Testing Cross-System Transferability of Fish Habitat Associations using *Cottus carolinae* (Banded Sculpin)

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Abstract - Assessing stream fish habitat associations across contrasting ecosystems can inform generality of habitat predictions. We tracked *Cottus carolinae* (Banded Sculpin) in Little Creek, TN, to test transferability of habitat predictions developed from independent studies. Predictions included shifting habitat use across size classes (prediction 1), over the diel period (prediction 2), and during variable flows (prediction 3), as well as maintaining associations with depth, velocity, and substrate gradients across scales (prediction 4). Size 1 (80–99 mm TL) and size 2 (100–140 mm TL) Banded Sculpin used similar habitats (prediction 1 not supported), shifted to pools with little cover at night (prediction 2 supported), and adjusted habitat uses according to flow (prediction 3 supported), and depth, velocity, and substrate associations were similar for small and large streams when size classes were combined (prediction 4 supported). Our synthesis highlights consistencies in fish habitat associations that manifest due to behavioral, morphological, and physiological constraints that operate across ecosystems.

Introduction

Ecological niche and species distribution modeling are useful tools for applying management decisions to the conservation of aquatic organisms because they allow for generating predictions for the distribution of stream fishes (Leftwich et al. 1997, Thomas and Bovee 1993). The framework for such modeling approaches is grounded in niche theory, which broadly states that biotic and abiotic determinants regulate the distribution and abundance of organisms (Chase and Leibold 2003). Soberón and Peterson (2005) described 4 classes of such determinants: (1) environmental conditions that impose physiological limits on species survival and reproduction (i.e., abiotic factors); (2) interactions between species that alter population maintenance (i.e., biotic factors); (3) the ability of a species to disperse and occupy new habitat (i.e., habitat accessibility); and (4) the ability of a species to adapt to new conditions (i.e., evolutionary capacity). Understanding the manner in which these determinants govern species distribution allows for transferring information among ecosystems. However, the generality or transferability of habitat

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associations for most fishes remains unstudied, especially for non-game species with minimal socioeconomic value (Clarkson et al. 2005, Minckley and Deacon 1991). Improved understanding of habitat transferability for cosmopolitan, non-game fishes with reported habitat associations from disparate ecosystems might lend insight into the prevalence of context-dependencies regarding habitat predictions (Hubert and Rahel 1989, Leftwich et al. 1997, Peterson 2006).

Stream fishes select optimal habitats to efficiently utilize resources and increase survival across multiple temporal and spatial scales (Schlosser 1991). Factors associated with stream fish habitat selection are classified as extrinsic (e.g., flow variability) or intrinsic (e.g., physiological) processes (Poff and Allan 1995). At fine scales, fishes respond to short-term variability in flow and diel fluctuations in water temperature and photoperiod by selecting habitats that maximize survival and growth (Schlosser 1991). At broad scales, fishes move among habitats required for reproduction and ontogenetic development (DeBoer et at. 2015, Hunt 1968, Lucas et al. 2001). Across these scales, stream fishes might be expected to exhibit predictable associations with substrates, depths, and current velocities, so that responses form along multiple habitat gradients simultaneously (Poff and Allan 1995). Resource management processes that rely on predictable ecological outcomes concerning fishes include restoration of stream channels (Rabeni and Sowa 1996), stream-flow regulation (Freeman et al. 1997), removal of instream barriers (DeBoer et al. 2015), and restoration of imperiled species (Nykänen and Huusko 2004). Research synthesizing habitat associations of widely distributed species can advance stream fish ecology by testing the transferability of qualitative and quantitative habitat associations across broad habitat gradients (Adams and Schmetterling 2007, Bond and Lake 2003). In the southeastern US, fishes in the family Cottidae are broadly distributed and generally locally abundant, and therefore present the opportunity to test the transferability of documented habitat associations measured at disparate localities (Gorman and Karr 1978, Hynes 1970, Norton 1991).

Cottus carolinae (Gill) (Banded Sculpin) inhabit upland streams in the lower Mississippi Valley from Illinois to Alabama and from Oklahoma to North Carolina. Across this range, habitat associations related to abiotic and biotic classes of determinants are reported from multiple locations (Fig. 1). For example, juvenile Banded Sculpin shifted between riffles and pools in search of suitable habitat and to avoid predation by larger individuals in Brawley's Fork, a 1st-order stream in central Tennessee (Koczaja et al. 2005). Greenberg and Holtzman (1987) found Banded Sculpin used cover for refuge during daylight hours and emerged at night to feed as ambush predators in the Little River, TN. Kessler et al. (1995) found Banded Sculpin associations with current velocities and depths varied with stream-flow magnitude in Russell Creek, KY, so that habitats occupied were constrained by availability across a flow-magnitude gradient. Finally, Hunt (1989) studied the velocity, depth, and substrate associations of Banded Sculpin in a regulated reach of the Caney Fork downstream of Center Hill Reservoir in Tennessee. Hunt (1989) concluded individuals over 80 mm TL were associated with a mean velocity of 0.18 m/s, a mean depth of 0.44 m, and over substrates including gravel and cobble. Collectively, previous studies describe qualitative and quantitative habitat associations

of Banded Sculpin. However, each of these patterns were documented in streams of varying size and across a broad geographic area, creating the possibility for context-dependent or site-specific patterns in habitat associations that might not be transferable to other streams.

The goal of this study was to assemble Banded Sculpin habitat associations developed from multiple independent studies and assess the transferability of habitat associations by testing 4 predictions. We predicted that Banded Sculpin would: (1) express size-specific habitat associations that minimize overlap among size classes (Koczaja et al. 2005); (2) show diel shifts in habitat associations including use of cover by day and open water by night (Greenberg and Holtzman 1987); (3) choose habitats in proportion to availability as increasing flows expand habitat availability and decreasing flows contract habitat availability (Kessler et al. 1995); and (4) associate with shallow habitats (mean = 0.44 m) with moderate velocities (mean = 0.18 m/s) over course substrates such as gravel and cobble (Hunt 1989). Because each of these predictions were developed from research conducted at independent study locations, assessing the occurrence of each at a new location effectively serves to synthesize Banded Sculpin habitat associations and test transferability across ecosystems.
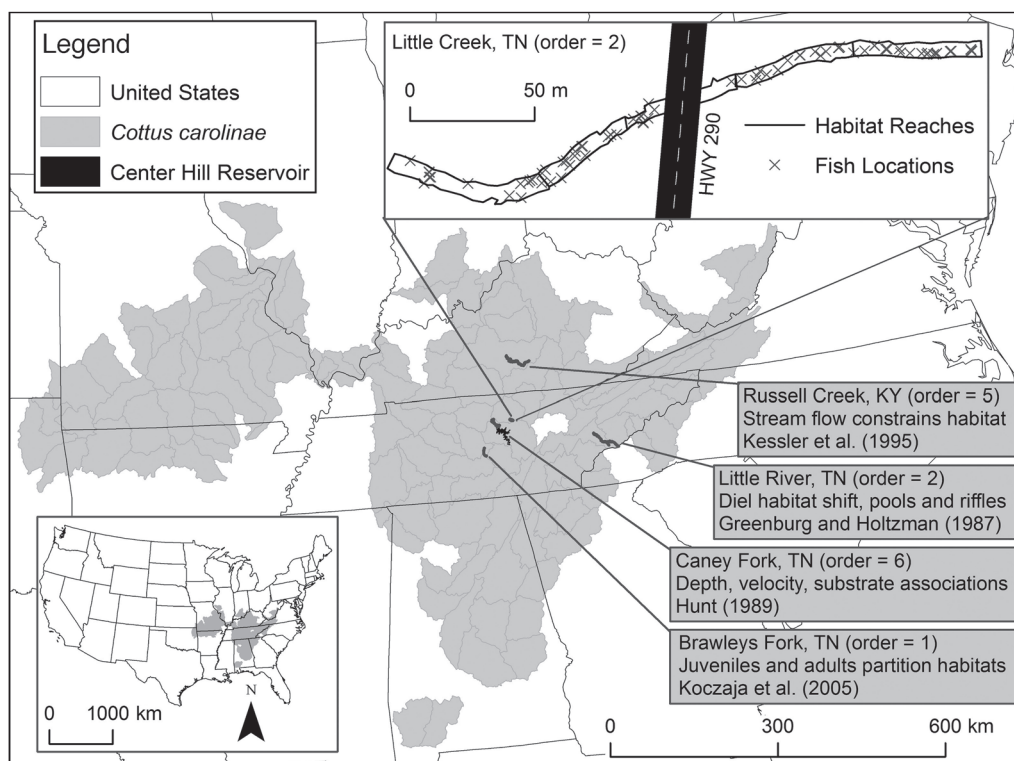

