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Microhabitat use, movements and abundance of gilt darters (*Percina evides*) in southern Appalachian (USA) streams

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Abstract – We examined microhabitat use by gilt darters (*Percina evides*) in two streams in the south-eastern USA. Darters were over-represented in erosional microhabitats with higher average velocities and more cobble. Male darters tended to show stronger selection than females. Size-based analyses showed that larger (≥60 mm) gilt darters tended to use microhabitats with more heterogeneous substrata and more boulder than smaller (≤59 mm) darters. We also conducted a short-term movement study and calculated population estimates based on mark–recapture data in autumn 2005. Darters moved both long and short distances with 40% of all recaptures occurring within 5 m of the initial capture point. Using Program MARK and model-averaged parameter estimates gilt darter density was 0.31 darters·m^{-2} (225 darters/730 m^2). Conservation of this species will require the preservation of erosional habitats in streams.

Key words: etheostoma; patch selection; habitat; habitat selection; fish

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Introduction

Temperate streams generally display high levels of spatial and temporal habitat heterogeneity, which renders them patchy environments (Petty & Grossman 1996). Habitat patches in streams vary in quantity and quality (Grossman et al. 1995; Wu & Loucks 1995) which can affect: (i) distribution (Thompson et al. 2001; Rieman et al. 2006), (ii) movements (Mundahl & Ingersoll 1983; Railsback et al. 1999; Petty & Grossman 2004) and (iii) habitat use (Freeman & Grossman 1993; Grossman et al. 2002; Resetarits 2005) of stream fishes. Despite the ubiquity of patchiness in streams, there are few studies that directly examine the effects of patchiness on habitat use in stream fishes (Grossman et al. 2002).

The general lack of information on habitat use patterns of stream fishes is a significant problem for conservation of these organisms, especially in regions of high diversity such as the south eastern USA. In fact, concomitant with increased land development in this region, a large number of south eastern stream fishes have decreased in abundance; with many being classified as imperiled (Margulies et al. 1980; Labbe & Fausch 2000; Warren et al. 2000). This trend is particularly evident within the highly speciose darter subfamily (Etheostomatinae: Warren et al. 1997; Scott & Helfman 2001).

As a consequence, we quantified a variety of habitat-related characteristics for the gilt darter (*Percina evides*). Gilt darters are relatively widespread with three disjunct regional populations: Eastern, Missouri/Upper Mississippi River and White River (Ozarks; Near et al. 2001). Despite their broad distribution, the range and general abundance of gilt darters has been declining for decades (Page 1983; Hatch 1985; NatureServe Explorer 2006) and this species is classified as imperiled/rare in some states (e.g. Georgia). Hence, we tested for nonrandom microhabitat use by gilt darters in two sites over several seasons. We addressed whether nonrandom microhabitat use varied seasonally or by fish sex or size. In addition, we conducted a short-term study of darter movements and abundances.

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Methods

Study sites

Our study sites were Coweeta Creek and Tellico Creek, located in Macon County, North Carolina. These streams are both tributaries of the Little Tennessee River (35°11'N; 83°23'W) and are relatively undisturbed (>97% forested land cover, Sutherland et al. 2002). Coweeta Creek is a fifth order stream with an average discharge of 1.26 $m^3 \cdot s^{-1}$ (Sutherland et al. 2002). Our study site was a 100 m section of the creek approximately 4 km downstream of the USDA Coweeta Hydrologic lab. The general physiognomy of the Coweeta Creek drainage has been described by Grossman et al. (1998). Tellico Creek is a third order stream, with an average discharge of 0.63 $m^3 \cdot s^{-1}$ (Sutherland et al. 2002). The Tellico study site was 110 m in length. Both study sites have riffle, run and pool morphologies typical of streams in the Blue Ridge Province of the southern Appalachians.

Microhabitat availability

We quantified microhabitat availability by collecting random samples between 20 and 200 cm from each darter's location. The direction of the microhabitat availability sample was randomly chosen from 0 to 24, corresponding to 30 min intervals on a clock face; we randomly selected the distance for the samples location using a number between 20 and 200. We considered random microhabitat availability samples to represent patches could have been occupied by darters (Petty & Grossman 1996).

Microhabitat measurements

We made fish microhabitat measurements in Coweeta Creek between 7 May and 7 June 2005 (spring sample) and in Tellico Creek between 9 and 28 August 2005 (summer sample) and 21 October to 5 November (autumn sample). The change in sites resulted from a loss of access to the Coweeta site. During the spring sample some gilt darters exhibited breeding behaviour, thus habitat use patterns during this period represent a mixture of breeding and nonbreeding patterns. We made fish observations during daylight hours (from ~0900 to ~1700) by entering the study site at a randomly determined location and snorkelling slowly upstream while searching for gilt darters. We covered the entire channel width by slowly moving laterally until the far bank was reached and then moving slowly upstream and repeating this procedure. Upon sighting an undisturbed fish we placed a painted lead weight at its location (Petty & Grossman 2004).

We measured a series of microhabitat parameters (mean water velocity, focal point velocity, depth, distance from substratum and substratum composition) using the methods of Grossman & Freeman (1987) and Petty & Grossman (1996). We quantified current velocity using a Marsh-McBirney Model 201 electronic velocity metre. We measured depth to the nearest 0.5 cm with a metre stick. We visually estimated substratum composition within a 400 cm^2 quadrat centered on the fish's position. Substrata were divided into seven categories (bedrock, boulder, cobble, gravel, sand, silt and debris). Because Coweeta data are from spring and Tellico data from summer and autumn, inter-site comparisons are confounded by a site X season interaction.

