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Factors Affecting Allopatric and Sympatric Occurrence of Two Sculpin Species across a Rocky Mountain Watershed

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We assessed factors related to the occurrence of allopatric and sympatric Paiute Sculpin (*Cottus beldingi*) and Mottled Sculpin (*Cottus bairdi*) in the Salt River watershed of Wyoming and Idaho, 1996–1997. Sympatric occurrences of Paiute Sculpin and Mottled Sculpin were found in downstream segments of tributaries across a wide range of elevations, stream temperatures, channel slopes, and stream sizes. Allopatric Paiute Sculpin was found in small, high-elevation streams with low summer water temperatures, high channel slopes, large rocky substrates, and low densities of Brown Trout (*Salmo trutta*). Allopatric Mottled Sculpin occurred in spring streams that were wide and deep, dominated by fine substrate, and supported high densities of Brown Trout. Mottled Sculpin was absent from all tributaries on the eastern side of the drainage where streams have low summer water temperatures, high-gradient channels, and barriers that can influence upstream movements. This study suggests that stream geomorphology, thermal characteristics, local habitat conditions, and nonnative fishes differentially influence the occurrence of Paiute Sculpin and Mottled Sculpin.

THE coexistence of ecologically similar species is a central focus of aquatic ecology, with a variety of abiotic and biotic mechanisms having been proposed to explain the coexistence of similar species (Werner, 1977; Gotelli, 1997). When two species use a common resource, abiotic disturbances or predation may suppress population densities so the resource does not become limiting (e.g., Wilson, 1990). Alternatively, sympatric species may partition resources such that both species coexist at a lower abundance than in allopatry (e.g., Wilson, 1990; Brown, 1991). Although these concepts are useful for exploring factors allowing coexistence of species on small scales, understanding factors related to the occurrence of allopatric and sympatric populations at large spatial scales is also important.

Sculpin (Cottidae) are an important component of fish assemblages in the western United States. Two species, Mottled Sculpin (*Cottus bairdi*) and Paiute Sculpin (*Cottus beldingi*), are native and often numerically dominate fish assemblages in streams of the interior Rocky Mountain region (Bailey, 1952; Jones, 1972). Mottled Sculpin is one of the most widespread sculpin species in North America (Lee et al., 1980). Paiute Sculpin has a limited geographic distribution in the Columbia River drainage, portions of the Lahontan and Bonneville basins, and a few areas in the upper Colorado River drainage (Lee et al., 1980). Both species are native to the Snake River system of Wyoming and Idaho and often occur in sympatry (Baxter and Stone, 1995). Trophic overlap between Mottled Sculpin and Paiute Sculpin is probably high because both species are benthic insectivores (Bailey, 1952; Johnson, 1985; Moyle and Vondracek, 1985). Mottled Sculpin inhabit a variety of habitats in both lotic and lentic systems (Lee et al., 1980) and occur in pools, runs, and riffles in lotic systems (Bailey, 1952). In contrast, Paiute Sculpin are found almost exclusively in lotic systems and are most common in fast-water habitats (e.g., riffles, rapids) with large rocky substrate (Jones, 1972; Johnson, 1985).

Our objective was to identify factors related to allopatric and sympatric occurrences of Paiute Sculpin and Mottled Sculpin in the Salt River drainage of Wyoming and Idaho. Specifically, we sought to determine whether large-scale variables (e.g., elevation, channel slope), thermal characteristics, local habitat characteristics (e.g., substrate composition), or nonnative species affect occurrence of the two sculpin species across the watershed.

Materials and Methods

Fish and habitat were sampled in streams throughout the Salt River watershed (Fig. 1). The Salt River is a tributary to the Snake River near the Wyoming-Idaho border. The mainstem of the Salt River is a fifth-order stream (after Strahler, 1957) that originates in the Salt River Range and flows northerly for approximately 45 km to its confluence with the Snake River at Palisades Reservoir. Numerous spring streams emerge from the alluvium adjacent to the Salt River and flow for short distances before joining

