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[Article]

Size-Dependent Territoriality of Mottled Sculpin in a Southern Appalachian Stream

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Abstract.—We quantified the space use behaviors of juvenile and adult mottled sculpin *Cottus bairdii* over a 3-year period in Shope Fork, western North Carolina. Our objectives were to (1) quantify home range size, (2) determine whether the fish exhibit territorial behaviors, (3) characterize the relative stability of territories, and (4) relate temporal variation in behaviors to environmental variability and population size structure. Adult behaviors were consistent with those of a strongly territorial organism. Adults exhibited nonrandom movements, restricted home ranges, and extremely low levels of spatial overlap with neighboring residents (<10% overlap). Territories were established in erosional microhabitats that were significantly more stable (as measured by seasonal shifts in dominant substrate composition) than randomly selected microhabitats in the study site. In contrast to adults, juveniles did not exhibit evidence of territoriality and instead occupied overlapping home ranges (16–36% overlap) in less-stable, depositional microhabitats along the stream margin. Mottled sculpin home range size, home range overlap, and territory abandonment rate were related to the density of large adults rather than flow variability or microhabitat stability. Adult territoriality and juvenile floating provide behavioral mechanisms capable of producing strong regulation of mottled sculpin populations in this system.

Nonbreeding territoriality is common in marine fishes and appears to be less common in freshwater species (Barlow 1993). In marine fishes, territorial individuals defend areas of high-quality food resources, predator refuges, and nesting sites (Roberts and Ormond 1992; Pitcher 1993; Barlow 1993; Goncalves and Almada 1998; Letourneur 2000). This behavior is common to only one family of freshwater fishes, the Salmonidae (Grant and Noakes 1987; Grant 1990; Hughes 1992; Nakano 1995; Steingrimsson and Grant 1999). Competitively dominant salmonids defend high-quality feeding territories and subdominant individuals are forced to use lower quality microhabitats. Territoriality in salmonids has been shown to influence population dynamics (Grant and Kramer 1990; Elliott 1994), interspecific interactions (Fausch and White 1981), and watershed-scale distribution patterns (Hughes and Reynolds 1994; Hughes 1998). Whereas territoriality has been extensively documented in salmonids, we have found no prior studies of territoriality in a North American benthic stream fish.

The existence of foraging territories is determined in large part by the distribution of food resources and the stability of that distribution (Lott 1991; Maher and Lott 2000). Territoriality is favored by patchily distributed food resources and may function to ensure that a dominant individual maintains exclusive access to high-quality patches. Numerous researchers have found that territoriality will persist as long as stable, high-quality food patches are present (Stamps and Krishnan 1995; Davies and Hartley 1996). By contrast, territoriality should not increase individual fitness if food resources are temporally variable (Lott 1991). In fact, Barlow (1993) suggested that territoriality should be rare in stream fishes because of highly variable resources in these habitats, although he also concluded that it would be logistically difficult to observe territorial behaviors in stream fishes.

Many streams display high levels of variation in resource availability (Hildrew and Giller 1994; Allan 1995; Fausch et al. 2002). For example, benthic macroinvertebrate densities and physical habitat characteristics are patchily distributed in streams across a wide range of spatial scales (Frissell et al. 1986; Downes et al. 1993; Grossman et al. 1995a). In addition, streamflow and microhabitat stability may vary daily, seasonally, and over decades (Poff and Ward 1989; Grossman et al. 1995a, 2006). Our own studies in the Coweeta Creek drainage, western North Carolina, demonstrate the combined importance of spatial variability of food resources and temporal variability in flows on stream fish foraging behavior, population dynamics, and community structure (Grossman et al. 1995a, 1998, 2006; Thompson et al. 2001; Petty and Grossman 2004).

Spatial and temporal variability of resources place

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conflicting pressures on the expression of territorial behavior by benthic stream fishes. Territoriality should increase an individual's fitness if high-quality patches are present but should reduce fitness if patch quality is unpredictable. Given the uncertainty of whether territoriality conveys a selective advantage and given a general lack of information on the behavior of benthic stream fishes, we conducted a study of the space use behaviors of mottled sculpin *Cottus bairdii*. Our objectives were to (1) quantify two-dimensional movements and home ranges; (2) quantify size-dependent territoriality; (3) characterize the physical characteristics and stability of territories; and (4) assess the effects of flow variability, microhabitat stability, and population structure on territoriality. Given the high degree of resource patchiness, we expected mottled sculpin to exhibit territorial behaviors that would be strongly modified by periods of high streamflows and low habitat stability.

The mottled sculpin is widely distributed across North America and frequently dominates stream fish assemblages in both abundance and biomass (see references in Grossman et al. 2006). Mottled sculpin are small (maximum standard length [SL] < 150 mm), sit-and-wait predators of benthic invertebrates (Stouder 1990). In the Coweeta Creek drainage, mottled sculpin reach ages greater than 7 years, have low fecundities (maximum = 166 eggs), spawn in early spring (typically late March–April), and display readily separable life history classes (Grossman et al. 2002, 2006). Small mottled sculpin occupy microhabitats dominated by silt, sand, and gravel. As they reach sizes greater than 5 cm, the fish move to deeper areas dominated by cobble and boulder substrata (Grossman and Ratajczak 1998). Macroinvertebrate prey distributions are patchy in the Coweeta Creek system (Petty and Grossman 1996; Thompson et al. 2001), and prey abundance within a patch is a good predictor of mottled sculpin patch (i.e., microhabitat) use (Petty and Grossman 1996). Finally, strong evidence exists to indicate that adult density influences a variety of population and behavioral characteristics of mottled sculpin in the Coweeta Creek drainage, including microhabitat use and population dynamics (Freeman and Stouder 1989; Petty and Grossman 2004; Grossman et al. 2006).

