each seasonal sample and tested for both interspecific and intraspecific seasonal and size-related differences in microhabitat use.

To determine whether darters occupied microhabitats with significantly higher invertebrate numbers or biomass than were randomly available, we compared invertebrate samples from darter and randomly selected microhabitats using Student's t-tests on log-transformed data. Tests were conducted separately for each season. We tested for interspecific and size-related analyses using ANOVA and Tukey–Kramer a posteriori tests (Zar 1997). Because dipterans dominate the diet of darters (Page 1983; Kuehne and Barbour 1983), we also analyzed the relationship between the percentage dipteran abundance (e.g., dipteran abundance divided by total macroinvertebrate abundance) in both fish and random samples. Because of the difficulty of characterizing invertebrate distributions and the low sample sizes of some species during the study we set alpha at 0.1 for this analysis (Zar 1997; Grossman et al 2006).

To determine the maximum prey size consumable by darters, we examined gape sizes of museum

specimens (University of Georgia Museum Natural History) encompassing the size range of specimens observed in the field (blackbanded darter 41–100 mm SL; turquoise darter 49–73 mm SL; and tessellated darter 28–56 mm SL). We used these data to set a size limit for prey items included in analysis. Gape sizes for all species were sufficiently large that all prey except Odonata were consumable by darters and hence, included in analyses.

Results

Site characteristics and seasonal variation in microhabitat availability

Low flow conditions prevailed during the study period and total annual precipitation for 2000 and 2001 was 86 and 89 cm respectively, whereas the 20 year mean was 132 cm (Henry 2006). Mean wetted widths of the site ranged from 15.2 to 19.4 m between fall 2001 and fall 2002, whereas water temperature varied from 10 to 23°C. In addition to blackbanded, turquoise, and tessellated darters we also observed yellowfin shiner, *Notropis lutipinnis*, creek chub, *Semotilus atromaculatus*, rosyface chub, *Hybopsis rubifrons*, bluehead chub, *Nocomis leptocephalus*, and northern hog sucker, *Hypentilium nigricans*, in the site.