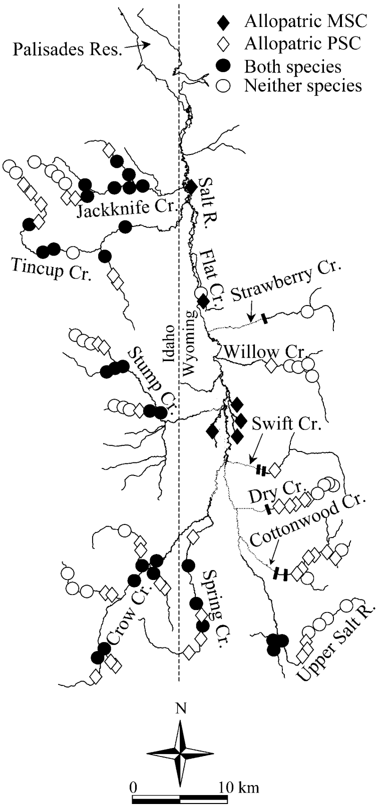

Fig. 1. Map showing the locations of reaches sampled and distributions of allopatric and sympatric Paiute Sculpin (PSC) and Mottled Sculpin (MSC) in the Salt River watershed of Wyoming and Idaho, 1996–1997. Open symbols represent sampling reaches and dark bars represent large (> 1 m high), permanent barriers to upstream movement by fishes. Stream segments represented as dotted lines indicate that reaches are frequently intermittent or dewatered.

the river. The basin is surrounded by mountain ranges that differ markedly in morphology (Isaak, 2001). The Salt River Range on the east side of the watershed is rugged with elevations exceeding 3300 m. The Gannett Hills to the south and Caribou and Webster ranges to the west are less rugged and elevations do not exceed 2800 m. Valleys in the Salt River Range are generally narrow and constrained, whereas those in other portions of the watershed are constrained in upstream segments and unconstrained in downstream stream segments. Consequently, streams on the eastern side of the watershed have straighter channels, larger substrates, and steeper channel slopes than those on the western side. Stream temperatures are much lower on the eastern side of the watershed compared to those in other areas of the basin (Isaak and Hubert 2001).

The native fish fauna of the Salt River drainage consists of 11 species: Mountain Whitefish (*Prosopium williamsoni*), Utah Sucker (*Catostomus ardens*), Mountain Sucker (*Catostomus platyrhynchus*), Longnose Dace (*Rhinichthys cataractae*), Speckled Dace (*Rhinichthys osculus*), Utah Chub (*Gila atraria*), Leatherside Chub (*Gila copei*), Redside Shiner (*Richardsonius balteatus*), Mottled Sculpin, Paiute Sculpin, and Cutthroat Trout (*Oncorhynchus clarki*; Baxter and Stone, 1995). Brown Trout (*Salmo trutta*), Rainbow Trout (*Oncorhynchus mykiss*), and Brook Trout (*Salvelinus fontinalis*) have been introduced and become naturalized in the watershed. Brown Trout are widespread, but Rainbow Trout are relatively rare, and Brook Trout are generally limited to headwater areas of mountain tributaries.

Lands in the main valley and lower mountain valleys are privately owned and are influenced by agricultural activities. Small diversion structures are common throughout the basin, and several large, permanent structures (> 1 m high) have been constructed to divert water for agricultural use (Fig. 1). Consequently, the lower segments of mountain streams, particularly on the east side of the basin, are frequently intermittent or completely desiccated during summer. Mountainous areas are publically owned and managed for recreation and livestock grazing.

Fish were sampled from 110 reaches during 1996 and 1997 (Fig. 1). Sampling began in early July after snowmelt and continued until mid-September of each year. Fish were sampled using a backpack electrofisher (Model 15-C, Smith-Root, Vancouver, Washington) from reaches 63–465 m in length (mean ± standard error; 194.2 ± 8.9 m). Most reaches (89%) were at least 100 m long. Multiple electrofishing passes (at least three passes) were conducted at 76% of the reaches, whereas one pass was conducted at the remaining reaches. All fish were identified in the field and noted as either present or absent, except for salmonids, which were enumerated.

Elevation (meters above mean sea level) of the study reaches was determined from 1:24,000-scale U.S. Geological Survey topographic maps (Table 1). Water temperatures (C) were recorded every 30 min using digital thermographs (model WTA32, Onset Computer Corporation, Pocasset, Massachusetts) deployed at opposite ends of each study stream. Stream temperatures were summarized as the mean temperature for July and August. Mean temperatures for reaches without thermographs were interpolated based on stream-specific rates of wa-

TABLE 1. MEAN, STANDARD ERROR, MINIMUM, AND MAXIMUM VALUES OF ELEVATION (METERS ABOVE MEAN SEA LEVEL), MEAN SUMMER WATER TEMPERATURE (JULY AND AUGUST, C), CHANNEL SLOPE (%), MEAN WETTED WIDTH (m), MEAN DEPTH (CM), THE PROPORTION OF BOULDER, COBBLE, GRAVEL, AND FINE SUBSTRATE (%), THE PROPORTION OF THE REACH COVERED BY AQUATIC VEGETATION, WOODY DEBRIS, AND TOTAL COVER (%), AND THE NUMBER OF BROWN TROUT (NUMBER/100 m) FOR REACHES SAMPLED IN THE SALT RIVER DRAINAGE OF WYOMING AND IDAHO.