Methods

Study area.—We conducted our study between 1 June 1994 and 1 November 1996 as part of a long-term investigation of mottled sculpin population dynamics in the Coweeta Creek basin (Petty and Grossman 2004; Grossman et al. 2006). The study area consisted of a 1-km segment on Shope Fork, a fourth-order tributary of Coweeta Creek at the U.S. Department of Agriculture Coweeta Hydrologic Laboratory. Shope Fork is a relatively undisturbed coldwater stream (maximum summer temperature <20°C) and is representative of many small streams in this region. It lies within a mixed hardwood–conifer forest with an understory of rhododendron *Rhododendron maximum*, mountain laurel *Kalmia latifolia*, and dogwood *Cornus florida*. At the downstream end of the study site, Shope Fork is approximately 800 m in altitude, drains a 2,185-ha watershed, has a mean annual discharge of 0.38 m^3/s, and has a mean wetted width of 5.5 m. The dominant substrata are boulder, cobble, and gravel, and habitat features include riffle–run–pool sequences. The resident fish assemblage of Shope Fork includes mottled sculpin, rainbow trout *Oncorhynchus mykiss*, longnose dace *Rhinichthys cataractae*, and rosyside dace *Clinostomus funduloides* (Freeman et al. 1988).

Mottled sculpin observations.—We observed fish while snorkeling and used mark–recapture techniques to quantify the spatial organization of resident mottled sculpin within a 1-km segment of Shope Fork. Mark–recapture sampling followed the "robust" design of Pollock et al. (1990), which consisted of sampling at both primary (seasonal) and secondary (successive days within seasons) time scales. During each year of the study (1994–1996), we completed four seasonal samples: early June (spring), late July (midsummer), early September (late summer), and late October (autumn). Each seasonal sample involved four sampling passes, yielding 16 passes/year (48 passes total). Passes made within each season were separated by 1–2 d, and seasonal samples were separated by approximately 45 d. We assumed that mottled sculpin populations were closed (i.e., no gains or losses) within a seasonal sample but open among samples (Pollock et al. 1990).

Intensive sampling of mottled sculpin populations was confined to a central 200-m core of the 1-km site. Each time a sampling pass was conducted, we observed mottled sculpin within the 200-m core (i.e., 4 passes/season within the core). We also sampled two 400-m buffer zones located immediately up- and downstream of the study core at the end of each season (i.e., 1 pass/season within the buffer zones). Buffer zones were sampled to capture marked individuals that may have moved out of the core site. However, because recaptures in the buffer zones of individuals originally marked in the core were rare (<2% of all fish marked in the core were recaptured in the buffer zones; Petty and Grossman 2004), data from buffer zone recaptures were not included in our analyses.

To begin a pass, we entered the site at a randomly determined location and snorkeled slowly upstream. The entire 200-m core area was sampled in a single day. When we located a mottled sculpin, we immediately captured it with a dip net and marked its focal position with a painted lead weight. At the time of first capture, individuals were anesthetized with tricaine methanesulfonate until they were sufficiently tranquil to be easily and individually marked with distinct subcutaneous injections of acrylic paint (Hill and Grossman 1987; Petty and Grossman 2004). A double-marking study in an adjacent stream reach using fin clips and acrylic paints indicated that mark retention by juveniles and adults was extremely high (>90%) for up to 16 months and did not differ significantly among size-classes (Petty and Grossman 2004). We measured SLs (nearest mm) of all newly captured and recaptured individuals, noted their individual marks, and classified each as a juvenile (SL $\leq$ 48 mm), small adult (49–64 mm), or large adult ($\geq$65 mm; Petty and Grossman 2004). The use of a consistent methodology for the capture and recapture of fish minimized sampling bias during collections and in subsequent statistical analyses.

After snorkeling the entire site, we mapped the exact location ($\pm$5 cm) of each captured individual via a network of permanent transect posts positioned along the stream margin (see Petty and Grossman 2004 for a detailed description of sampling methodology). We also quantified microhabitat characteristics at the focal position of each captured mottled sculpin (Grossman and Ratajczak 1998). Microhabitat measurements included depth ($\pm$1 cm), average velocity ($\pm$0.1 cm, determined with an electronic current velocity meter), and a visual estimate of the percentage contribution of seven substratum classes to the total substratum within a 400-cm^2 quadrat (Grossman and Ratajczak 1998). Substratum classes included bedrock (embedded substratum with a maximum dimension >30.0 cm), boulder (unembedded substratum with a maximum dimension >30.0 cm), cobble (2.6–30.0 cm), gravel (0.3–2.5 cm), sand ($\leq$0.2 cm), silt (material capable of suspension in the water column), and debris (organic material of any size). Average velocity for quadrats with depths no greater than 75 cm was quantified with one measurement taken at 0.6 × water column depth, whereas for quadrats deeper than 75 cm the average velocity was calculated as the mean of measurements made at 0.2 and 0.8 × depth (Bovee and Milhaus 1976). After completion of microhabitat measurements, we returned all mottled sculpin to their position of last capture.