Movements and population size

During the autumn 2005 sampling, we also quantified short-term movements and conducted a mark–recapture population estimate for gilt darters in Tellico Creek. We captured gilt darters with dip nets, anaesthetised them, and then marked them with a unique subcutaneous acrylic paint mark (magenta, orange, light pink and turquoise). Darters were marked using a combination of three marks at four possible body locations (left and right anal fin, left and right caudal peduncle; Hill & Grossman 1987; Roberts & Angermeier 2004). We weighed each fish with an electronic balance (nearest 0.1 g) and measured length with a straightedge (nearest mm, standard length, SL). After marking, gilt darters were kept in a live well to monitor injuries and mortality. If fish displayed 'typical' behaviour and had no physical injuries, we replaced them in their exact capture location in the stream.

We made three sequential passes through the Tellico Creek site on 21–22 October, 29–30 October and 3–5 November. Each pass employed relatively equal sampling effort and consisted of 3–4 h of effort per 15 m of the site, or until we captured all darters observed. After capture, we examined all gilt darters for marks, and marked all previously unmarked fish. We triangulated the exact capture location (±1 cm) of each fish using permanent benchmarks placed at 5 m intervals along the stream bank. We then compared recapture locations to derive an estimate of linear movement between captures (Petty & Grossman 2004). At the end of the third pass, we snorkelled 25 m sections both directly above and below the study site to capture marked individuals that moved out of the study site (Albanese et al. 2003).

Data analysis

Microhabitat availability and use

We tested for differences in both microhabitat habitat availability both within and among sites and between darter use and availability using the Principle Component Analysis (PCA) technique (correlation matrix solution) of Grossman & Freeman (1987) and Grossman & de Sostoa (1994). We used PCA because microhabitat data represent a constellation of correlated factors that are unlikely to be perceived as independent variables and PCA is the least biased multivariate technique for detecting patterns in this type of data (Grossman et al. 1991). In the PCA analysis the darter's focal water velocity was analogous to the bottom velocity because all the darters encountered were on the bottom substratum. Both linear and per cent data were transformed using ln and arcsine-square root transforms respectively. We only reported ecologically interpretable components with eigenvalues >1 (Grossman & Freeman 1987). To test for significant differences we plotted means and 95% confidence ellipses for the sample(s) of interest (i.e. seasonal microhabitat availability, seasonal microhabitat use, site, sex, size, etc.) for each pair of components (Grossman & de Sostoa 1994). If the 95% confidence ellipses did not overlap, the samples were considered significantly different (equivalent to a *t*-test, Johnson 1999).

Gilt darters have sexually dimorphic colouration and sex is correlated with size (Skyfield & Grossman, unpublished data). Juvenile gilt darters (approximately <45 mm SL) all appear to have female colouration, although by ~50mm SL sexually dimorphic coloration is present (Hatch 1982). Although all darters between 45 and 50 mm had female colouration, almost all gilt darters >60 mm displayed male colouration. Consequently, sex-based comparisons only were made on fish 51–59 mm where both sexes are represented. We also assumed that external colouration represented the true sex of the individual (i.e. there were no males that mimicked female colouration). We also performed size-linked analyses but recognise that size and sex are confounded in these analyses.

Movement

We quantified movements of darters using linear movement distances calculated with ARCView 3.2 (Environmental Systems Research Institute, CA, USA). We tested for significant differences in the number of darters making upstream versus downstream movement as well as mean upstream and downstream distances moved using Wilcoxon rank sum tests. Movement differences among gilt darters recaptured at varying sampling intervals (i.e. pass 1 – pass 2, pass 2 – pass 3 and pass 1 – pass 3) were quantified using a Wilcoxon ANOVA with *a posteriori* Tukey's Honestly Significant Difference, (HSD) tests on ranked data. Finally, we used Wilcoxon rank sum tests and Wilcoxon ANOVA with Tukey's HSD tests respectively, to examine differences in movement distances on both a sex and size-related (≤50 mm, 51–59 mm and ≥60 mm) basis.

Population size

We used Program MARK (White & Burnham 1999; Program MARK) to derive a population size estimate and 95% confidence interval (CI) from mark–recapture data from Tellico Creek in autumn 2005. We used a closed population model with a Huggins estimator to calculate capture and recapture probabilities, and population size separately. To evaluate the relative fit of the candidate models, we used Akaike's Information Criteria corrected for small samples (AIC_c). The relative fits of the candidate models were determined by calculating the Akaike weights, with the best fitting model having the highest weight. We then examined parameter estimates and CIs to select the best model(s). We ran the analysis using 111 marked gilt darters.

Results

Microhabitat availability

Inter-site and seasonal variation in habitat availability
More than half (61%) of the variance in the microhabitat availability data set for both sites was explained by the first four factors from the PCA. Both Coweeta spring and Tellico summer samples possessed faster average and bottom velocities with more cobble than Tellico autumn samples (Appendix 1, Fig. 1a and b. In addition, Tellico Creek contained more boulder and gravel than was available in Coweeta Creek (Appendix 1, Fig. 1a and b). Finally, Coweeta Creek in spring was significantly deeper than Tellico Creek in either summer or autumn (Appendix 1, Fig. 1b).