Microhabitat availability differed significantly among all three seasons (Fig. 1). The PCA extracted five significant components that explained 72.3% of the variance in the data set. However, only the first two components were ecologically interpretable (28 and 14% variance explained respectively). These two components elucidated a velocity–depth–substratum gradient (PC1) and a gradient contrasting bedrock areas with little sand versus sandy areas with little bedrock (PC2). In spring 2002, the site was deepest with the highest average and bottom current velocities, increasing amounts of cobble, bedrock and vegetation substratum and little silt and debris. Summer 2002 displayed the opposite suite of habitat characteristics (e.g. shallowest, lowest velocities, etc.), whereas fall 2001 possessed intermediate habitat values (Fig. 1).
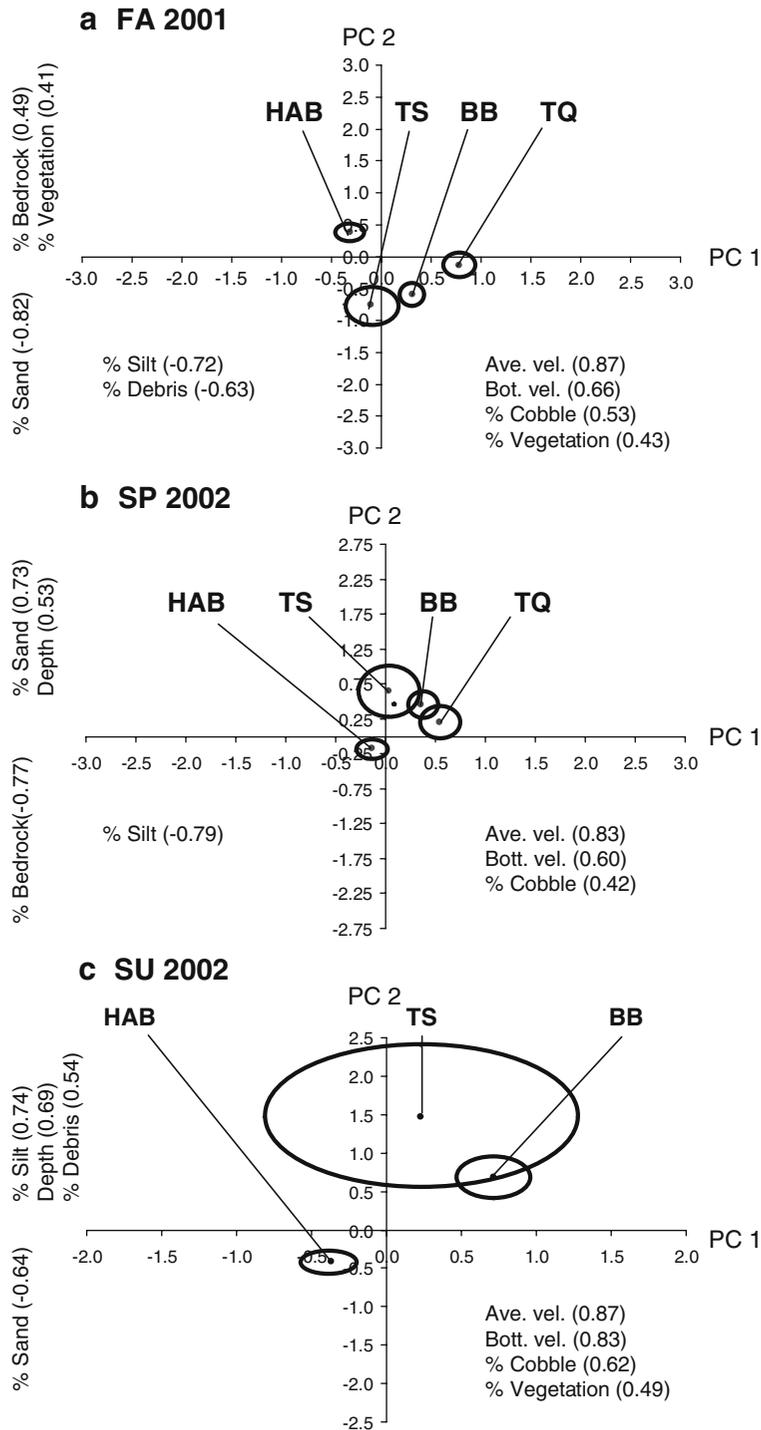
Microhabitat use