Figure 1. Distribution of Banded Sculpin in the southeast United States, including locations for previous studies (gray boxes) and the current study area in Little Creek, TN. Gray polygons represent 8-digit hydrologic unit codes inhabited by Banded Sculpin according to NatureServe (Natureserve, 2016) and "x"-symbols in insert closeup represent recapture locations for Banded Sculpin in Little Creek, TN.

Methods

Study area

Little Creek is a 2nd-order stream in the Eastern Highland Rim ecoregion of north-central Tennessee. This study was conducted on a reach of Little Creek that runs through Tennessee Technological University's Shipley Farm north of Cookeville, TN, in Putnam County. The study reach was buffered by riparian vegetation and surrounded by agricultural (i.e., row-crop and cattle rangeland) and residential land uses (Wells et al., in press). We measured habitat associations of Banded Sculpin in a 200-m reach of stream during the months of April and May 2015 to assess fine-scale, detailed habitat associations at the population scale (Fig. 1 inset).

Habitat use

Using 2 backpack electrofishing units moving upstream in tandem (100–125 volts direct current), we collected 79 Banded Sculpin throughout the 200-m study reach on 31 March 2015. Captured individuals were tagged using passive integrated transponders (PIT) following the methods of Ruetz et al. (2006) and released back to the site of capture as described in detail by Wells et al. (in press). Recapture occasions occurred every Tuesday and Saturday (13 occasions; 4 April–16 May) and spanned a duration of 46 days, after which time most individuals were no longer recaptured within the study reach. All Saturday recapture occasions except 4 April occurred during night (20:00–02:00), and all Tuesday recapture occasions occurred during daytime hours (09:00–14:00). For each recapture occasion, researchers started at the downstream boundary and scanned the stream from bank to bank in an upstream direction with a multi-directional antenna mounted on a 3-m telescopic pole, connected to a portable PIT tag reader and tuning box (model no. FS2001F-ISO; Biomark, Boise, ID). Scanning methods followed previous applications of similar equipment to track benthic stream organisms including crayfish and *Cottus* fishes (Black et al. 2010, Breen et al. 2009, DeBoer et al. 2015). In particular, disturbance to adjacent fishes was minimized by always beginning downstream and moving upstream, limiting the number of researchers in the water, and using the telescoping pole to reduce habitat disturbance (Wells et al., in press). When a PIT-tagged fish was detected, we recorded the PIT tag number, global positioning system (GPS) coordinates with sub-meter accuracy (using a Trimble GeoExplorer 6000 GPS; Trimble Navigation Limited, Sunnyvale, CA), whether or not the fish was visually observed, and multiple habitat variables including velocity (m/s) measured at 60% of water depth, depth (m), presence or absence of filamentous algae, and substrate type (i.e., silt, sand, gravel, cobble, boulder, and bedrock) as classified according to Bovee (1982) (Table 1).

Habitat availability

We measured habitat availability weekly on Tuesdays for 6 weeks (7 April through 12 May) and streamflow at hourly intervals using a pressure transducer. To measure habitat availability, we spaced 50 transects 4-m apart along the bank for the entire 200-m reach. Within each transect, we measured 5 evenly spaced points

perpendicular to the bank (250 points total weekly) while being careful to avoid disturbing relocated fish. At each point along transects, the habitat protocol used during fish sampling was repeated, including recording depth (m), velocity (m/s), substrate classification, and presence/absence of filamentous algae. To capture hourly water levels, we measured streamflow with a HOBO Water Level Logger (Model U20L, Onset Computer Corporation, Bourne, MA) and a metered stage that was positioned downstream of the study reach. Stage height and discharge were recorded every Tuesday, including depth and velocity measurements at 20 evenly spaced points across the wetted width of the stream following the United States Geological Survey protocol described by Turnipseed and Saurer (2010). We then calculated discharge as the summation of depth (m) and velocity (m/s) at all 20 points to procure the volume of water (m^3/s) and constructed a rating curve from the metered stage and discharge measurements to model continuous streamflow. Daily precipitation values were obtained for the duration of our study from the Upper Cumberland Regional Airport near Sparta, TN (USAF WBAN ID: 723274 99999; NOAA 2015).

Statistical analyses

We simultaneously assessed size-specific and diel differences in habitat associations for all habitat variables recorded at fish positions through the use of multiple factor analysis (MFA; Escofier and Pagès 1994). This approach allowed for multivariate analysis of both continuous and discrete classes of habitat variables. We used 4 classes of variables including depth and velocity (class 1: continuous), presence or absence of algae (class 2: binomial), the 6 substrate categories (class 3: polynomial), and fish classified as using no cover (observed in open) or some form of cover (hidden below cover) (class 4: binomial). We parameterized the model using the 4 variable classes for all individuals detected at least 3 times during the study (i.e., the minimum number of observations needed for at least 1 diurnal and at least 1 nocturnal habitat observation per fish) and conducted MFA using Program R function 'MFA' from package 'FactoMineR' (Lê et al. 2008). We used a scree

Table 1. Descriptions of variables used to measure habitat use of Banded Sculpin in Little Creek, TN, and corresponding multiple factor analysis (MFA) axes scores.