Variable	Mean	SE	Minimum	Maximum
Elevation	2060.9	14.6	1736.2	2500.9
Temperature	10.9	0.3	5.2	17.9
Slope	2.4	0.2	0.1	10.0
Width	4.6	0.2	1.3	14.8
Depth	20.4	1.1	7.3	71.4
Boulder	6.0	0.8	0	36.0
Cobble	48.8	2.7	0	98.0
Gravel	34.8	2.2	0	89.0
Fine	10.6	1.7	0	87.0
Aquatic vegetation	0.8	0.1	0	7.0
Woody debris	0.1	0.1	0	2.0
Total cover	0.9	0.1	0	7.0
Brown Trout	2.2	0.5	0	24.9

ter temperature change that were calculated by dividing the difference in elevation between upstream and downstream thermographs into the difference in mean water temperature at those sites. Additional studies indicate that the method provided accurate predictions at reaches lacking thermographs (DJI, unpubl. data). Channel slope (%) was estimated using an Abney level following Isaak and Hubert (1999). Wetted width was measured to the nearest centimeter along transects placed perpendicular to the streamflow at 10-m intervals along the length of each reach. Depth was measured to the nearest centimeter and substrate characteristics were identified at points spaced at 25%, 50%, and 75% of the transect length. Substrate categories included fine (< 2 mm in diameter), gravel (2–64 mm), cobble (65–256 mm), and boulder (> 256 mm) substrate. Length and width were measured for all cover patches that were within 1 m of each transect. Cover was defined as overhanging cover, woody debris, or aquatic vegetation in water at least 15 cm deep. Habitat characteristics in a reach were summarized as the mean of each variable across all transects.

Reaches were placed into one of four categories based on the occurrence of Paiute Sculpin and Mottled Sculpin: (1) Paiute Sculpin in allopatry; (2) Mottled Sculpin in allopatry; (3) Paiute Sculpin and Mottled Sculpin in sympatry; or (4) neither species present. Using these categories, the distribution of each species was plotted on a map. Associations between the occurrence of each species and abiotic and biotic characteristics of the reach were analyzed using canonical discriminant analysis (CDA; Johnson, 1998). The analysis consists of grouped observations (sculpin occurrence categories) and independent variables (abiotic and biotic characteristics). The CDA derives canonical variates (i.e., linear combinations of independent variables) that have the highest possible multiple correlation with the defined groups to maximally separate the groups. Thus, we used CDA to determine the variables that best discriminated among the four categories of sculpin occurrence. To reduce the influence of redundant and correlated variables, we examined bivariate plots of all combinations of variables. Variables that showed no relationship with other variables and had correlation coefficients less than or equal to $|0.60|$ were retained in the analysis. Independent variables used in the analysis included mean summer temperature, elevation, mean wetted stream width, total cover (i.e., all cover types combined), the proportion of fine substrate, and the relative abundance of Brown Trout (i.e., number of Brown Trout on the first electrofishing pass/100 m). Mean depth and width were highly correlated (r = 0.66, P = 0.0001); thus, only mean width was included because it is a measure of channel morphology shown to influence the occurrence of coldwater fishes (Bozek and Hubert, 1992). We used the proportion of fine substrate to reflect substrate composition because it was correlated with all other substrate categories and because the amount of fine substrate is an indication of sediment deposition associated with land use. Nu-

TABLE 2. CORRELATION (r) BETWEEN CANONICAL VARIABLES (CAN1 AND CAN2) AND MEAN SUMMER TEMPERATURE (JULY AND AUGUST, C), ELEVATION (METERS ABOVE MEAN SEA LEVEL), MEAN WIDTH (m), FINE SUBSTRATE (%), TOTAL COVER (% OF TOTAL AREA), AND THE ABUNDANCE OF BROWN TROUT (NUMBER/100 m) FOR REACHES SAMPLED IN THE SALT RIVER DRAINAGE OF WYOMING AND IDAHO. Numbers in parenthesis represent P-values. Percentage of the total variation and the eigenvalues (λ) for each canonical axis are also provided.