Microhabitat use in Coweeta and Tellico Creeks

Gilt darters displayed nonrandom microhabitat use during all three seasons of the study. The PCA for spring 2005 data extracted four interpretable components (61% variance explained); however, only components 1 and 2 showed differences between use and availability data. Gilt darters occupied microhabitats with greater amounts of cobble and lower quantities of boulders and depositional substrata, than randomly available (Fig. 2a). The

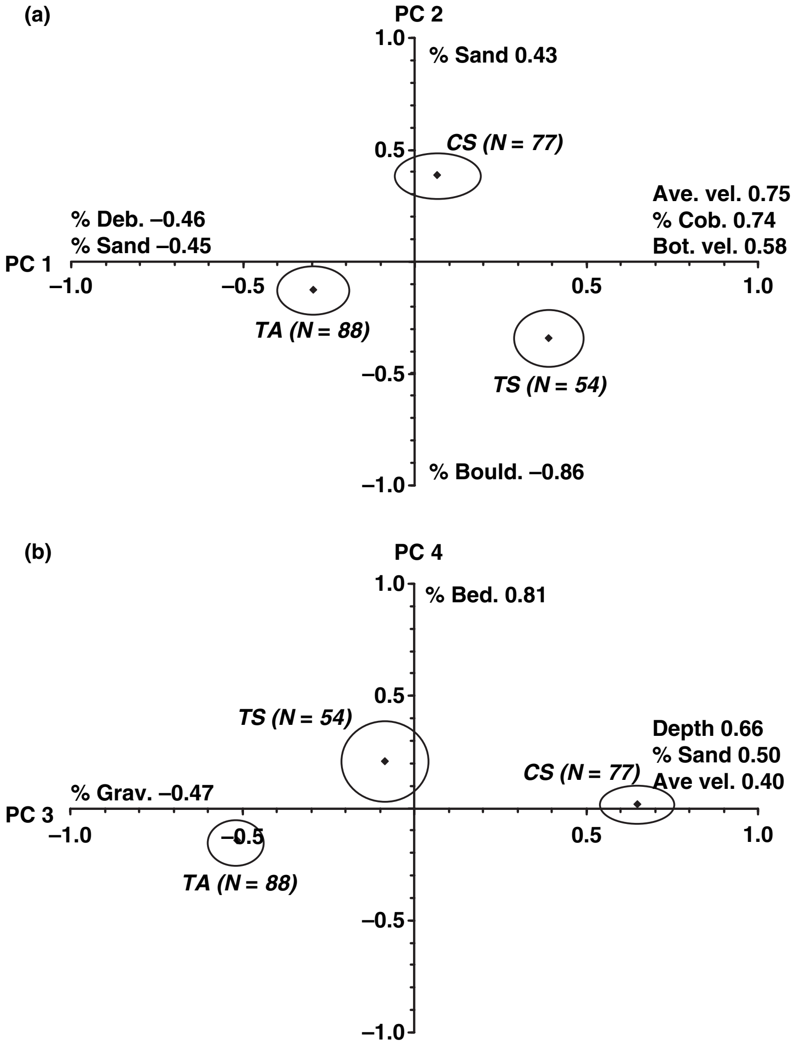

Fig. 1. Inter-site differences in habitat availability, PC 1–4. PC 1 and 2 (a), PC 3 and 4 (b). Centroids represent sample means and ellipses are 95% confidence intervals. Only loadings ≥0.40 are presented. CS, Coweeta spring; TS, Tellico summer; TA, Tellico autumn. Ellipses that do not overlap represent samples that are significantly different at the 0.05 level using a *t*-test.

summer 2005, PCA also extracted four interpretable components (66% variance explained). Again, only components 1 and 2 showed differences between use and availability. PC1 and PC2 indicated that gilt darters occurred in microhabitats with higher percentages of cobble and gravel and lower amounts of boulder/bedrock and depositional substrata than randomly available (Fig. 2b). Finally, the autumn 2005 PCA identified three components (49% variance explained); however, differences in use only were displayed on PCs 1 and 2. Gilt darters were over-represented in higher velocity microhabitats with greater amounts of cobble and less boulder, sand and debris than randomly available (Fig. 2c).

Sex-linked differences in microhabitat use

Our sex-based microhabitat comparisons only included fish 51–59 mm SL because this was the only size class in which the sexes showed overlap in all seasons (personal communication). PCA analysis for Coweeta Creek spring data identified three components (PCA – 66% variance explained); however, differences in use only were displayed on PCs 1 and 2. Male gilt darters occupied microhabitats with higher average and bottom velocities, greater amounts of cobble and less sand and boulder than females (Appendix 2, Fig. 3a). PCA analysis for Tellico Creek summer data also identified three components (PCA – 69% variance explained), with differences in use only displayed on PCs 1 and 2. Analysis of Tellico Creek autumn data, however, identified four components (PCA – 73% variance explained) with differences displayed on PCs 1, 2 and 4. Male and female darters occupied distinct microhabitats in Tellico Creek during both summer and autumn. In summer, male gilt darters utilised microhabitats with more cobble, higher average velocities, and less boulder than females (Fig. 3b). In autumn, male gilt darters used microhabitats with lower average and bottom velocities and greater amounts of cobble and less boulder than females (Appendix 2, Fig. 3c).