Fall 2001

The PCA extracted five components that accounted for 68% of the variance in the microhabitat availability data, with the first two components being ecologically interpretable (Fig. 2a). Component one (26% variance explained) depicted a velocity–substratum gradient, whereas PC2 (13% variance explained) elucidated a sand, bedrock, vegetation
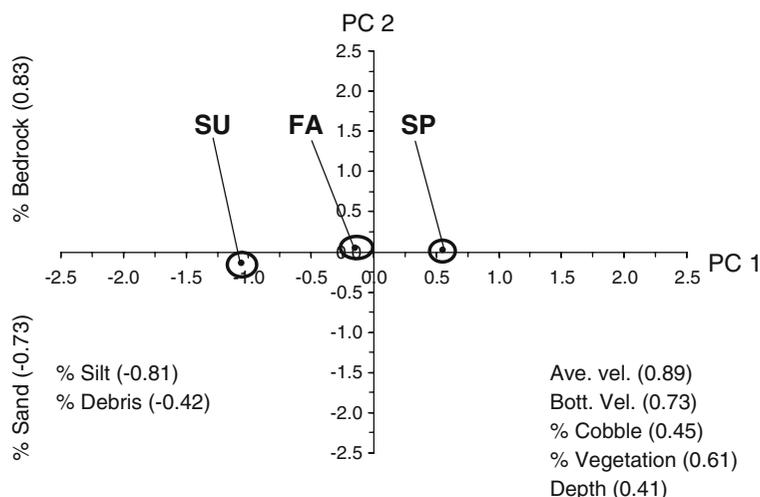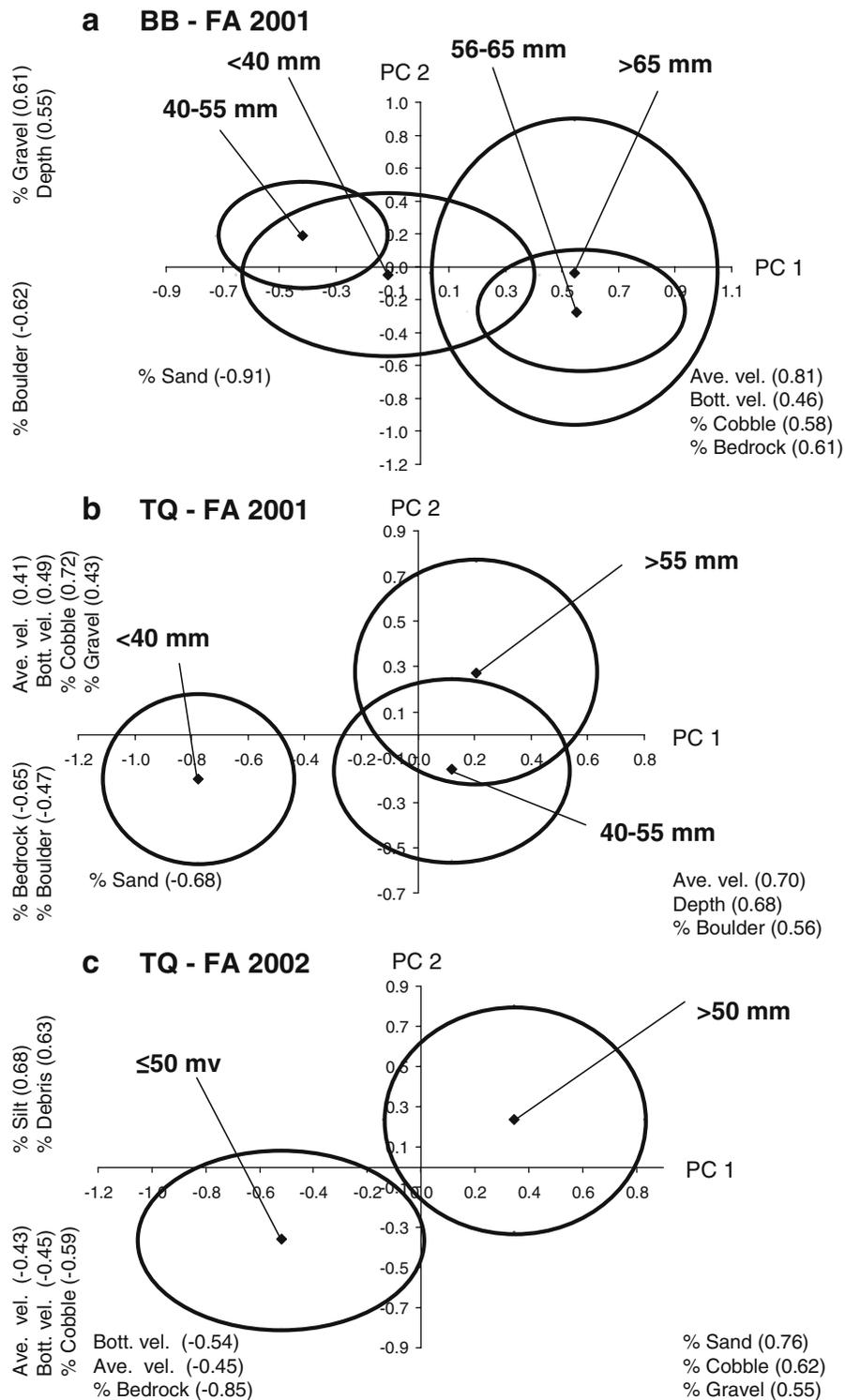