Variable	Description	MFA Axis 1	MFA Axis 2
Velocity	Current velocity in m/s	-0.996	0.172
Depth	Total depth in m	1.355	-0.020
Algae	Filamentous algae present	-0.807	-0.095
No algae	Filamentous algae absent	0.981	0.359
Silt	Substrate <0.06 mm	2.852	-1.712
Sand	Substrate 0.06–2.0 mm	0.245	0.040
Gravel	Substrate 2.0–75.0 mm	-0.158	-0.349
Cobble	Substrate 75.0–254.0 mm	-0.224	-1.061
Boulder	Substrate >254.0 mm	-0.440	1.712
Bedrock	Substrate solid rock	5.982	-0.995
Cover	Fish concealed during recapture	-0.010	-0.574
No cover	Fish visually observed during recapture	0.035	1.310

plot to determine the number of MFA axes retained for analysis and illustrated the results with a bi-plot of ordinated sample points shown at their centroids (i.e., 4 dimensional centers of coordinates for each class of variables).

The output from the MFA allowed for testing predictions regarding Banded Sculpin size-specific diel habitat associations. The 2 size classes assigned to Banded Sculpin were based on Craddock (1965) and grouped age-1 individuals as 80–99 mm total length (size 1) and age-2+ individuals as ≥100 mm total length (size 2). We did not include age-0 fish because of size-limitations associated with using PIT tags (Ruetz et al. 2006), though age-0 habitats are known to differ from older age classes (Koczaja et al. 2005). We used ordinated coordinates (centroids) for individually marked Banded Sculpin to calculate mean (and standard deviation) MFA axis scores across all diurnal and all nocturnal observations and assessed non-independent differences between diurnal and nocturnal MFA scores utilizing Cohen's effect size (Cohen 1988) following the methods of Dunlop et al. (1996). We illustrate the directionality of habitat shifts in multivariate space between diurnal and nocturnal observations at the scale of individually marked Banded Sculpin, in which a value of zero represent no shift, a negative value represents a negative shift along the MFA axis, and a positive value represents a positive shift along the MFA axis. Finally, we compared nocturnal shifts and diel recapture rates for size 1 and 2 Banded Sculpin to assess size-specific habitat associations.

We tested predictions for constrained availability and associations with habitats during low flows using univariate analyses. We estimated habitat availability and habitat use by both size classes for each Tuesday because both use and availability were measured on these days. Change in the distributions of available velocities and depths among weeks was tested using Kruskal-Wallis tests, and change in substrate categories was tested using a 6 x 6 contingency table. To test for differences between habitat availability and use, we classified depth and velocity values into bins using the Sturges (1926) equation and substrate bins ranked by grain size (silt = 1, sand = 2, gravel = 3, cobble = 4, boulder = 5, and bedrock = 6). We plotted depth, velocity, and substrate availability versus use for each size class by week to show proportion of habitats available and utilized through time. We then tested for differences in frequency distributions for habitat availability and use with the Kolmogorov-Smirnov (KS) test for depths, velocities, and substrates in the 'Matching' package in Program R (Petty and Grossman 2004).

We tested for transferability of depth, velocity, and substrate observations from Caney Fork, TN (stream order = 6), to Little Creek, TN (stream order = 2). Raw data from Caney Fork were obtained from Hunt (1989). We used the Sturges (1926) equation to calculate bin intervals for depth and velocity by combining all individuals we encountered 3 or more times in Little Creek, in addition to all individuals from Caney Fork with a TL ≥80 mm. Hunt (1989) data included some individuals assigned using combined substrates (e.g., sand/boulder, gravel/cobble, and gravel/boulder). Because Hunt (1989) and our study followed Bovee (1982) substrate classifications, we reasoned that it was acceptable to split in half the combined substrates in Hunt (1989) data (e.g., if gravel/cobble = 30, then 15

individuals were labeled using gravel and 15 individuals labeled using cobble). We tested the differences in frequency between Little Creek and Caney Fork using Kolmogorov-Smirnov (KS) tests in the 'Matching' package in Program R (Petty and Grossman 2004). All statistical analyses were conducted in Program R version 3.1.2 (R Core Team 2015).

Results

Thirty-nine Banded Sculpin were recaptured 3 or more times and retained for analyses. Individuals measured and weighed during the tagging ranged in total length from 80 to 137 mm and in weight from 5.9 to 32.5 g, with 16 individuals categorized as size 1 and 23 as size 2. The environmental template of Little Creek shifted during our tracking study as precipitation events caused elevated stream flows, and there were 3 punctuated high-pulse events on 5 April, 11 April, and 17 April (Fig. 2A). After 17 April, discharge diminished through time, and only 2 additional, smaller pulses in discharge occurred on 24 April and 5 May. Distributions differed among weeks for depths (Kruskal-Wallis: $X^2 = 105$, df = 5, $P < 0.01$) and velocities ($X^2 = 158$, df = 5, $P < 0.01$), including constrained depths and velocities during the second half of the study (Fig. 2B). The distribution of substrates did not differ among weeks (6 x 6 contingency table: $X^2 = 38,874$, $P = 0.46$), and bedrock substrate dominated observations (Fig. 2C).

MFA results illustrated consistent shifts in habitat associations over the diel period for both size classes. The first 2 MFA axes captured 30% of spatiotemporal variance in stream habitat used by Banded Sculpin. Axis 1 captured 17% of variance and represented a riffle-pool gradient in which sculpin that associated with algae, higher velocities, and shallower depths were arranged negatively, and sculpin associated with no algae, greater depths, lower velocities, and fine or smooth substrates (silt, bedrock) were arranged positively (Fig. 3A, B). Axis 2 captured 13% of variance and represented a cover gradient in which sculpin that associated with cobble, cover, and gravel were arranged negatively, and sculpin that associated with boulder substrate and no cover were arranged positively (Table 1). Effect sizes for habitat shifts along MFA 1 were positive (i.e., shift towards pools at night) for 29 sculpin (75%), including 12 (75%) for size 1 and 17 (74%) for size 2 individuals (Fig. 3C). Effect sizes for habitat shifts along MFA 2 were positive (i.e., shift toward no cover at night) for 33 sculpin (85%), including 15 (94%) for size 1 and 18 (78%) for size 2 individuals (Fig. 3D). The mean (± standard deviation) proportion of recaptures during night was 0.46 (± 0.07) for size 1 and 0.38 (± 0.09) for size 2 fish, but the mean (± standard deviation) number of recaptures per fish was 9 (± 2) for size 1 and 6 (± 2) for size 2 (Fig. 3E).