Movement analysis.—Our first objective was to quantify the two-dimensional movement patterns of mottled sculpin residing in the study reach. We used mark–recapture data to quantify mottled sculpin movements by recording the x and y coordinates of each sequential capture of an individual within a given year (Turchin 1998). Individual movements could then be represented as a two-dimensional vector, where elements of the vector include the distance between two consecutive capture locations (d_t) and the turning angle (α_t) resulting from three consecutive captures. Because movement distances within a year were not significantly correlated with time between recaptures (r = 0.01–0.06), we quantified movement in units of linear distance (i.e., m) rather than as a rate (e.g., m/d; Turchin 1998).

We combined information from all 3 years and constructed cumulative frequency distribution curves of movement distance for each mottled sculpin age-class. We then compared mottled sculpin movements to a simple model of random movement. If mottled sculpin move randomly within the study site, then the distribution of turning angles (i.e., α_t) exhibited by the fish should be uniform (Turchin 1998). However, if mottled sculpin movements are nonrandom, then the distribution of α_t should deviate from uniformity. We used log-likelihood tests (Sokal and Rohlf 1995) to compare observed turning angle distributions with a uniform distribution. Finally, we calculated the frequency of juvenile and adult movements with turning angles greater than or less than 90° for a series of movement distance intervals (0.5–1.0, 1.0–1.5, 1.5–2.0, 2.0–2.5, 2.5–3.0, and >3.0 m) and used replicated, log-likelihood goodness-of-fit tests to determine whether turning angles varied as a function of movement distance. All tests were run separately on juveniles and adults (significance level = 0.05). Turning angle frequencies were calculated for individuals captured at least three times within a year. For individuals captured more than three times, we randomly selected a series of three consecutive captures and the associated turning angle to avoid bias from analyzing multiple observations from the same individuals (Turchin 1998).

Home range size and territoriality.—Our second objective was to quantify mottled sculpin home range size and overlap and determine whether mottled sculpin were territorial. We used the program CAL-HOME (Kie et al. 1994) and the minimum convex polygon approach to calculate home range sizes (m^2) of all mottled sculpin captured four times or more in a given year. This approach has been used successfully to quantify home ranges in a variety of vertebrate species (Bowers et al. 1996; Anders et al. 1998). There was a significant relationship between home range size and number of captures for mottled sculpin captured three or more times ($r = 0.4$, $P = 0.04$, $n = 420$) but not for fish captured four or more times (r = 0.18, P > 0.05, n = 340). Consequently, individuals captured only three times within a year were not included in estimates of home range size.

Following Maher and Lott (1995, 2000), we defined territoriality as the exclusive use of a geographic area by an individual. We quantified the degree of territoriality exhibited by mottled sculpin as the percent home range overlap among neighboring residents. Ideally, demonstration of territoriality would include evidence of aggressive defense; however, when a species is cryptic or when aggressive interactions are highly infrequent (the case for mottled sculpin), territoriality can be inferred from exclusive use (Maher and Lott 1995). Total and percentage home range overlap was calculated in the spatial analysis extension of ArcGIS version 8.3 (ESRI 2003). Home range size and percent overlap were calculated separately for each age-class in each year. We performed analyses of variance (ANOVAs) and post hoc Tukey's tests on home range size (log transformed) and percentage overlap (arcsine–square-root transformed) to test for significant differences among juvenile, small-adult, and large-adult mottled sculpin across the 3 years of the study. We assessed the relative degree of territoriality exhibited by each age-class by comparing observed home range overlaps with critical thresholds identified by Lott (1991): over 25% overlap for nonterritorial organisms, 15–25% for weakly territorial organisms, and less than 15% for strongly territorial organisms.

Characteristics of mottled sculpin territories.—Our third objective was to quantify the physical microhabitat characteristics and temporal stability of mottled sculpin territories. We compared the physical microhabitat characteristics of patches inhabited by juvenile, small-adult, and large-adult mottled sculpin with patches available in the study area. Microhabitat availability within the 200-m core site of Shope Fork was quantified at the end of each seasonal mottled sculpin sampling period (i.e., total of four samples each year). We made physical microhabitat measurements in 400-cm^2 quadrats at 1-m intervals along transects running perpendicular to streamflow within the active stream channel (i.e., area of the stream channel consisting of scoured substrata). Transects were spaced every 5 m (approximately one mean stream width) throughout the 200-m segment of Shope Fork (41 total transects; 205 total quadrats). We collected an identical suite of microhabitat measurements from both availability quadrats and mottled sculpin locations.

Microhabitat data were analyzed by subjecting data from transect sampling to a principal components analysis (PCA; in the Statistical Analysis System) using the methods of Grossman and Ratajczak (1998). We analyzed components with eigenvalues greater than 1 and ecologically interpretable loadings. Before analysis, depth, average current velocity, and substratum data were $\log(x + 1)$ or arcsine–square-root transformed to meet the normality assumptions of PCA (Grossman and Freeman 1987). This analysis quantified microhabitat availability in Shope Fork. We then compared component scores for availability quadrats and mottled sculpin focal positions to test for nonrandom microhabitat use. Because the physical microhabitat use patterns of mottled sculpin are known (Grossman and Freeman 1987; Petty and Grossman 1996; Grossman and Ratajczak 1998), we constrained our analysis to late summer of each year.