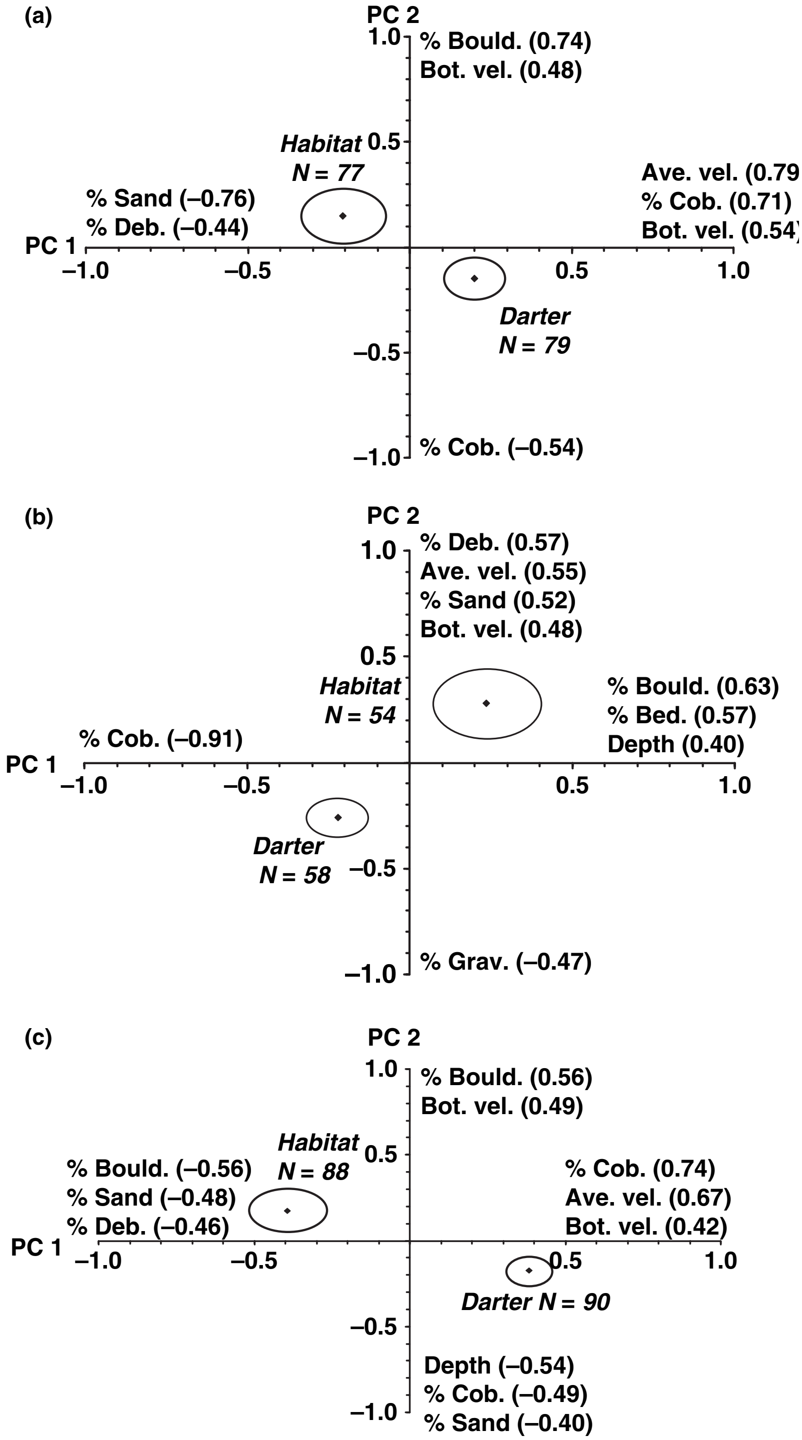

Fig. 2. Test for nonrandom microhabitat use by gilt darters during spring in Coweeta Creek (a), summer in Tellico Creek (b), and autumn in Tellico Creek (c) (see Fig. 1 for full details).

Size-linked differences in microhabitat use

We also observed size-related differences in microhabitat use by gilt darters in all three seasons. The PCA for Coweeta Creek in spring extracted three factors (58% variance explained), medium gilt darters (51–59 mm) occupied microhabitats with higher bottom velocities, deeper water and greater amounts of cobble and less depositional substrata than either large (≥60 mm) or small (≤50 mm) fish (Appendix 3, Fig. 4a). Gilt darters in Tellico Creek in summer also displayed size-related differences in microhabitat use (PCA – four components, 68% variance explained, Fig. 4b). Small (≤50 mm) and medium (51–59 mm) gilt darters occupied microhabitats with greater amounts of cobble than large (≥60 mm) gilt darters (Appendix 3, Fig. 4b). Microhabitats used by medium gilt darters (51–59 mm) had higher bottom