Banded Sculpin responses to temporal variability in flows illustrated constrained habitat use during flow attenuation. Univariate gradients of depth and velocity generally followed availability, whereas substrates were always used in disproportion to availability. Stream depths occupied by both size classes did not differ from availability for 5 of 6 recaptures, with the exception of 21 April when size class 1 (D = 0.63, $P < 0.01$) and size class 2 (D = 0.56, $P < 0.01$) fish used
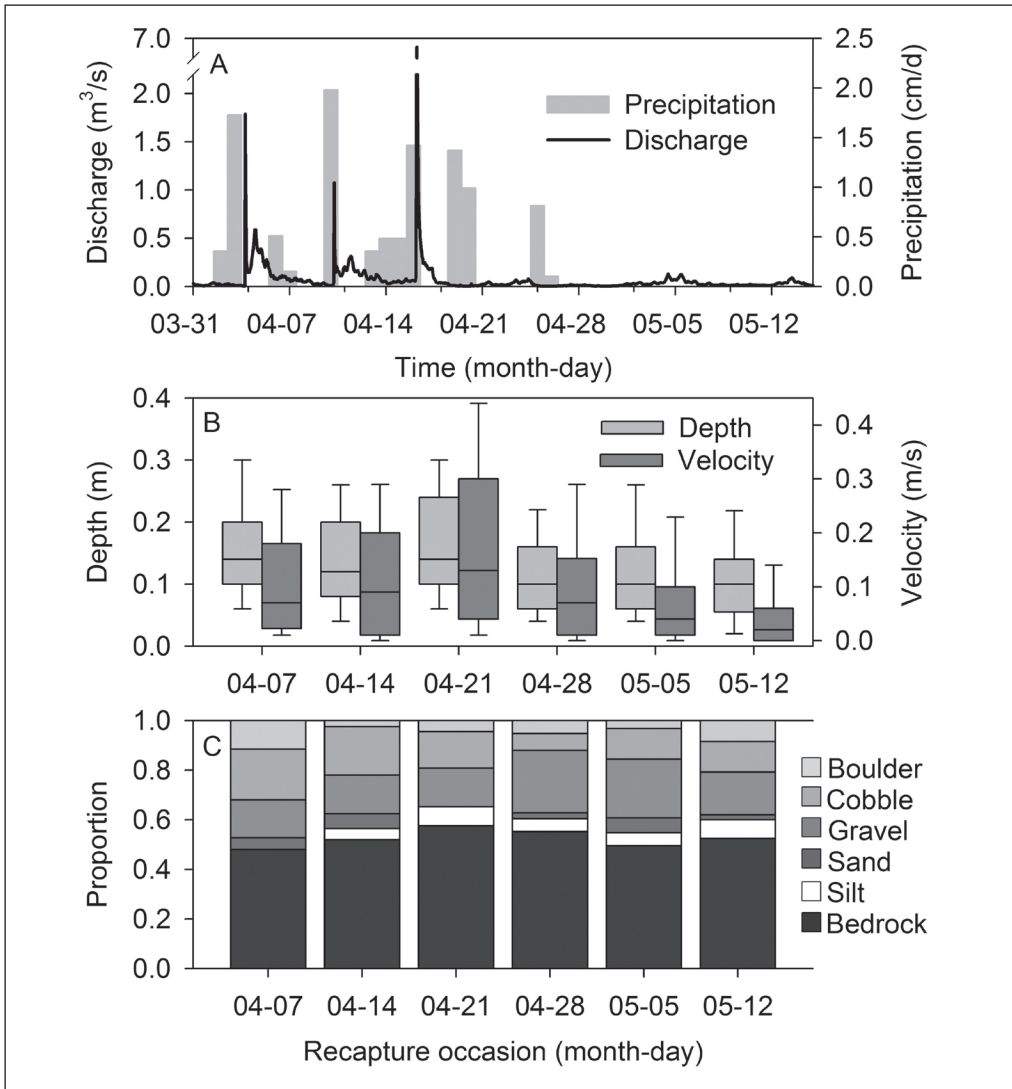
Figure 2. (A) Daily precipitation (gray bars) and hourly stream discharge (black line) for Little Creek, TN, during 31 March–16 May 2015. (B) Boxplots summarizing available depths (light gray) and velocities (dark gray), and (C) proportion of available substrates for 6 weeks during which Banded Sculpin habitat associations were measured.

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Figure 3 [following page]. (A) Multiple factor analysis (MFA) biplot for MFA 1 (17% variance) versus MFA 2 (13% variance) illustrating Banded Sculpin habitat associations during diurnal ("day"; gray) and nocturnal ("night"; black) observations. (B) The timing of diurnal (gray) and nocturnal (black) habitat observations ("Obs") with respect to sunrise and sunset. Effect sizes for habitat shifts along (C) MFA 1 and (D) MFA 2 illustrate magnitude of shifts between day (control) and night (treatment) for each of 39 individually marked Banded Sculpin. (E) Number of recaptures per individual during day (gray) and night (black), total length ("TL"; solid dark gray line), and size classes split (dotted line): size 1 (80-99 mm TL) and size 2 (>100 mm TL).
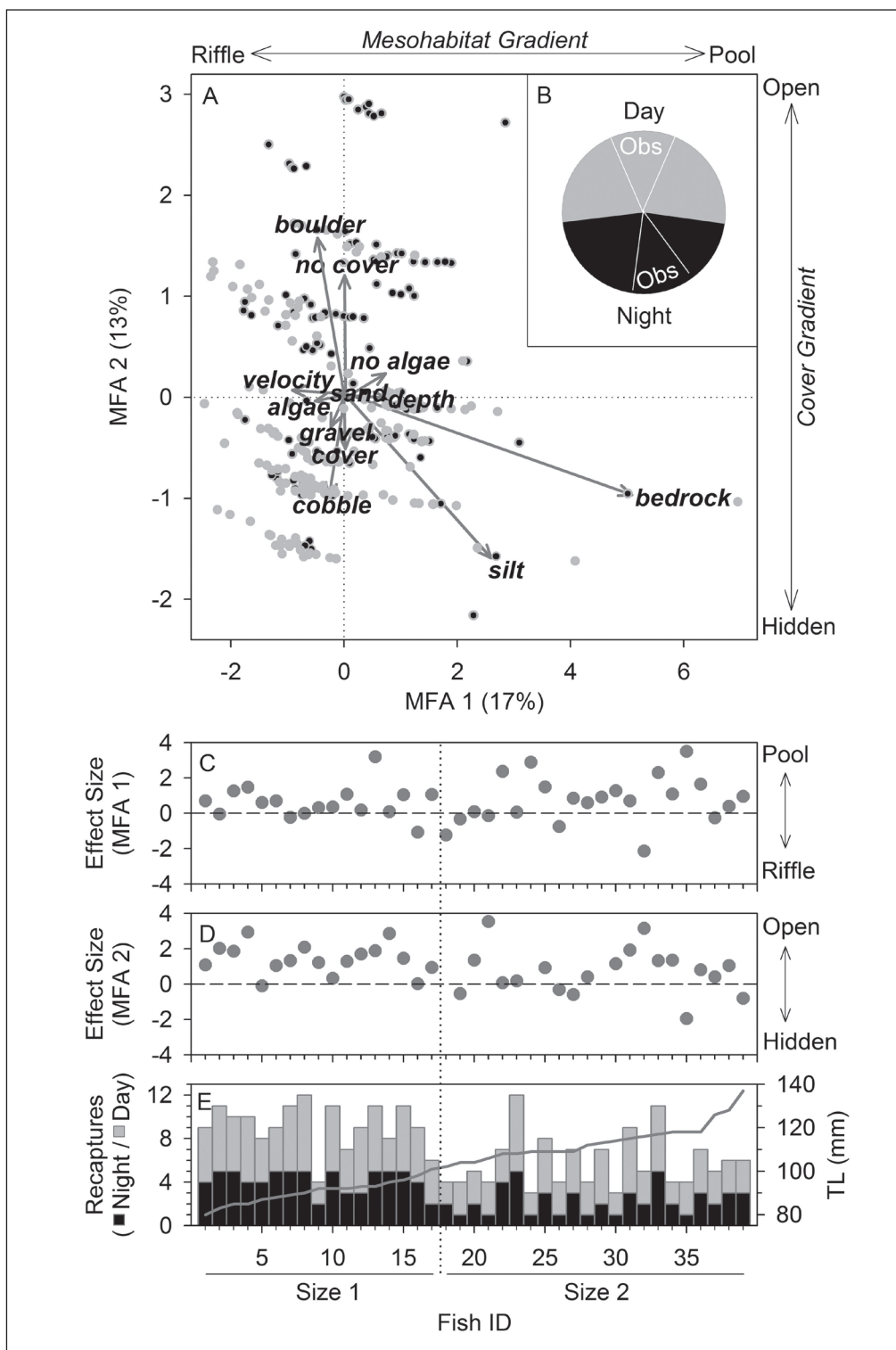
Figure 3. Caption on previous page.