We also used microhabitat data collected along transects to quantify microhabitat stability. During each season, we classified each quadrat by its dominant substratum (bedrock–boulder, cobble–gravel, sand–silt, debris, or dry) using the method of Grossman et al. (1995a). Microhabitat stability was calculated as the number of times the dominant substrate composition of a quadrat changed from one sample date to the next (Grossman et al. 1995a). After quantifying the relative stability of each quadrat, we used mottled sculpin distribution data to identify quadrats that were intensively used (i.e., occupied in more than 7 of the 12 seasonal sampling events). We recorded the size-classes in each quadrat and then classified all quadrats with respect to whether they were used primarily by juveniles, small adults, or large adults. Given that juveniles and adults rarely occupied overlapping home ranges (see Results), the classification of patches as juvenile or adult was relatively straightforward. In cases where both juveniles and adults were observed in the same quadrat, we assigned the quadrat to the size-group that was the most frequent occupant. Finally, we used χ^2 analysis to test the hypothesis that different age-classes occupied territories with higher substrate stability than was generally available in the study site.

Environmental variability, population age structure, and territory abandonment.—Preliminary analyses indicated that adult mottled sculpin were highly territorial and exhibited two distinct movement patterns: short (<2 m), area-restricted movements within a patch or territory and longer (>2 m), directional movements from one territory or patch to another (patch abandonment). We also observed a high degree of temporal variability in territoriality and territory abandonment rates. Consequently, our final objective was to quantify the effects of temporal variability in streamflow, microhabitat stability, and population size and age structure on mottled sculpin territory use.

We monitored stream discharge in Shope Fork from gauge height data obtained from a U.S. Forest Service gauging station located immediately upstream of the study site. Flow data were used to calculate maximum flow each month, monthly average daily maximum flow, monthly average daily mean flow, and the number of high-flow events each month. We considered flows greater than 0.71 m^3/s to represent high-flow events (see Grossman et al. 1998). This flow level has a recurrence interval of 10–77 events/year.

Mark–recapture data from multiple passes (four) within each season were used to obtain seasonal estimates of mottled sculpin density and age structure. We used removal estimators for closed captures in the program MARK to estimate density (White et al. 1982). Akaike's model selection criterion was used to assess the interactive effects of season and age on mottled sculpin capture probability and determine which models provided the most appropriate estimates of season- and age-specific population size (Burnham and Anderson 2002). We calculated age structure each season as the proportion of the total population made up of each age-class (juvenile, small adult, and large adult).

Finally, we quantified season- and age-specific territory abandonment rates by calculating the proportion of the resident population that abandoned their original territory (i.e., made directional movements >2 m) over the course of each seasonal time step. We then used linear correlation to examine the effects of population age structure (i.e., proportion of the total population consisting of large adults), flow variability (i.e., number of high-flow events), and microhabitat stability (i.e., proportion of quadrats experiencing a shift in dominant substrate type) on territory abandonment rates. We also used correlation ($n = 3$) to relate year-to-year variation in percentage spatial overlap (i.e., territoriality) to streamflow, microhabitat stability, and population size structure.

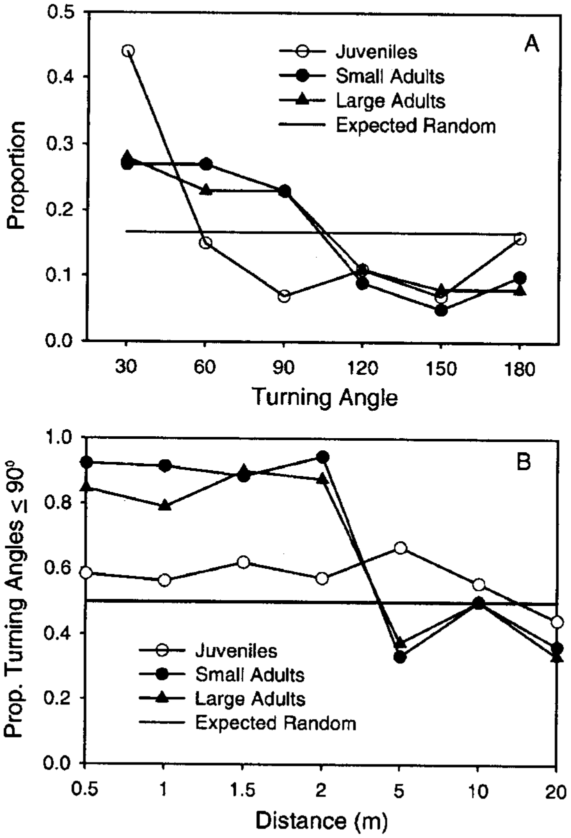

FIGURE 1.—Two-dimensional movement patterns of mottled sculpin inhabiting Shope Fork, North Carolina, 1994–1996: (A) frequency distribution of fish turning angles and (B) relationship between turning angle and the preceding movement distance. Straight solid lines represent the movement pattern expected under a model of random movement.

Results

Movement

We marked and released a total of 604 mottled sculpin within the core 200-m area. Of these, 308 individuals were captured at least three times within a year and were included in movement analyses. Analysis of movement distance indicated that mottled sculpin were extremely sedentary; median movement distance of all age-classes combined was 1.42 m, and more than 80% of all movements were less than 3 m in linear distance.