Fig. 1 Seasonal differences in microhabitat availability. Mean component scores are presented for each season, as well as a 95% confidence ellipse. Axis loadings >0.40 are listed. Seasonal abbreviations are as follows: FA = fall 2001 (*n*=198); SP = spring 2002 (*n*=227); and SU = summer 2002 (*n*=93)

Fig. 2 Interspecific differences in microhabitat use, **a** fall 2001, **b** spring 2002, and **c** summer 2002. Mean component scores are presented for each species, as well as 95% confidence ellipses. Axis loadings > 0.40 are listed. Species abbreviations are as follows: BB = blackbanded, TQ = turquoise, TS = tessellated, HAB = microhabitat availability

Fig. 3 Size-related differences in microhabitat use, **a** blackbanded, fall 2001, **B** turquoise, fall 2001, and **c** turquoise darters, fall 2002. Mean component scores are presented for each species, as well as 95% confidence ellipses. Axis loadings > 0.40 are listed

gradient. Habitat use by all three species differed significantly from random and from each other (Fig. 2a), and interspecific differences occurred along a velocity–substratum gradient. Both blackbanded and turquoise darters occupied microhabitats with higher velocities, increasing amounts of cobble, sand and vegetation and lower amounts of silt and debris than randomly available (Fig. 2a). By contrast, tessellated darters occurred over areas with more sand and less bedrock and vegetation than random quadrats or turquoise darters (no difference on PC2 between tessellated and blackbanded darters, Fig. 2a).

Spring 2002

Five components were obtained from the PCA, explaining 66% of the variance in the data, although only two were ecologically interpretable. Component one (20% variance explained) also depicted a velocity–substratum gradient with cobble and silt substrata (Fig. 2b). Component two (15% variance explained) depicted a depth–sand–bedrock gradient. Microhabitat use by all species differed significantly from what was randomly available, but only tessellated and turquoise darters differed significantly in interspecific microhabitat use. Turquoise and blackbanded darters used microhabitats that were slightly faster and deeper with more sand (blackbanded only), cobble and less bedrock and silt than available by chance (Fig. 2b). Tessellated darters occupied deeper, sandier microhabitats with less bedrock than random quadrats. Turquoise darters occupied microhabitats that were faster with more cobble and less silt than tessellated darters (Fig. 2b).

Summer 2002

Microhabitat availability during this season was similar to fall 2001 with only components one and two (29 and 16% variance explained respectively) being ecologically interpretable. These components elucidated velocity–depth–substratum gradients (Fig. 2c). Wetted area in the site had decreased substantially and fish densities were low. We did not observe sufficient turquoise darters for statistical analysis ($N < 5$). Habitat use for both blackbanded and tessellated darters differed significantly from habitat availability (Fig. 2c), but not from each other. Both darter species tended to occupy deeper micro-

habitats with high velocities, more silt and cobble and less sand than were randomly available. Blackbanded darters also occupied microhabitats with more vegetation and cobble than expected by chance (Fig. 2c).

All species displayed significant seasonal variation in microhabitat use. These shifts, however, always reflected seasonal shifts in microhabitat availability rather than true seasonal shifts in microhabitat use.

Size-related variation in microhabitat use

Sample sizes were sufficient to quantify size-related variation in microhabitat use only for blackbanded and turquoise darters. During fall 2001, large blackbanded darters (>55 mm) occupied faster microhabitats with more erosional substrata and less sand than intermediate sized fish (40–55 mm) (Fig. 3a). There were no significant size-related differences for blackbanded darters in other seasons. During fall 2001, large turquoise darters (≥40 mm) used deeper microhabitats with higher velocities and more erosional substrata than individuals <40 mm (Fig. 3b). During fall 2002, large turquoise darters (>50 mm) used microhabitats with lower velocities and greater amounts of cobble and depositional substrata than smaller specimens (Fig. 3c).
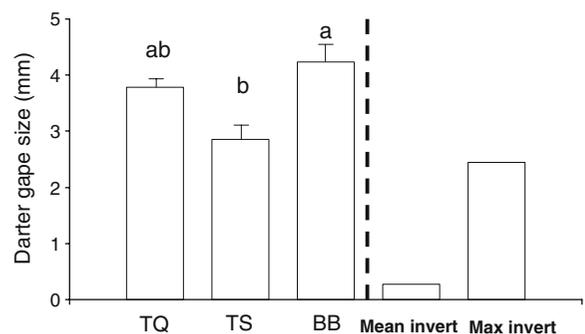