depths in disproportion to availability (Table 2). In general, the frequency of avail-ability and use of depths were consistent across the study (Fig. 4A–F). Velocities used by size 1 fish significantly differed from availability on 21 April (D = 0.73, $P < 0.01$) and 12 May (D = 0.67, $P = 0.04$); whereas, size 2 fish only differed on 12 May (D = 0.78, $P < 0.01$). In general, the frequency of availability and use of

Table 2. D-values and *P*-values from Kolmogorov-Smirnov (KS) test for significance comparing available versus used habitat variables (depth, velocity, and substrates) for each Tuesday recapture occasion 7 April–12 May in Little Creek, TN. * indicates significant values for size 1 (80–99 mm TL) and size 2 (>100 mm TL) fish.

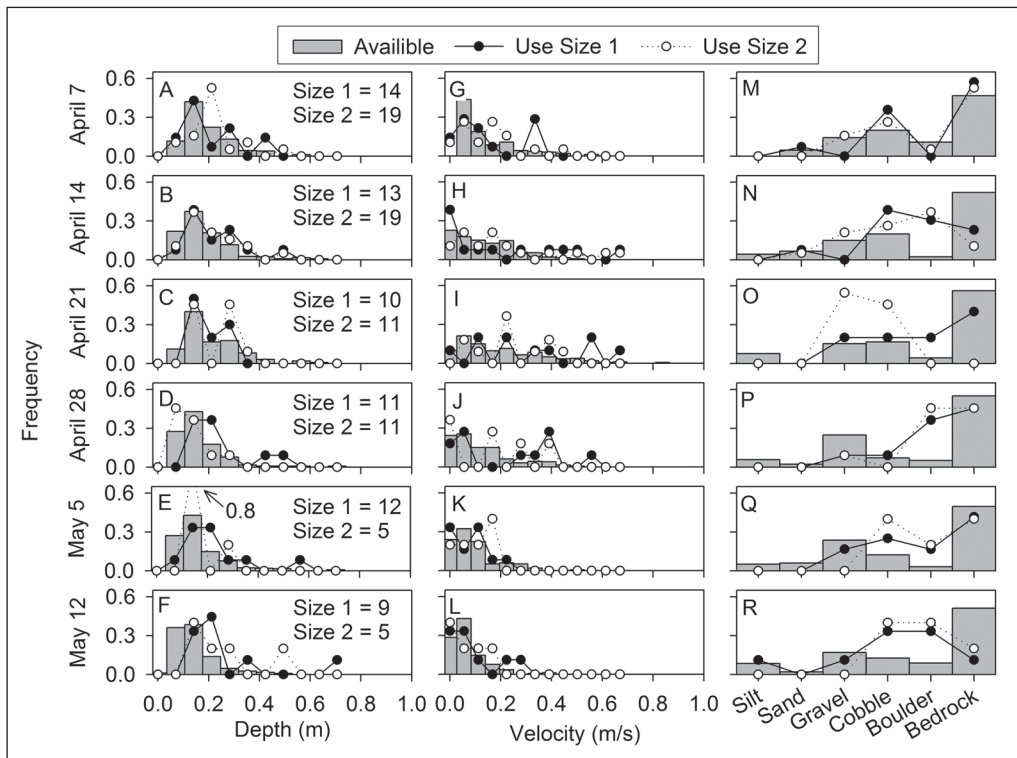| | Depth | | | | Velocity | | | | Substrate | | | |
| | Size 1 | | Size 2 | | Size 1 | | Size 2 | | Size 1 | | Size 2 | |
Date	D	P	D	P	D	P	D	P	D	P	D	P
7-Apr	0.60	0.18	0.60	0.13	0.64	0.12	0.64	0.06	0.83	0.03*	0.83	0.03*
14-Apr	0.55	0.08	0.45	0.21	0.50	0.16	0.50	0.16	1.00	<0.01*	0.83	0.03*
21-Apr	0.63	<0.01*	0.56	<0.01*	0.73	<0.01*	0.55	0.08	0.83	0.03*	0.83	0.03*
28-Apr	0.50	0.16	0.60	0.05	0.46	0.13	0.46	0.13	1.00	<0.01*	1.00	<0.01*
5-May	0.44	0.34	0.56	0.12	0.38	0.29	0.47	0.10	1.00	<0.01*	1.00	<0.01*
12-May	0.57	0.20	0.71	0.06	0.67	0.04*	0.78	<0.01*	1.00	<0.01*	1.00	<0.01*

Figure 4. Proportion of available habitat (gray bars) and used habitat (black circles = size 1, 80-99 mm TL; white circles = size 2, >100 mm TL) for Banded Sculpin from 7 April through 12 May in Little Creek, TN, including (A–F) depth, (G–L) velocity, and (M–R) substrate. Size-specific, weekly sample sizes are given in panels A–F.

velocities declined during the study (Fig. 4G–L). Both size classes disproportionally used larger substrates (cobble and boulder) to a greater extent than available and typically used silt less than available across all recapture occasions (Table 2, Fig. 4M–R).

Testing for transferability of habitat associations between Caney Fork and Little Creek revealed consistencies in use for depth, velocity, and substrate gradients. Banded Sculpin association with depth gradients was similar (D = 0.54, P = 0.08) between Caney Fork and Little Creek despite rare use of greater depths in Caney Fork (Fig. 5A). Distributions in the velocities used by sculpin were similar (D = 0.56, P =0.12) in Caney Fork and Little Creek (Fig. 5B). Sculpin substrate associations were similar (D = 0.67, P = 0.14) in Caney Fork and Little Creek despite greater used of bedrock in Little Creek (Fig. 5C).