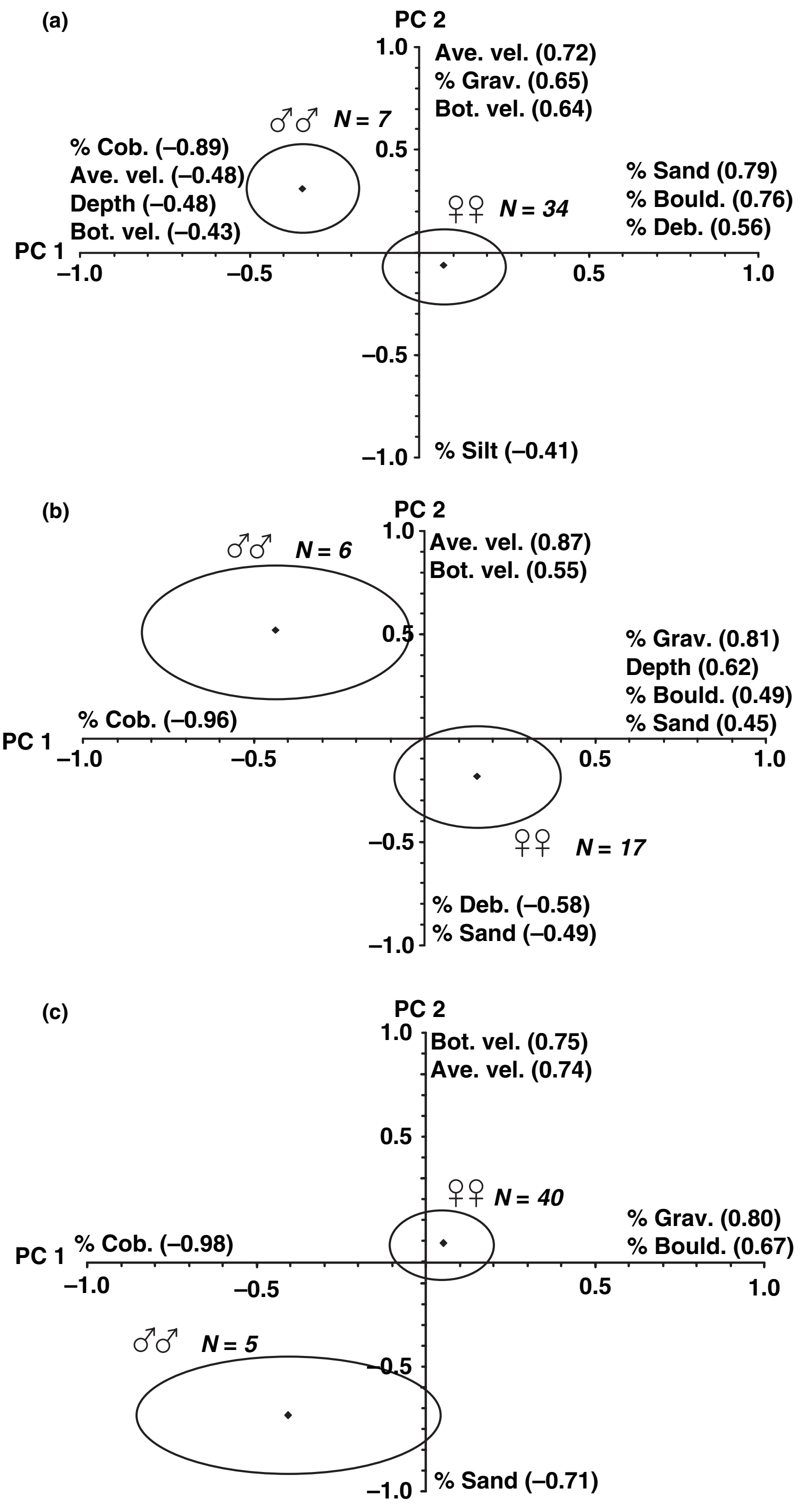

Fig. 3. Test for sex-linked differences in microhabitat use by gilt darters during spring – Coweeta Creek (a), summer – Tellico Creek, (b) and autumn, Tellico Creek (c) (see Fig. 1 for full details).

velocities than those used by either large (≥60 mm) or small (≤50 mm) gilt darters (Appendix 3, Fig. 4b). Finally, large (≥60 mm) gilt darters were found over more gravel and large erosional substrata than either small (≤50 mm) or medium (51–59 mm) fish (Appendix 3, Fig. 4b). In contrast to summer, only small (≤50 mm) and medium (51–59 mm) gilt darters differed in microhabitat use during autumn in Tellico Creek (PCA – four components, 69% variance explained, Appendix 3, Fig. 4c). Small (≤50 mm) gilt darters occupied microhabitats with lower average velocities and more boulder and sand than those used by medium (51–59 mm) gilt darters (Appendix 3, Fig. 4c).