Fig. 4 Test of darter gape size. Histograms represent mean darter gape size of museum specimens. Vertical lines represent ± 1 standard error. Maximum and mean invertebrate head capsule widths are included for reference. Species abbreviations are as follows: TQ = turquoise ($n=16$), TS = tessellated ($n=9$), BB = blackbanded ($n=16$) darters respectively. "Max invert" denotes head capsule width of the largest non-odonate invertebrate sampled. Differing letters indicate significant pairwise differences (Tukey–Kramer, F-value=5.62, p=0.0073)

Gape size and macroinvertebrate analyses

Gape size differed among darter species (Fig. 4); blackbanded darters had significantly larger gapes than tessellated darters, but turquoise darter gapes did not differ from the other species. Nonetheless, the gape of all species was sufficiently large enough to consume the largest non-odonate prey item sampled.

Invertebrate biomass was significantly lower in fall 2001 than in spring 2002, however the opposite result obtained with biomass of percent dipteran composition (Fig. 5a, b). The remaining comparisons were non-significant. Although blackbanded darters used microhabitats with significantly lower macroinvertebrate biomass and numbers than randomly available in fall 2001, (Fig. 6a), they did occupy

microhabitats with significantly higher percentages of Diptera (biomass and numbers) than found in random samples (Fig. 6b). In spring 2002, in comparison to random samples, all three darters occupied microhabitats with significantly lower macroinvertebrate biomass and numerical abundance (blackbanded and tessellated only, Fig. 7a). Blackbanded darters also occupied microhabitats with significantly lower percentages of dipterans (Fig. 7b). Nonetheless, tessellated darters occupied microhabitats with significantly higher biomass percentages of Diptera (Fig. 7b). There were no interspecific differences in biomass, numbers, or percent dipteran composition during this season. There were no significant size-related differences in macroinvertebrate abundance in microhabitats occupied by any size classes of any darter species.
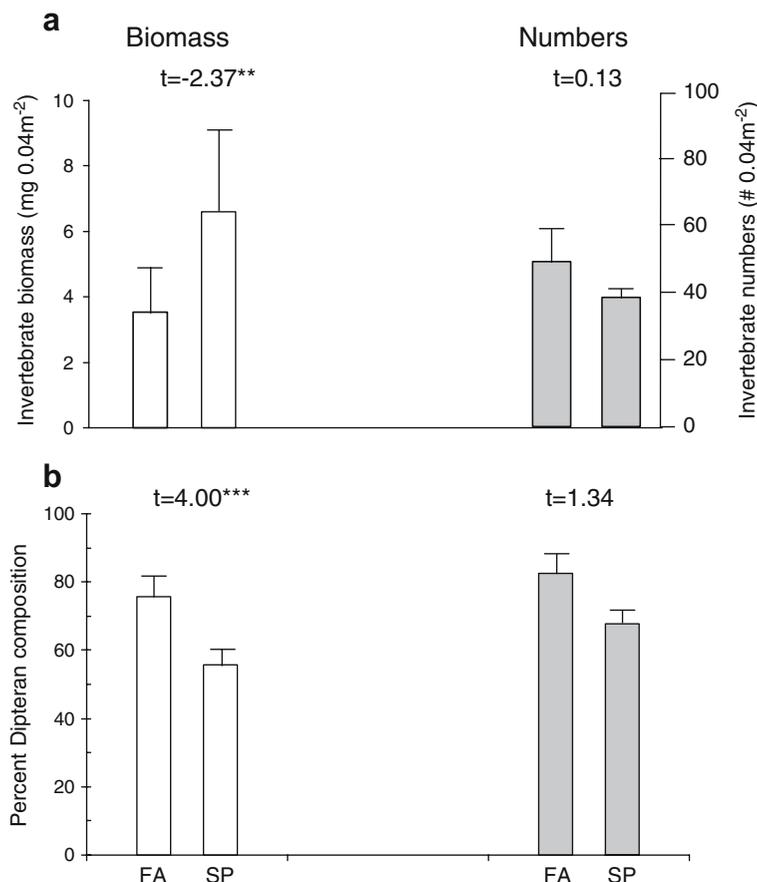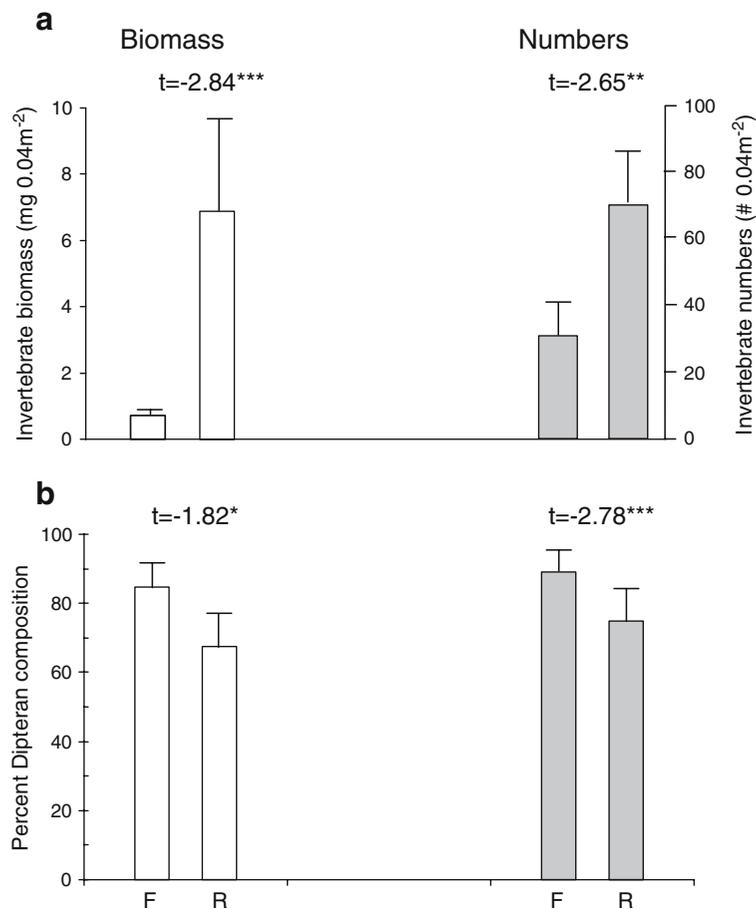

Fig. 5 Test for differences in invertebrate abundance between fall 2001 ($n=48$) and spring 2002 ($n=116$). Histograms represent mean invertebrate biomass (**a** – left), invertebrate numbers (**a** – right), and mean ratio of dipteran/total biomass (**b** – left) and number (**b**– right). Vertical lines represent ± 1 standard error. *$p≤$ 0.10, **$p<0.05$, ***$p<0.01$