Discussion

Our study provides a regional multi-system synthesis of Banded Sculpin habitat associations and suggests most habitat associations are consistent across ecosystems. We predicted size-specific shifts in habitat use for age-1 and age-2+ fish (Koczaja et al. 2005), movement from cover during the day to the open at night (Greenberg and Holtzman 1987), expansion and contraction of habitats coincident with expansion and contraction of flows (Kessler et al. 1995), and, regardless of size, consistent use of depth, velocity and substrate gradients across stream sizes (Hunt 1989). We found that size 1 and 2 individuals exhibited similar shifts over the diel period as fish moved from cover within riffles during the day to the open habitat within pools at night. Both size classes similarly adjusted habitat associations as flows constricted over a 2-month period, and analysis of both size classes combined showed that sculpin used similar depths, velocities, and substrates regardless of stream size. These findings suggest 3 of the 4 predictions were supported by observations in Little Creek, with the exception being size-specific habitat associations. Our study differs from the work that first described size-selective habitat use because our analysis of sizes was limited to "adults" (sensu Koczaja et al. 2005) and essentially ignored potential differences in habitat selection and use between adults and young of the year. Consequently, our finding of consistent habitat use by 2 relatively large size classes builds on previous work by documenting consistencies of habitat use for multiple adult size classes. However, we found consistently lower recapture rates for size 2 fish, suggesting some size-specific differences in either detection or habitat use even among adult fish. Our study highlights structured habitat shifts by sculpin across the diel period, as flows expand and contract, and across streams of contrasting size.

The concept of diurnal and flow-dependent habitat shifts by *Cottus* and other stream fishes is not a pioneering idea. Cottidae species of various size classes use cover during the day and associated with lithic surfaces during night to facilitate nocturnal foraging (Finger 1982, Freeman and Stouder 1989, Grossman and Freeman 1987). Improved prediction of fish responses to physical habitat manipulation and availability through space and time represents an increasing area of interest

for natural resource management (Freeman et al. 1997, Schlosser and Toth 1984). In large, regulated streams, flow might directly be controlled by dam operations to optimize available fish habitat (Brown and Ford 2002, Kiernan et al. 2012, Standford et al. 1996). In smaller and unregulated streams, physical channel adjustments (e.g., restoration) might be employed to optimize fish habitats (Bond and Lake 2003, Deboer et al. 2015). Regardless of the mechanism applied to manage physical

Figure 5. Proportion of (A) depth, (B) velocity, and (C) substrate habitats used by Banded Sculpin in Caney Fork (black bars; Hunt 1989) and Little Creek (white bars; this study), TN.
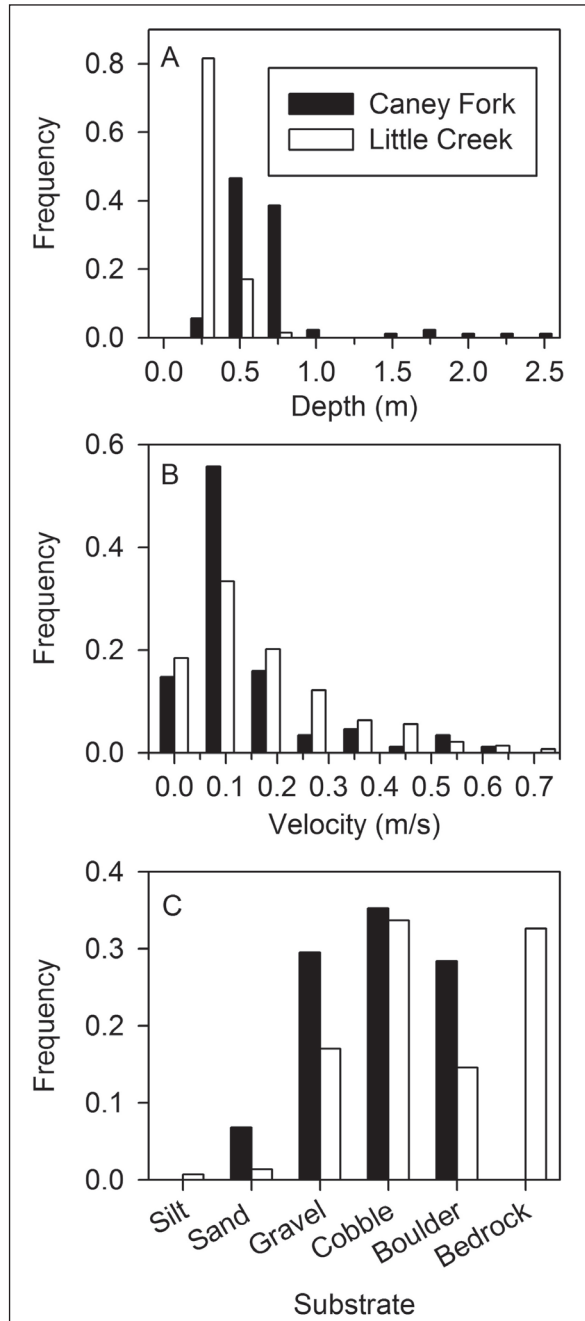
habitat, there is an explicit need to include representative habitat associations for targeted species, communities, or assemblages (Edwards and Cunjak 2007, Gorman and Karr 1978). For intermediate streams such as Little Creek that undergo seasonal drying, fish habitat associations will depend upon the period during which observations are made (Davey and Kelly 2007, Driver and Hoeinghaus 2016) because fishes might shift habitat use as drying progresses (Kraft 1972, Perkin et al. 2010). If fishes are relegated to sub-optimal habitats during low flows, then observations made during these periods represent only a fraction of habitat associations in a dynamic system (Labbe and Fausch 2000). The timing of our study captured a gradient of flows ranging from stable discharge maintained by precipitation to a period of sustained drying during which flows declined to near-zero. Because of this type of natural environmental variability in streams, fishes generally use gradients of depth and velocity that vary according to spatiotemporal environmental heterogeneity (Bain et al. 1988, Matthew and Hill 1979, this study). However, habitat associations remain restricted by biotic constraints that act upon fish to force unifying responses regardless of stream contexts.

Morphological, behavioral, and physiological determinants constrain fish habitat associations to yield broadly transferrable expectations. These 3 classes of intrinsic constraints likely contributed to our observed support for quantitative habitat predictions, and are related to the mechanisms that constrain range-wide descriptions of Banded Sculpin habitat use (e.g., Anderson 1985, Etnier and Starnes 1993, Mammoliti 2014, Pflieger 1997). Anatomical and morphological constraints on Banded Sculpin include no gas bladder and consequently little buoyance control, and enlarged pectoral fins that act as hydrofoils to hold fish in place across a range of current velocities (Kerfoot and Schaefer 2006). The aforementioned morphological constraints relegate local occurrence of *Cottus* fishes to benthic zones generally in riffle habitats (at least for lotic *Cottus* spp.) and might act as compensatory mechanisms for weak swimming abilities (Natsumeda 2007). Behaviorally, Banded Sculpin are ambush predators that depend on cryptic coloring for camouflage and thus require microhabitats that provide sufficient camouflage capability (Armbruster and Page 1996). Low-velocity microhabitats with homogenous fine substrates such as silt and sand might be avoided because these habitats do not support optimal foraging or survival (Mundahl et al. 2012). Similarly, daily changes in light levels during sunset can synchronize and initiate foraging activity for nocturnal predators to produce consistent foraging behaviors across ecosystems (Helfman 1986). From a physiological perspective, thermal tolerances and metabolic rates represent widely studied ecological characteristics for *Cottus* species that constrain species abundances outside of preferred habitats (Walsh et al. 1997). Movement to local habitats that maximize energy conservation, including temperature-based microhabitat selection or flow-induced movements, have been documented for *Cottus* fishes across stream locations and sizes (Hudy and Shiflet 2009; Wells et al., in press).