Mottled sculpin exhibited nonrandom two-dimensional movement patterns within the study site (Figure 1). All age-classes exhibited acute turning angles (i.e., <90°) at a greater rate than expected by chance alone (juveniles: Kolmogorov–Smirnov statistic [KS] = 0.3, $P = 0.04$; small adults: KS = 0.30, $P = 0.03$; large adults: KS = 0.25, $P = 0.05$; Figure 1A). In addition, we observed a significant relationship between turning angle and movement distance for small adults ($G = 38.7$, df = 6, $P < 0.01$) and large adults ($G = 15.93$, df = 6, $P < 0.05$) but not for juveniles ($G = 1.04$, df = 6, $P > 0.10$; Figure 1B). For example, 80–90% of adult movements less than 2 m were followed by movements back toward the initial location and represented area-restricted movements (Figure 2). However, when adults moved distances greater than 2 m, they failed to show evidence of area-restricted movements (i.e., movement patterns were not significantly different from random and represented abandonment of the patch; Figures 1B, 2). In contrast, the tendency of juveniles to exhibit acute turning angles was independent of movement distance and statistically consistent with a model of random movement (Figure 1B).

Home Range Size and Territoriality

The total area used by adult mottled sculpin while exhibiting area-restricted movements remained relatively constant over the course of the study, ranging

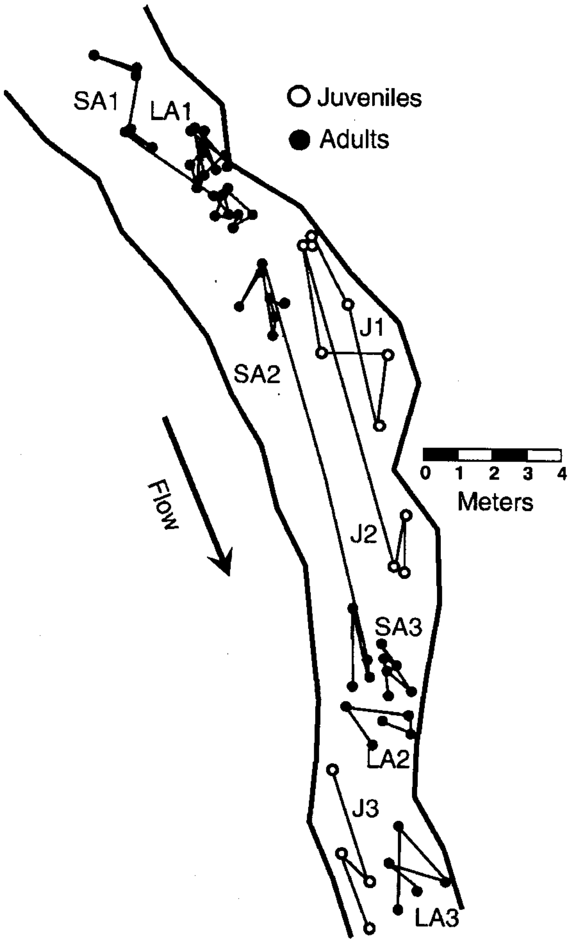

FIGURE 2.—Representative movement patterns of juvenile (J; ≤48 mm SL), small-adult (SA; 49–64 mm), and large-adult (LA; ≥65 mm) mottled sculpin inhabiting a 30-m reach of the Shope Fork, North Carolina. Locations are for nine individuals captured over a 7-month period in 1995.

from a low of 0.92 m^2 in 1996 to 1.02 m^2 in 1994. However, home range size (i.e., total area used within a year) varied significantly among age-classes and over time (Table 1). Home range sizes of juveniles and small adults were significantly larger than those of large adults in 1994 and 1995 (1994: $F = 5.4$, df = 2, $P = 0.006$; 1995: $F = 3.1$, df = 2, $P = 0.05$). Home range sizes did not differ among age-classes in 1996 ($F = 0.4$, df = 2, $P = 0.69$); juveniles and small adults used dramatically smaller areas in 1996 than in previous years (Table 1).

Spatial overlap of home ranges also varied significantly, both annually and among age-classes (Table 1; Figure 3). Mean spatial overlap of juveniles ranged from a low of 11% in 1996 to a high of 35% in 1995 and differed significantly from that of small and large adults in 1994 and 1995 but not 1996 (1994: $F = 5.4$, df = 2, $P = 0.006$; 1995: $F = 3.1$, df = 2, $P = 0.05$; 1996: $F = 3.1$, df = 2, $P = 0.05$). Juveniles were either weakly territorial (overlap of 15–25% in 1996) or nonterritorial (overlap > 25% in 1994 and 1995). In contrast, small and large adults always displayed the low spatial overlap (<15% in all years) consistent with strong territoriality (Table 1). Figure 3 illustrates the tendency for individuals to shift from using overlapping home ranges as juveniles to using nonoverlapping home ranges as adults. Finally, there was a strong tendency for juvenile home ranges to overlap with those of other juveniles, whereas overlap between juvenile and adult ranges was extremely rare. Of the total overlap observed, 72% was juvenile–juvenile overlap, 20% was adult–adult overlap, and 8% was juvenile–adult overlap.

Characteristics of Mottled Sculpin Territories

Principal components analysis of microhabitat availability data identified two significant components

TABLE 1.—Mean (±SE) home range size and percentage spatial overlap of mottled sculpin residing in Shope Fork, North Carolina, 1994–1996. Differing letters indicate significant differences among age-classes within a given year.