Discussion

Our results demonstrated that blackbanded, tessellated and turquoise darters in Cloud Creek use microhabitat in a non-random manner, generally choosing areas with faster current velocities and more complex substrata. In addition, all species occupied distinct microhabitats in fall 2001 but these differences were less distinct in spring 2002 (two *Etheostoma spp.* different) and had disappeared by summer 2002. Seasonal differences in microhabitat use for the three species were attributable to seasonal differences in microhabitat availability. We also observed size-related differences in microhabitat use in both blackbanded and turquoise darters. With the exception of turquoise darters in fall 2002, smaller

darters tended to use slower microhabitats with greater quantities of depositional substrata. Finally, although both blackbanded and tessellated darters occasionally occupied microhabitats with higher proportions of chironomids, in general darters did not select microhabitats with higher prey abundances. Our results almost certainly were affected by the highly variable environmental conditions observed during the study with both drought (fall 2001 early fall 2002) and higher flow conditions (mid – fall 2002) present. This variation, besides its effect on the biota, also prevented us from collecting both benthic samples during summer and habitat availability data in fall 2002 (rains broke the drought), which likely made detection of biological relationships more difficult.
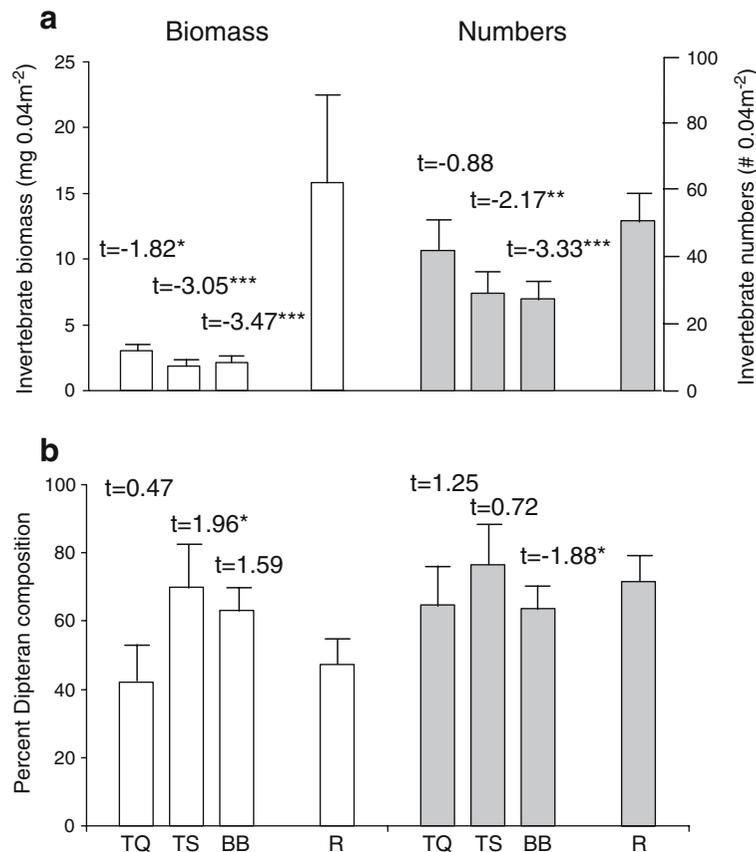

Fig. 6 Test for differences in invertebrate abundance between blackbanded (*n*=25) darter microhabitats (*F*) and randomly selected (*n*=22) microhabitats (*R*) in fall 2001. Histograms represent mean invertebrate biomass – darter vs. random (*top left*), invertebrate numbers – darter vs. random (**a**), and mean dipteran/total biomass – darter vs. random (**b**) and mean dipteran/total number – darter vs. random (*bottom right*). Vertical lines represent ±1 standard error. *$p \leq 0.10$, **$p < 0.05$, ***$p < 0.01$

Comparisons of habitat use patterns of other darters with our data reveal both similarities and differences. For example, Van Snik Gray and Stauffer (1999) observed tessellated darters in deeper habitats than other darters, and depth selection by this species varied among sites. In our study, tessellated darters used different velocities from either blackbanded or turquoise darters during at least one season, but there were no interspecific differences in depth. Van Snik Gray and Stauffer (2001) and Van Snik Gray et al. (2005) found that interspecific competition with the introduced banded darter, *E. zonale*, caused tessellated darters to shift from larger to smaller substrata in aquarium studies, a pattern later confirmed in the field. Their field studies also suggest tessellated darters were aggressively displaced by banded darters from preferred deeper faster microhabitats to slower,