In summary, we found that 3 of the 4 determinants of species occurrence described by Soberón and Peterson (2005) represent mechanisms that produce

transferable elements for predicting local Banded Sculpin occurrence regardless of stream size or location, including abiotic factors, biotic factors, and habitat accessibility. The fourth element, evolutionary capacity, might be measured with molecular techniques applied across populations (Day et al. 2016). The potential for transferring habitat predictions across ecosystems for other *Cottus* species, especially threatened and endangered species (e.g., *Cottus paulus* J.D. Williams [Pygmy Sculpin] and *Cottus specus* G.L. Adams & Burr [Grotto Sculpin]), is a valuable framework for enhancing conservation and management approaches for native fishes (Adams and Schmetterling 2007).

Acknowledgments

Literature Cited

Adams, S.B., and D.A. Schmetterling. 2007. Freshwater sculpins: Phylogenetics to ecology. Transactions of the American Fisheries Society 136:1736–1741.

Anderson, C.S. 1985. The structure of sculpin populations along a stream-size gradient. Environmental Biology of Fishes 13:93–102.

Armbruster, J.W., and L.M. Page. 1996. Convergence of cryptic saddle pattern in benthic freshwater fishes. Environmental Biology of Fishes 45:249–257.

Bain, M.B., J.T. Finn, and H.E. Booke. 1988. Streamflow regulation and fish community structure. Ecological Society of America 69:382–392.

Black, T.R., S.S. Herleth-King, and H.T. Mattingly. 2010. Efficacy of internal PIT tagging of small-bodied crayfish for ecological study. Southeastern Naturalist 9:257–266.

Bond, N.R., and P.S. Lake. 2003. Characterizing fish–habitat associations in streams as the first step in ecological restoration. Austral Ecology 28:611–621.

Bovee, K.D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. US Fish and Wildlife Service Biological Services Program Report FWS/OBS-82/26. US Fish and Wildlife Service, Fort Collins, CO. 248 pp.

Breen, M.J., C.R. Ruetz, K.J. Thompson, and S.J. Kohler. 2009. Movements of Mottled Sculpin (*Cottus bairdii*) in a Michigan stream: How restricted are they? Canadian Journal of Fisheries and Aquatic Sciences 66:31–41.

Brown, L.R., and T. Ford. 2002. Effects of flow on the fish communities of a regulated California river: Implications for managing native fishes. River Research and Applications 18:331–342.

Chase, J.M., and M.A. Leibold. 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press, Chicago, IL. 221 pp.

Clarkson, R.W., P.C.Marsh, S.E. Stefferud, and J.A. Stefferud. 2005. Conflicts between native fish and nonnative sport fish management in the southwestern United States. Fisheries 30:20–27.

Cohen, J. 1988. Statistical Power Analysis for the Behavioral Sciences, Second Edition. Lawrence Earlbaum Associates, Hillsdale, NJ. 400 pp.

Craddock, J.E. 1965. Some aspect of life history of the Banded Sculpin, *Cottus carolinae carolinae*, in Doe Run, Meade County, Kentucky. Ph.D. Dissertation. University of Louisville, Louisville, KY. 157 pp.

Davey, A.J., and D.J. Kelly. 2007. Fishes community responses to drying disturbances in an intermittent stream: A landscape perspective. Freshwater Biology 52:1719–1733.

Day, J., J.E. Gerken, and G.L. Adams. 2016. Population ecology and seasonal demography of the endangered Grotto Sculpin (*Cottus specus*).Ecology of Freshwater Fish 25:27–37.

DeBoer, J.A., J.M. Holtgren, S.A. Ogren, and E.B. Snyder. 2015. Movement and habitat use by Mottled Sculpin after restoration of a sand-dominated 1st-order stream. The American Midland Naturalist 173:335–345.

Driver, L.J., and D.J. Hoeinghaus. 2016. Fish metacommunity responses to experimental drought are determined by habitat heterogeneity and connectivity. Freshwater Biology 61:533–548.

Dunlop, W.P., J.M. Cortina, J.B. Vaslow, and M.J. Burke. 1996. Meta-analysis of experiments with matched groups or repeated measures designs. Psychological Methods 1:170–177.

Edwards, P.A., and R.A. Cunjak. 2007. Influence of water temperature and streambed stability on the abundance and distribution of Slimy Sculpin (*Cottus cogatus*). Environmental Biology of Fishes 80:9–22.

Escofier, B., and J. Pagès. 1994. Multiple factor analysis (AFMULT package). Computational Statistics and Data Analysis 18:121–140.

Etnier, D.A., and W.C. Starnes. 1993. The Fishes of Tennessee, 2nd Printing. University of Tennessee Press, Knoxville, TN. 689 pp.

Finger, T.R. 1982. Interactive segregation among three species of Sculpins (*Cottus*). Copeia 1982:680–694.

Freeman, M.C., and D.J. Stouder. 1989. Intraspecific interactions influence size specific depth distribution in *Cottus bairdii*. Environmental Biology of Fishes 24:231–236.

Freeman, M.C., Z.H. Bowen, and J.H. Crance. 1997. Transferability of habitat-suitability criteria for fishes in warmwater streams. North American Journal of Fisheries Management 17:20–31.

Gorman, O.T., and J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59:507–515.

Greenberg, L.A., and D.A. Holtzman. 1987. Microhabitat utilization, feeding periodicity, home range and population size of Banded Sculpin, *Cottus carolinae*. Copeia 1987:19–25.

Grossman, G.D., and M.C. Freeman. 1987. Microhabitat use in a stream fish assemblage. Journal of Zoology 212:151–176.

Helfman, G.S. 1986. Fish behaviour by day, night and twilight. Pp. 366–387, *In* T.J. Pitcher (Ed.). The Behaviour of Teleost Fishes. Springer, New York, NY. 716 pp.

Hubert, W.A., and F.J. Rahel. 1989. Relations of physical habitat to abundance of four nongame fishes in high-plains streams: A test of habitat suitability index models. North American Journal of Fisheries Management 9:332–340.

Hudy, M., and J. Shiflet. 2009. Movement and recolonization of Potomac Sculpin in a Virginia stream. North American Journal of Fisheries Management 29:196–204.

Hunt, R.L. 1968. Effects of habitat alteration on production, standing crops and yield of Brook Trout in Lawrence Creek, Wisconsin. Research Report No. 31. Department of Natural Resources, Madison, WI. 45 pp.