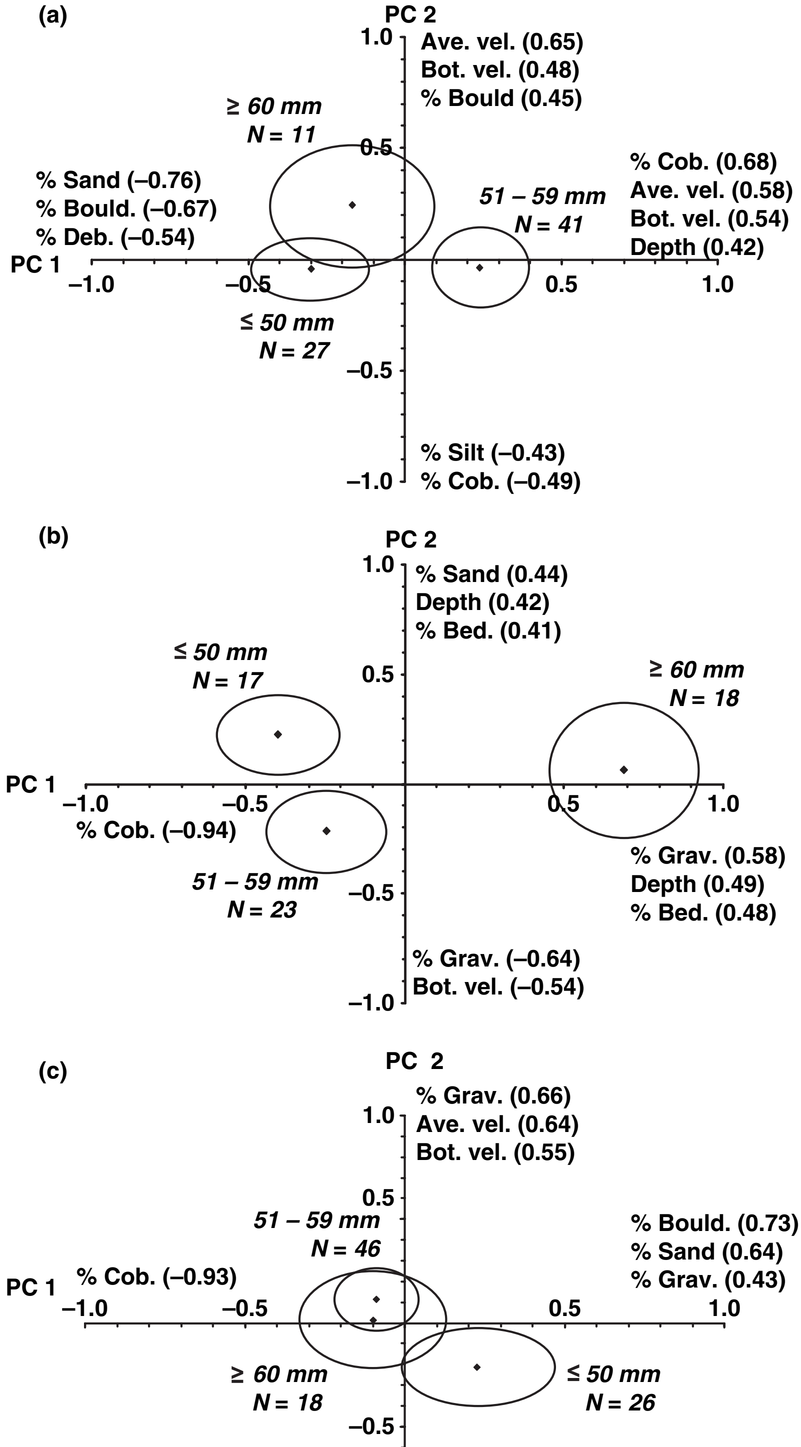

Fig. 4. Test for size-linked differences in microhabitat use by gilt darters during spring – Coweeta Creeek (a), summer – Tellico Creek, (b) and autumn, Tellico Creek (c) (see Fig. 1 for full details).

Movement

We marked 164 darters and recaptured 35 identifiable individuals (total recaptures = 43). The vast majority of recaptured fish had identifiable marks. Net movement for these darters ranged from 28 m downstream to 58 m upstream, with the majority of movements occurring within 8 m of the capture site (Fig. 5). Totally 40% of the recaptured darters remained within 5 m of the initial capture site. During our study, gilt darters did not exhibit significant differences (Wilcoxon test, all P-values > 0.05) in: (i) frequency of

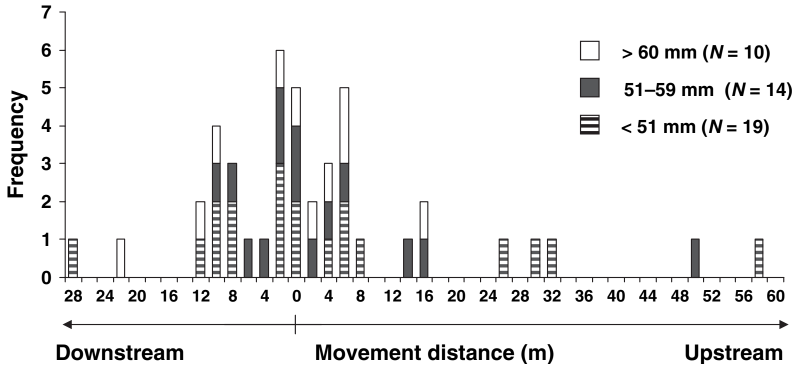

Fig. 5. Movement data for small (45–50 mm), medium (50–59 mm) and large (>60 mm) gilt darters in Tellico Creek during autumn sampling.

Table 1. Akaike Information Criterion (AIC) models of varying capture–recapture probabilities used to estimate population size in Tellico Creek, autumn 2005.

Model	K	Log L	AIC_c	ΔAIC_{ci}	w_i	Mean	Lower CI	Upper CI
Population size = capture probability varies, recapture probability is constant	4	1.00	598.5	0.00	0.608	239	164	54488
Population size = capture and recapture probability vary	5	0.405	600.3	1.81	0.247	201	164	24914
Population size = capture probability and recapture probability are equal and constant	**1**	**0.113**	**602.897**	**4.35**	**0.069**	**240**	**213**	**284**
population size = capture probability and recapture probability are constant but not equal	**2**	**0.089**	**603.382**	**4.84**	**0.054**	**212**	**185**	**271**
Population size = capture probability is constant and recapture probability varies	**3**	**0.036**	**605.171**	**6.63**	**0.022**	**212**	**185**	**271**

K is the number of parameters, Log L is the log likelihood value, AIC_c represents Akaike Information Criterion for small samples, ΔAIC_c represents the difference in AIC values for two models, w_i is the Akaike weight, mean is mean population size and CI represents the 95% confidence interval. Values in bold represent models in the confidence set.

upstream or downstream movement, (20 upstream vs. 21 downstream), (ii) mean distances moved upstream and downstream, (iii) distances moved while at large for differing time periods (e.g. recaptures on pass 2 vs. pass 3), (iv) movements by males and females or (v) movement distances of small, medium or large gilt darters (Fig. 5).

Population size

Because AICc weights were low, and CI extremely wide for the two models with the highest w_i values, we model averaged from the remaining models in the confidence set to obtain our parameter estimates (Table 1). Model averaged parameter estimates yielded a mean of 225 (95% CI: 167–282) individuals within an area of 730 m^2, for a density of 0.31 gilt darters·m^{-2}.