Variable	CAN1	CAN2
Temperature	0.48 (0.0001)	0.77 (0.0001)
Elevation	−0.61 (0.0001)	−0.48 (0.0001)
Width	0.61 (0.0001)	−0.03 (0.72)
Fine substrate	0.91 (0.0001)	−0.27 (0.005)
Total cover	−0.06 (0.55)	0.09 (0.36)
Brown Trout	0.51 (0.0001)	0.24 (0.02)
Variance (%)	73.07	26.01
λ	3.13	1.12

merous sculpin species have been shown to be sensitive to interactions with nonnative fishes (e.g., Maret et al., 1997), and piscivorous Brown Trout often have a negative influence on native species (e.g., Jones, 1972). Because Brown Trout were the most common and abundant piscivorous fish in the system, relations between sculpin occurrence and Brown Trout abundance were examined.

RESULTS

Paiute Sculpin was more common than Mottled Sculpin and was found in 64% of all reaches, 38% in allopatry, and 26% in sympatry with Mottled Sculpin (Fig. 1). Mottled Sculpin was found in allopatry at only six reaches, all of which were in spring streams. The two species were found in sympatry in downstream reaches of streams, with either allopatric Paiute Sculpin or no sculpins in upstream reaches (Fig. 1). Paiute Sculpin was not sampled in any of the spring streams and was the only sculpin species sampled in eastern tributaries.

Reaches where neither sculpin species was present occurred across a wide range of temperatures and elevations, but they generally had a lower mean summer temperature and were at higher elevations than those where either species was found. Allopatric Paiute Sculpin occurred in high-elevation reaches with low temperatures. Sympatric occurrences generally occurred in reaches with high summer temperatures across a wide range of elevations.

Both species appeared to have a lower thermal boundary. Paiute Sculpin was absent from reaches with mean summer temperatures less than 6 C; whereas Mottled Sculpin was absent from reaches with summer temperatures less than 10 C. Similar thresholds were observed with regard to elevation. Paiute Sculpin was absent from reaches above 2300 m in elevation, and Mottled Sculpin was absent from reaches above 2150 m. Upper thermal and lower elevational boundaries were not observed for either species.

The first two canonical axes cumulatively explained 99% of the variation in the occurrence of the two sculpin species (Table 2). The first canonical axis explained the highest proportion of the variation and was comprised of mean width, percentage of fine substrate, abundance of Brown Trout, and elevation, whereas the second axis was comprised of mean summer water temperature. The first canonical axis discriminated reaches with allopatric Mottled Sculpin from the other categories. Reaches with allopatric Mottled Sculpin were wide and dominated by fine substrate, and they had high abundance of Brown Trout (Fig. 2). Discrimination based on the second axis indicated that reaches without either species and those with allopatric Paiute Sculpin occurred across a wide range of temperatures, but most reaches had low mean summer water temperatures. Reaches with both species had relatively high summer temperatures.

DISCUSSION

Distributions of Paiute Sculpin and Mottled Sculpin were explained by elevation, channel morphology and local habitat conditions, and thermal characteristics. Paiute Sculpin has been associated with fast-water habitats (e.g., rapids, riffles) and large rocky substrates (Jones, 1972; Johnson, 1985; Moyle and Vondracek, 1985). Paiute Sculpin occurred throughout the Salt River watershed where fast-water habitats were common in nearly all tributary streams. Mottled Sculpin can occur in a wide variety of environments (Bailey, 1952; Lee et al., 1980), but de-

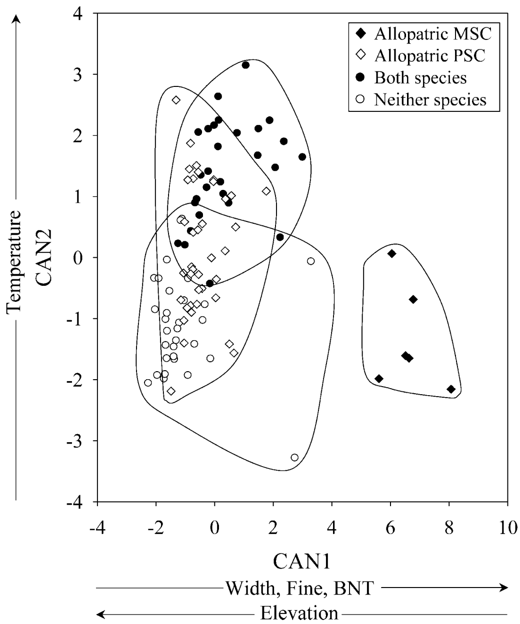

Fig. 2. Canonical discriminant analysis used to identify factors related to the occurrence of allopatric and sympatric Paiute Sculpin (PSC) and Mottled Sculpin (MSC) in the Salt River watershed of Wyoming and Idaho, 1996–1997. The first canonical axis (CAN1) was primarily comprised of mean wetted width (m), the proportion of fine substrate (%), the abundance of Brown Trout (number/100 m), and elevation (meters above mean sea level). The second canonical axis (CAN2) was primarily comprised of mean summer water temperature (July and August, C).