Hunt, T.D. 1989. Microhabitat selection and some aspects of the life history of the Banded Sculpin, *Cottus carolinae* (Gill): M.Sc. Thesis. Tennessee Technological University, Cookeville, TN.

Hynes, H.B.N. 1970. Ecology of Running Waters. University of Toronto Press, Toronto, ON, Canada. 555 pp.

Kerfoot, J.R., Jr., and J.F. Schaefer. 2006. Ecomorphology and habitat utilization of *Cottus* species. Environmental Biology of Fishes 76:1–13.

Kessler R.K., A.F. Casper, and G.K. Weddle. 1995. Temporal variation in microhabitat use and spatial relations in the benthic fish community of a stream. American Midland Naturalist 134:361–370.

Kiernan, J.D., P.B. Moyle, and P.K. Crain. 2012. Restoring native fish assemblages to a regulated California stream using the natural flow-regime concept. Ecological Applications 22:1472–1482.

Koczaja, C., L. McCall, E. Fitch, B. Glorioso, C. Hanna, J. Kyzar, M. Niemiller, J. Spiess, A. Tolley, R. Wyckoff, and D. Mullen. 2005. Size-specific habitat segregation and interspecific interactions in Banded Sculpin (*Cottus carolinae*). Southeastern Naturalist 4:207–218.

Kraft, M.E. 1972. Effects of controlled flow reduction on a trout stream. Journal of the Fisheries Board of Canada 29:1405–1411.

Labbe, T.R., and K.D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774–1791.

Lê, S., J. Josse, and F. Husson. 2008. FactoMineR: An R package for multivariate analysis. Journal of Statistical Software 25:1–18.

Leftwich, K.N., P.L. Angermeier, and C.A. Dolloff. 1997. Factors influencing behavior and transferability of habitat models for a benthic stream fish. Transactions of the American Fisheries Society 126:725–734.

Lucas, M.C., E. Baras, T.J. Thomas, A. Duncan, and O. Slavík. 2001. Migration of Freshwater Fishes Vol. 47. Blackwell Science, Oxford, UK. 440 pp.

Mammolitti, C.S. 2014. Banded Sculpin *Cottus carolinae* Gill 1861. Pp 347–348, *In* Distler, D.A, M.E. Eberle, D.R. Edds, K.B. Gido, S.G. Haslouer, D.G. Huggins, T.D. Mosher W.J. Stark, J.R. Tomelleri, J.R. Triplett, E.O. Wiley, and W.J. Matthews. Kansas Fishes. University Press of Kansas, Lawrence, KS. 518 pp.

Matthew, W.J., and L.G. Hill. 1979. Influence of physico-chemical factors on habitat selection by Red Shiners, *Notropis lutrensis* (Pisces: Cyprinidae). American Society of Ichthyologists and Herpetologists 1979:70–81.

Minckley, W.L., and J.E. Deacon. 1991. Battle Against Extinction: Native Fish Management in the American West. University of Arizona Press, Tucson, AZ. 517 pp.

Mundahl, N.D., D.E. Mundahl, and E.C. Merten. 2012. Success of Slimy Sculpin reintroductions in Minnesota trout streams: Influence of feeding and diets. The American Midland Naturalist. 168:162–183.

National Oceanic and Atmospheric Administration (NOAA). 2015. Climate data. Available online at: http://www.ncdc.noaa.gov/cdo-web/. Accessed 28 June 2015.

Natsumeda, T. 2007. Movement patterns of Japanese Fluvial Sculpin in a headwater stream. Transactions of the American Fisheries Society 136:1769–1777.

Natureserve. 2016. NatureServe Web Service. Arlington, VA. Available online at http:// services.natureserve.org. Accessed 1 January 2016.

Norton, S.F. 1991. Habitat Use and community structure in an assemblage of Cottidae Fishes. Ecology 72:2181–2192.

Nykänen, M., and A. Huusko. 2004. Transferability of habitat preference criteria for larval European Grayling (*Thymallus thymallus*). Canadian Journal of Fisheries and Aquatic Sciences 61:185–192.

Perkin, J.S., Z.R. Shattuck, P.T. Bean, T.H. Bonner, E. Saraeva, and T.B. Hardy 2010. Movement and microhabitat associations of Guadalupe Bass in two Texas Rivers. North American Journal of Fisheries Management 30:33–46.

Peterson, A.T. 2006. Uses and requirements of ecological niche models and related distributional models. Biodiversity Informatics 3:59–72.

Petty, J.T., and G.D. Grossman. 2004. Restricted movement by Mottled Sculpin (Pisces: Cottidae) in a southern Appalachian stream. Freshwater Biology 49:631–645.

Pflieger, W.L. 1997. The Fishes of Missouri. Missouri Department of Conservation, Jefferson City, MO. 372 pp.

Poff, N.L., and J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76:606–627.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria. Available online at http://www.R-project.org/. Accessed 1 September 2015.

Rabeni, C.F., and S.P. Sowa. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. Canadian Journal of Fisheries and Aquatic Sciences 53:252–259.

Ruetz, C.R., III, M.E. Brendan, and S.L. Kohler. 2006. Evaluating passive integrated transponder tags for marking Mottled Sculpins: Effects on growth and mortality. Transactions of the American Fisheries Society 135:1456–1461.

Schlosser, I.J. 1991. Stream fish ecology: A landscape perspective. BioScience 41:704–712.

Schlosser, I.J., and L.A. Toth. 1984. Niche relationships and population ecology of Rainbow (*Etheostoma caeruleum*) and Faintail (*E. flabellare*) Darters in a temporally variable environment. Oikos 42:229–238.

Soberón, J., and A.T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2:1–10.

Standford, J.A., J.V. Ward, W.J. Liss, C.A. Frissell, R.N. Williams, J.A. Lichatowich, and C.C. Coutant. 1996. A general protocol restoration of regulated rivers. Regulated Rivers: Research and Management 12:391–431.

Sturges, H.A. 1926. The choice of a class interval. Journal of the American Statistical Association 21:65–66.

Thomas, J.A., and K.D. Bovee. 1993. Application and testing of a procedure to evaluate transferability of habitat suitability criteria. Regulated Rivers: Research and Management. 8:285–294.

Turnipseed, D.P., and V.B. Sauer. 2010. Discharge measurements at gaging stations. US Geological Survey Techniques and Methods, Book 3, Chapter A8. Pp. 1–87. Available online at http://pubs.usgs.gov/tm/tm3-a8/. Accessed 15 October 2015.

Walsh, S.J., D.C. Haney, and C.M. Timmerman.1997. Variation in thermal tolerance and routine metabolism among spring- and stream-dwelling freshwater sculpin (Teleostei: Cottidae) of the southeastern United States. Ecology of Freshwater Fish 6:84–94.

Wells, G.W., T.C. Johnson, A.E. Gebhard, R.T.R. Paine, L.A. Hix, H.N. Ferrell, A.N. Engel, and J.S. Perkin. In press. March of the sculpin: Measuring and predicting short-term movement of Banded Sculpin *Cottus carolinae*. Ecology of Freshwater Fish.