Discussion

The gilt darters of both Coweeta and Tellico Creeks exhibited nonrandom microhabitat use in all sites and seasons. In general, gilt darters selected microhabitats with higher average velocities, greater amounts of cobble and to a lesser extent, gravel. Gilt darters always were found on the substratum (benthic guild, *sensu* Grossman & Freeman 1987) and generally avoided microhabitats with substantial amounts of depositional substrata (sand, silt or debris). In addition, gilt darters appeared to select deeper microhabitats in Coweeta Creek: however, this may be due to seasonal, site-specific or reproductive requirements of this species. Although we have no direct evidence, it is possible that gilt darters are over-represented in high-velocity microhabitats dominated by cobble, because cobble substrata may provide excellent habitat for invertebrate colonisation (Mattingly & Galat 2004), a phenomenon that has been demonstrated for other benthic fishes in this system (see Petty & Grossman 1996; Thompson et al. 2001). In addition, cobbles provide extensive interstitial spaces which may serve as refuges from both high velocities and predators (Harding et al. 1998).

Gilt darters displayed relatively consistent microhabitat use patterns despite differences in microhabitat availability and the abundances of benthic species in the two streams. For example, mottled sculpin (*Cottus bairdi*) were much more abundant in Coweeta Creek than in Tellico Creek (J. Skyfield, personal communication). This suggests that interspecific interactions with mottled sculpin may have little effect on microhabitat use by gilt darters. Similar results have been found in microhabitat use studies for other species in Coweeta Creek (i.e. few interspecific effects, Grossman et al. 1998).

Given the between-stream and seasonal consistency of microhabitat use patterns for gilt darters, it is possible that our results are relevant to other gilt darter populations (Glozier et al. 1997). Our data also are consistent with studies that have identified important habitat types for other darters (Bowen et al. 1998;

Freeman et al. 2001) such as shallow-coarse (<35 cm deep, gravel or larger substrate) and shallow-slow (<35 cm deep, <35 cm·s^{-1}) habitats. Nonetheless, without replication of seasonal and site-related patterns the potential transferability of our microhabitat results are limited (*sensu* Rosenfeld 2003; Rosenfeld et al. 2005).

In addition to the microhabitat use patterns observed in all darters, we detected significant size-related and sex-related differences in microhabitat use, although these differences were confounded by a size–sex interaction. Sexual dimorphism in colouration or morphology are not common in stream fishes, thus, there are few studies documenting sexual differences in microhabitat use. Nonetheless, male gilt darters occupied microhabitats with greater amounts of cobble overall sites and seasons, and also tended to occur in higher velocity microhabitats over less boulder substrata than female darters. During autumn in Tellico Creek, however, male gilt darters shifted to slower, deeper microhabitats than females.

Size-related analyses indicated that large gilt darters selected microhabitats with greater amounts of boulder and more heterogeneous substrata than small gilt darters (and sometimes medium-size darters) in both Coweeta Creek and Tellico summer samples. Size-related differences were less pronounced for Tellico autumn samples and medium and large gilt darters did not differ in microhabitat use during this season. It is possible that the greater amounts of depositional microhabitats (more debris, shallower and slower water) during this season reduced the amount of preferred microhabitat for large darters. Previous researchers have found that larger stream fish are more likely to inhabit areas that either maximise energy gain or minimise energy expenditure (Hill & Grossman 1993; Petty & Grossman 1996; Page 2000; Thompson et al. 2001; Grossman et al. 2002; Rosenfeld 2003; Mattingly & Galat 2004; Wildhaber & Lamberson 2004). This may explain the differences observed in size-related analyses, although we cannot test this hypothesis directly.

Our microhabitat findings are similar to those of other investigators who have studied microhabitat use in darters. The use of cobble substrata by gilt darters is well documented (Hatch 1985; Greenberg 1991) and other species of darters are known to exhibit selection for cobble-sized substrata (Chipps et al. 1994; Grossman & Ratajczak 1998; van Snik Gray & Stauffer 2001). Similar to our results, Hatch (1985) also found that gilt darters avoided depositional substrata.

Movement data and population estimates for gilt darters were based on a single season and hence, must be viewed as tentative. Nevertheless, little is known about darter movements, population sizes or densities. We observed both long and short movements by gilt darters with 40% of fish being recaptured within 5 m of their original capture location. The Tellico Creek gilt darter population appeared to include both movers and stayers (Gowan et al. 1994; Fraser et al. 2001; Rodriguez 2002; Petty & Grossman 2004), with little evidence of sex or size-based patterns in movement behaviour. The sole exception is that large fish never moved more than 21 m from their site of capture. We found no fish that had moved in the 25 m buffer zones surrounding our site, suggesting that most fish may have remained in the study area; however, we could not detect movements out of the study site >25 m. Gilt darter density in Tellico Creek generally were lower than densities recorded by Hatch (1982) for Minnesota populations (0.2–1.55 darters·m^{-2}). Nonetheless, however the temporal and phylogenetic differences (i.e. south eastern gilt darters belong to a different monophyletic group, Near et al. 2001) render these comparisons moot.

Gilt darters are a species of special concern within some south eastern states (e.g. Georgia) and their declining abundances (Margulies et al. 1980; Hatch 1982) may be due to a variety of factors including habitat degradation. Declines in stream habitat quality such as increased turbidity and sedimentation may negatively affect stream fishes by reducing prey abundance or foraging success or degrade spawning or nonspawning habitats (Hatch 1985; Sutherland et al. 2002; Tabit & Johnson 2002; Bolliet et al. 2005). Given that gilt darters avoided depositional substrata, anthropogenic sedimentation is likely to negatively influence gilt darter fitness and population persistence.