	1994		1995		1996	
Variable and size-class	*N*	Mean (SE)	*N*	Mean (SE)	*N*	Mean (SE)
Home range size (m^2)						
Juvenile[a]	29	9.1 (2.9) z	29	10.9 (2.9) z	29	1.6 (0.6) z
Small adult[b]	54	8.7 (1.8) z	55	8.5 (1.8) z	55	0.8 (0.1) z
Large adult[c]	14	2.8 (0.8) z	17	1.7 (0.4) y	17	2.8 (0.4) z
Spatial overlap (%)						
Juvenile	29	26.8 (3.8) z	29	35.1 (4.6) z	29	15.6 (6.5) z
Small adult	54	12.0 (1.4) y	55	13.5 (2.9) y	55	5.5 (1.9) z
Large adult	14	11.8 (2.5) y	17	4.4 (1.7) x	17	0.8 (0.4) z

[a] SL ≤ 48 mm.
[b] SL = 49–64 mm.
[c] SL ≥ 65 mm.

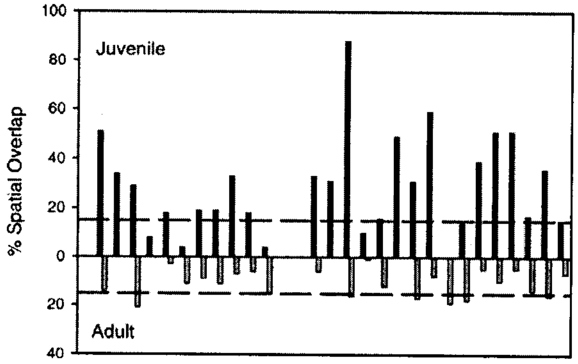

FIGURE 3.—Percent spatial overlap of 29 individual mottled sculpin that were observed as juveniles and subsequently established territories as adults in Shope Fork, North Carolina. The area within the dashed horizontal lines identifies overlap levels indicative of strong territoriality (Lott 1991).

that explained nearly 55% of the total variance in the data set (Table 2). Principal component 1 (PC1) represented an erosional–depositional continuum, whereas PC2 represented a continuum from boulder- to gravel-dominated substrata (Table 2). The ANOVAs on mean PC1 and PC2 scores detected significant differences in microhabitats used by juvenile, small-adult, and large-adult mottled sculpin in all 3 years of the study (PC1: $F = 8.2$–13.6, $P = 0.02$–0.001; PC2: $F = 5.6$–7.6, $P = 0.04$–0.006). We found that small and large adults occupied territories that were deeper and that had higher current velocities and higher amounts of cobble and boulder than areas used by juveniles (Figure 4).

Territories of small and large adults also were more likely to be positioned in areas of stable substrate than expected by chance alone (small adults: $\chi^2 = 17.32$, df $= 6$, $P = 0.01$; large adults: $\chi^2 = 20.76$, df $= 6$, $P = 0.005$; Figure 5). Over 80% of quadrats used intensively by large adults and 60% of those used by small adults never experienced a shift in their dominant substrate composition and never went dry. In contrast, fewer than 20% of the available quadrats remained stable from season to season throughout the study period (Figure 5). Juveniles tended to occupy areas that were considerably less stable than those used by adults and slightly, but not significantly, less stable ($\chi^2 = 5.32$, df $= 6$, $P = 0.5$) than randomly sampled quadrats in the study area (Figure 5).

Environmental Variability, Population Age Structure, and Territory Abandonment

We observed a high degree of flow variability in Shope Fork over the course of this study. The number of high-flow events occurring in a given month ranged from 0 to 10, and there was a high correlation between high-flow event occurrence, average mean daily flow ($r = 0.87$), and maximum daily flow ($r = 0.93$). Mottled sculpin population size (±95% confidence interval) remained relatively stable, ranging from 145 ± 18 individuals in August 1994 to 220 ± 23 individuals in June 1995. However, population size structure shifted over the course of the study; large adults comprised only 11% of the total population in spring 1994 and 36% of the total population in fall 1996.

We observed no significant correlations between territory abandonment rates, home range size, or home range overlap and any flow or microhabitat stability measures ($r = -0.25$ to 0.19). However, we found that seasonal territory abandonment rates increased as the percentage of large adults in the population increased. This pattern was highly significant for small ($r = 0.70$, $P = 0.01$, $n = 12$) and large adults ($r = 0.81$, $P < 0.001$, $n = 12$) but not for juveniles ($r = 0.45$, $P = 0.05$, $n = 12$). We observed similar patterns for home range size and percent spatial overlap: both behavioral attributes decreased as large-adult numbers increased ($r = 0.72$–0.85).

TABLE 2.—Means (±SE) of microhabitat variables from randomly selected available patches and patches used by juvenile, small-adult, and large-adult mottled sculpin in Shope Fork, North Carolina, 1994–1996. Also presented are the significant variable loadings (≥|0.40|) from principal components (PCs) 1 and 2. See text for substrate particle sizes.

Patch type	N	Depth (cm)	Velocity (cm/s)	Bedrock (%)	Boulder (%)	Cobble (%)	Gravel (%)	Sand (%)	Silt (%)	Debris (%)
Available	172	13 (1)	31 (2)	0 (0)	11 (2)	61 (2)	13 (1)	4 (1)	6 (1)	5 (1)
Juvenile[a]	50	17 (1)	38 (3)	0 (0)	13 (2)	58 (3)	18 (1)	5 (1)	4 (1)	3 (1)
Small adult[b]	61	19 (1)	47 (2)	0 (0)	18 (3)	63 (3)	13 (1)	1 (1)	1 (1)	3 (1)
Large adult[c]	32	20 (1)	48 (4)	0 (0)	19 (4)	54 (4)	18 (3)	3 (1)	2 (1)	4 (1)
PC1		0.46	0.87			0.54		−0.61	−0.84	−0.47
PC2					0.80		−0.53			

[a] SL ≤ 48 mm.
[b] SL = 49–64 mm.
[c] SL ≥ 65 mm.