shallower microhabitats (Van Snik Gray and Stauffer 2001). Despite many hours of underwater observation we did not observe any interspecific aggression among blackbanded, tessellated or turquoise darters in Cloud's Creek. Patterns of microhabitat segregation also were not indicative of interspecific competition, because the greatest amount of habitat specialization occurred in the season with intermediate levels of microhabitat availability rather than when microhabitat availability was lowest. Similarly, Stauffer et al. (1996) found that darters showed the greatest specialization during the month with the greatest habitat availability. Finally, Bayou, orangefin and spotted darters displayed similar habitat use patterns to darters in Cloud's Creek with non-random use occurring along a substratum size and depth gradient (Kessler and Thorp 1993; Slack et al. 2004).

Fig. 7 Test for differences in invertebrate abundance between blackbanded (BB – $n=49$), turquoise (TQ – $n=17$) and tessellated (TS – $n=13$) darter microhabitats and randomly selected (R – $n=37$) microhabitats in spring 2002. Histograms represent mean invertebrate biomass - darter vs. random (**a**), invertebrate numbers - darter vs. random (top right, shaded), and mean dipteran/total biomass - darter vs. random (**b**) and mean dipteran/total number - darter vs. random (bottom right, shaded). Vertical lines represent ± 1 standard error. * = $p \leq 0.10$, ** = $p < 0.05$, *** = $p < 0.01$

Similar to other stream fishes, we observed length-related differences in darter microhabitat use (Grossman and Ratajczak 1998). Although Grossman and Ratajczak (1998) did not detect length related differences in microhabitat use by *E. blennioides*, in a southern Appalachian stream (Coweeta Creek, NC), length-related differences were common among other species. Freeman and Stouder (1989) suggested that length-related depth preferences of *Cottus bairdi* in Coweeta Creek were influenced by intraspecific competition, which was confirmed by the field removal experiments of Grossman et al. (2006). We cannot speculate on the causal mechanisms producing length-related shifts in microhabitat use by blackbanded and turquoise darters although they may be related to ontogeny or intraspecific competition (Grossman and Freeman 1987; Grossman and Ratajczak 1998).

We originally hypothesized that darters would occupy microhabitats with higher abundances of prey as has been shown for other benthic species in Coweeta Creek (Petty and Grossman 1996; Thompson et al 2001). Our results, however, did not support this hypothesis, except for two cases in which both blackbanded and tessellated darters occupied patches with higher proportions of chironomids. The reasons for the differences among studies are unclear, although macroinvertebrate abundance, especially that of large macroinvertebrates was much lower in Cloud Creek than in Coweeta Creek (Hill and Grossman 1993; Petty and Grossman 1996). In addition, neither of the previous studies were conducted during droughts of the magnitude observed in Cloud Creek (Grossman et al. 1998). It was not surprising that the only positive results involved chironomids because Diptera are a major prey for darters (Matthews et al. 1982; Hlohowskyj and White 1983; McGehee 1989; Van Snik Gray et al. 1997).

Quantification of microhabitat use by stream fishes is of use from both basic and applied perspectives. Our data indicate that all three darter species differentially used microhabitats with higher current velocities and more complex substrata, and suggest that actions reducing the availability of these microhabitats probably would negatively affect these species. Turquoise darters, which naturally exhibit a narrow geographical distribution, also used more specialized scour microhabitats than blackbanded or tessellated darters. Anthropogenic changes that reduce

discharge have a greater impact on riffles and riffle-like stream habitats, in contrast to deeper habitats (e.g., pools). Therefore, darters that require scour microhabitats may be more prone to the effects of drought, or dewatering of streams. The fact that we observed only one turquoise darter within the site during summer 2002 provides support for this hypothesis. Microhabitat data such as these should aid managers in determining minimum flow levels for dam operations and other diversions. In addition, changes in land management practices that decrease stream sedimentation may help prevent homogenization of complex substrata required by many darter species.

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