In conclusion, we have shown that gilt darters were over-represented in faster microhabitats with greater amounts of erosional substrata. Microhabitat use by gilt darters differed by sex (cobble and boulder) and size (substratum variables) although there was little apparent seasonal variation. Gilt darters showed both restricted and relatively long-distance movements, although 40% of recaptured individuals were found within 5 m of their capture site. Densities of gilt darters in this relatively natural stream were 0.31 darters·m^{-2}. Given the paucity of information on this species of special concern, our data should be of use to both state and federal resource management agencies.

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Appendix

Appendix 1. Univariate mean and standard deviation of microhabitat availability and overall darter use data for all sites and seasons.

Site, season, habitat	*N*	Depth (cm)	Average velocity (m·s^{-1})	Bottom velocity (m·s^{-1})	% Bedrock	% Boulder	% Cobble	% Gravel	% Sand	% Silt	% Debris
Coweeta spring habitat	77	47 (18)	0.41 (0.19)	0.15 (0.13)	1 (7)	10 (22)	49 (32)	9 (13)	26 (28)	1 (8)	3 (11)
Coweeta spring Darter use	79	51 (16)	0.42 (0.17)	0.13 (0.09)	0	5 (14)	65 (29)	11 (11)	14 (16)	0 (1)	1 (3)
Tellico summer habitat	54	36 (11)	0.39 (0.18)	0.17 (0.12)	3 (16)	22 (32)	55 (33)	14 (17)	5 (13)	0	0 (1)
Tellico summer darter use	58	39 (9)	0.40 (0.16)	0.14 (0.13)	1 (6)	6 (11)	71 (22)	20 (19)	2 (5)	0	0
Tellico autumn habitat	88	29 (13)	0.27 (0.19)	0.11 (0.11)	1 (9)	20 (29)	47 (30)	14 (14)	11 (17)	0 (1)	5 (14)
Tellico autumn darter use	90	33 (10)	0.32 (0.18)	0.10 (0.10)	0 (2)	8 (13)	69 (22)	17 (15)	5 (8)	0	1 (3)

Appendix 2. Univariate mean and standard deviation of male and female darter (51–59 mm) microhabitat use for all sites and seasons.

Site, season, habitat	*N*	Depth (cm)	Average velocity (m·s^{-1})	Bottom velocity (m·s^{-1})	% Bedrock	% Boulder	% Cobble	% Gravel	% Sand	% Silt	% Debris
Coweeta spring 51–59 mm male darter	7	46 (7)	0.50 (0.12)	0.17 (0.12)	0	0	80 (9)	12 (9)	7 (6)	0	0
Coweeta spring 51–59 mm female darter	34	57 (17)	0.41 (0.19)	0.14 (0.11)	0	6 (18)	68 (30)	13 (14)	13 (15)	0 (1)	0 (1)
Tellico summer 51–59 mm male darter	6	35 (7)	0.54 (0.08)	0.15 (0.15)	0	0	84 (19)	15 (16)	2 (3)	0	0
Tellico summer 51–59 mm female darter	17	37 (9)	0.38 (0.14)	0.20 (.16)	0	3 (7)	74 (17)	20 (17)	3 (4)	0	0
Tellico autumn 51–59 mm male darter	5	38 (13)	0.28 (0.13)	0.01 (0.01)	0	0	78 (18)	18 (19)	4 (4)	0	0
Tellico autumn 51–59 mm female darter	40	30 (9)	0.34 (0.18)	0.12 (0.10)	1 (3)	8 (11)	70 (20)	17 (15)	4 (6)	0	1 (2)

Appendix 3. Univariate mean and standard deviation of microhabitat use by darter size classes for all sites and seasons.

Site, season, habitat	N	Depth (cm)	Average velocity ($m \cdot s^{-1}$)	Bottom velocity ($m \cdot s^{-1}$)	% Bedrock	% Boulder	% Cobble	% Gravel	% Sand	% Silt	% Debris
Coweeta spring $x \leq 50$ darter	27	48 (16)	0.40 (0.16)	0.11 (0.07)	0	5 (11)	60 (31)	9 (8)	17 (21)	0	2 (4)
Coweeta spring $51 < x < 59$ darter	41	55 (16)	0.43 (0.18)	0.14 (0.11)	0	5 (16)	70 (28)	13 (13)	12 (14)	0	0 (1)
Coweeta spring $x \geq 60$ darter	11	41 (12)	0.44 (0.15)	0.13 (0.07)	0	7 (14)	61 (27)	10 (9)	11 (11)	0	1 (2)
Tellico summer $x \leq 50$ darter	17	42 (11)	0.37 (0.16)	0.10 (0.08)	0	3 (6)	81 (16)	15 (14)	0 (1)	0	0
Tellico summer $51 < x < 59$ darter	23	37 (9)	0.43 (0.14)	0.19 (0.16)	0	2 (6)	76 (18)	18 (16)	3 (4)	0	0
Tellico summer $x \geq 60$ darter	18	40 (8)	0.39 (0.18)	0.13 (0.11)	4 (10)	12 (16)	54 (23)	27 (24)	3 (9)	0	0 (1)
Tellico autumn $x \leq 50$ darter	26	34 (12)	0.26 (0.18)	0.10 (0.10)	0	12 (17)	64 (27)	16 (17)	6 (9)	0	1 (2)
Tellico autumn $51 < x < 59$ darter	46	31 (10)	0.32 (0.18)	0.11 (0.10)	0 (3)	7 (10)	71 (19)	17 (15)	4 (7)	0	1 (2)
Tellico autumn $x \geq 60$ darter	18	34 (6)	0.39 (0.16)	0.07 (0.08)	0	6 (10)	71 (20)	17 (14)	4 (7)	0	2 (5)