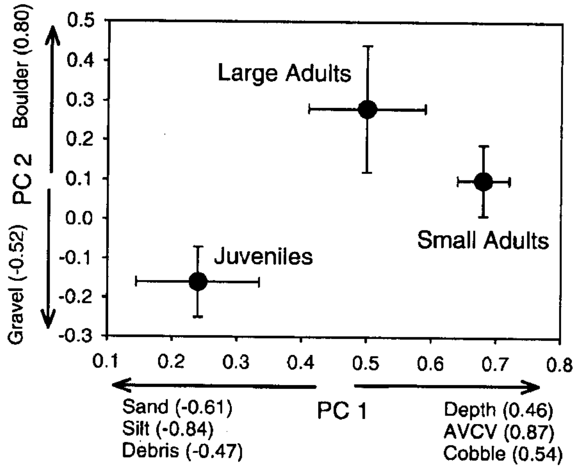

FIGURE 4.—Differences in microhabitat use by juvenile (≤48 mm SL), small-adult (49–64 mm), and large-adult (≥65 mm) mottled sculpin in Shope Fork, North Carolina, during late summer 1995, as indicated by principal components analysis. Data presented are mean (±SE) principal component (PC) 1 and PC2 scores. Also presented are factor loading scores of significant microhabitat variables on both PCs.

Discussion

Size-Dependent Territoriality

Our results indicate that adult mottled sculpin respond to spatial and temporal variability in resource availability and behave in a manner that ensures exclusive access to the highest-quality patches available. Adult mottled sculpin exhibited nonrandom movement behaviors that coupled short movement distances (i.e., <2 m) with acute turning angles. Combined, these behaviors tend to maintain mottled sculpin activities within relatively small areas (approximately 1-m^2 patches). The patches used by adults were characterized by extremely low overlap with neighboring residents, a behavior that is indicative of strong territoriality (Lott 1991). We know from previous research that adults occupy patches with relatively high invertebrate prey concentrations (Petty and Grossman 1996). Consequently, restricted home ranges combined with territoriality are behaviors that should enable mottled sculpin to maintain exclusive access to high-prey patches.

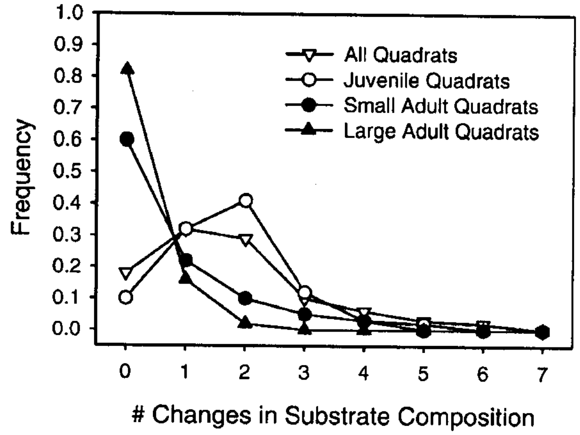

FIGURE 5.—Relative stability of patches (measured as change in substrate composition between seasonal samples) and frequency of patch use by mottled sculpin in Shope Fork, North Carolina, 1994–1996.

The space usage behaviors of juvenile mottled sculpin were consistently different from those of nearby adults. Juveniles exhibited random movement patterns along the stream margins and did not exhibit clear patterns of patch use and abandonment. Furthermore, juveniles had less-restricted home ranges and exhibited significantly higher spatial overlap with other juveniles. Consequently, while adult behaviors were consistent with those of a territorial organism, juvenile behaviors more closely matched those of floating individuals (Lott 1991). Floaters are defined as individuals in a population that are forced to inhabit areas of marginal quality, where they wait for territories of higher quality to become available (López-Sepulcre and Kokko 2005). Studies of birds, mammals, and fishes have provided evidence of territorial and floater strategies across a broad range of natural ecosystems (see Lott 1991; Maher and Lott 1995, 2000).

To our knowledge, this study provides some of the first evidence of territorial and floating behaviors in a benthic stream fish. However, the mottled sculpin behaviors that we observed are quite similar to those documented in studies of salmonid behavior (Fausch and White 1981; Grant and Noakes 1987; Hughes and Dill 1990; Nakano 1995). For example, Nakano (1995) conducted an observational study of competitive interactions among individual red-spotted masu salmon *Oncorhynchus masou ishikawai* in a Japanese stream. In this system, large, dominant individuals defended small home ranges in habitats with the best locations for drift feeding. Social dominance followed a strict size-related hierarchy in which smaller individuals occupied successively lower-quality patches. At some point in the hierarchy, subdominant fish were forced to abandon territoriality and switched to a nonterritorial, opportunistic foraging behavior (Nakano 1995). Mottled sculpin appear to exhibit many of the behavioral interactions observed by Nakano (1995).

Despite a lack of research demonstrating foraging-related territoriality, numerous studies have documented spawning-related territoriality in mottled sculpin populations (Downhower and Brown 1979, 1980; Natsumeda 1998, 1999, 2001). Several sculpin species are known to exhibit male parental care, and male–male competition is an important determinant of mottled sculpin distributions during the spawning season (Downhower and Brown 1980; Natsumeda 2001). Our results demonstrate that mottled sculpin also display intraspecific competition for feeding sites. Barlow (1993) argued that foraging-related territoriality appears to be derived from spawning-related territoriality in freshwater fishes but that the opposite is true for marine fishes. Future studies should determine whether foraging-related territoriality is common in benthic fish species that also exhibit parental care and competition for nest sites.

We hypothesize that the behavioral differences observed between juvenile and adult mottled sculpin is the result of size-dependent social interactions. An alternative hypothesis is that mottled sculpin behaviors are the result of size-dependent habitat preferences. It is possible that juveniles prefer low-velocity depositional patches, because high-velocity erosional patches are too energetically costly for them to use. However, the experimental and descriptive work of Facey and Grossman (1990, 1992) demonstrates that high velocities do not impose substantial energetic constraints on habitat selection by mottled sculpin in the Coweeta Creek drainage. In addition, both Freeman and Stouder (1989) and Grossman et al. (2006) demonstrated experimentally that juvenile and adult mottled sculpin prefer similar microhabitats in this system.

A second alternative to the social interaction hypothesis is that predator avoidance behaviors rather than competitive interactions control patch use by juveniles. Higher predation risk from cannibalistic adults may force juveniles to use marginal habitats. Predation risk is known to affect habitat selection by fishes in other systems (Power 1984; Gilliam and Fraser 1987). Despite these examples, it seems unlikely that patch use by juveniles is primarily a response to predation risk from adults, because previous work shows little effect of predators on microhabitat selection by mottled sculpin in this system (Grossman et al. 1995b, 1998). Although the largest adults (i.e., >80 mm) may pose a predatory threat to small juveniles, these individuals represent a very small percentage (<5%) of the population. In addition, dietary studies of mottled sculpin suggest that cannibalism is extremely rare in this system (Stouder 1990; G.D.G., unpublished data). Consequently, we believe the best explanation for size-dependent behaviors is that intraspecific competitive interactions between adults and juveniles limit juvenile access to high-quality patches. Nevertheless, the behavioral and population-level consequences of competition versus predatory threat may be the same.

Territoriality, Environmental Variability, and Mottled Sculpin Population Dynamics

Barlow (1993) hypothesized that territoriality should be selected against in streams, such as Shope Fork, because high variation in resource availability would render it unprofitable. In Shope Fork, mottled sculpin displayed territoriality despite high variability in flows and substratum stability. Territorial mottled sculpin persist in this system because adults are able to maintain territories in patches that are relatively stable and highly profitable. Unstable patches were avoided by large adults and tended to be inhabited by smaller, nonterritorial individuals. Consequently, our study supported Barlow's (1993) hypothesis that habitat instability should prevent the selective advantaged obtained by territoriality. However, our results also demonstrate that the economic defensibility hypothesis should incorporate spatial heterogeneity in its predictions. For example, many streams probably have both stable and unstable patches, and the consequences of territoriality in each would differ. We predict that territoriality will be the most prevalent in fishes inhabiting highly stable streams dominated by coarse substrata, whereas highly overlapping home ranges will be favored in streams characterized by high flow variability and less-stable substrates.

As an extension of Barlow's (1993) hypothesis, we predicted that mottled sculpin behaviors would be influenced by seasonal and year-to-year variation in streamflow and microhabitat stability. We expected increased patch abandonment rates, home range sizes, and spatial overlap during periods of high flow variability. However, we found no evidence that flow variability influenced the behaviors of juveniles or adults. Instead, behaviors were consistently influenced by variation in the density of large adults in the population. Increasing dominance of large adults resulted in reduced home range sizes and reduced spatial overlap of all age-classes. Increases in the density of large adults also produced increases in territory abandonment rates.

These results underscore the importance of intraspecific interactions to mottled sculpin populations relative to the effects of streamflow and environmental variability. Variability in environmental features, especially streamflow, is unquestionably a dominant influence on stream fish communities (Grossman et al. 1982, 1985, 1990, 1998; Poff and Ward 1989; Mérigoux et al. 1999; Oberdorff et al. 2001). However, mottled sculpin populations in the Coweeta Creek drainage seem to be largely immune to these effects, probably because they are dominated by the highly stable adult segment of the population (Grossman et al.

2006). Nonetheless, age-0 density and interactions between age-0 fish and juveniles are strongly dependent upon interannual variation in flow (Grossman et al. 2006). In most riverine ecosystems, spatiotemporal variability in juvenile recruitment is translated through the entire population (Mérigoux and Ponton 1999; Spina 2001; Cattanéo et al. 2002; Petty et al. 2005). Mottled sculpin in the Coweeta Creek drainage, however, do not fit this general pattern.

Numerous studies in other systems have demonstrated that territoriality combined with subdominant floaters in marginal habitats can produce strongly regulated population dynamics (Kokko and Sutherland 1988; Hunt 1998; López-Sepulcre and Kokko 2005; Penteriani et al. 2005). For example, López-Sepulcre and Kokko (2005) demonstrated that the presence of floaters forms a buffer against population fluctuations. In our system, dominant mottled sculpin are territorial in stable, highly profitable areas of the stream, whereas subdominant fish float along the margins. The floating subpopulation is able to move into higher-quality patches as they become available. Floating mottled sculpin also are available to take advantage of unpredictable changes in the distribution of profitable patches. Consequently, the combination of territoriality and floating may explain the high degree of stability in mottled sculpin population dynamics in the Coweeta Creek system (Freeman et al. 1988; Grossman et al. 2006).

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