spite their plasticity some streams in the Salt River drainage appeared to lack suitable habitat. Mottled Sculpin was absent from all tributary streams on the east side of the drainage and high-elevation reaches in western and southern tributaries where high current velocities and large rocky substrates dominate. This suggests that Mottled Sculpin require relatively slow-water habitats for some portion of their life history.

Eastern tributaries also differed from other tributaries in the watershed in that they were affected by large dams (i.e., > 1 m high) that divert water for agricultural use. Consequently, the presence of movement barriers provides an alternative hypothesis for the absence of Mottled Sculpin in eastern tributaries. However, Mottled Sculpin never occurred in reaches with water temperatures less than 10 C. In addition to the physical habitat differences of eastern tributaries, all reaches on the east side of the basin had mean summer temperatures less than or equal to 10 C. The most plausible explanation for the absence of Mottled Sculpin from eastern tributaries is the lack of slow-water habitats and cold water temperatures.

The only area in the Salt River watershed where Paiute Sculpin was absent and Mottled Sculpin was present was in spring streams near the mainstem of the Salt River. Spring streams were wide, deep, low-gradient (i.e., < 0.01%) streams dominated by fine substrates. Spring-stream habitat consisted almost entirely of pools and runs with few riffles and little large rocky substrate. In addition, Brown Trout abundance was high in spring streams. Thus, the absence of Paiute Sculpin in spring streams may be based on a lack of fast-water habitat with large rocky substrate, high abundance of predatory Brown Trout, or a combination of these factors.

Various studies have provided a conceptual basis for explaining the occurrence of species over large spatial scales. In aquatic systems, the concepts of hierarchical faunal filters, longitudinal zonation, and species additions have been proposed (e.g., Matthews, 1998). The concept of hierarchical faunal filters suggests that a series of screens or filters serves to eliminate species from faunal pools such that the presence of a species at a location is the cumulative result of passage through an array of filters. Filters are first comprised of large-scale (i.e., spatial and temporal) characteristics (e.g., zoogeography, physiology) followed by subsequently smaller-scale features (e.g., reach-scale habitat, biotic interactions). The concept of faunal filters is relevant to the concept of longitudinal zonation and species additions in stream systems in that species have different physiological tolerances, habitat requirements, and abilities to interact with other species. In our study, Paiute Sculpin occurred throughout the watershed, whereas Mottled Sculpin occurred in the lower reaches of tributaries. Consequently, our results suggest that elevation and water temperature are important features influencing the occurrence of sculpin species in the watershed, likely because of the action of a large-scale faunal filter (e.g., physiologic tolerances). Because Paiute Sculpin occurred across nearly the entire length of tributaries, the presence of Mottled Sculpin was largely the result of a species addition. In eastern tributaries, however, water temperatures were extremely low and probably functioned more like the headwaters of tributaries in the western and southern portions of the drainage, where Mottled Sculpin were also absent. In contrast, the only patterns associated with the absence of Paiute Sculpin was in relation to spring streams. Water temperatures in spring streams were within the tolerances of Paiute Sculpin, but reach-scale habitat (i.e., a small-scale faunal filter) was apparently not suitable for Paiute Sculpin occurrence. High densities of Brown Trout in spring streams may have also acted as an additional or alternative filter that excluded Paiute Sculpin. Therefore, it appears that Paiute Sculpin have the ability to occur across the landscape (i.e., aside from spring streams and the highest of elevations), whereas Mottled Sculpin are limited by thermal constraints and are simply added to the fish assemblage in downstream reaches. Thus, sympatric occurrences are the end result of processes that occur on both large and small scales.

Although our study does not reveal the specific interactions between Paiute Sculpin and Mottled Sculpin in sympatry, others have investigated mechanisms related to the coexistence of sculpin species and identified differences in microhabitat associations (Finger, 1982; Brown, 1991). As observed by others, differential microhabitat use likely allows Mottled Sculpin and Paiute Sculpin to coexist in the Salt River drainage, with Paiute Sculpin residing in fast-water habitat and Mottled Sculpin residing in slow-water habitat. When Mottled Sculpin use fast-water habitat, they probably segregate from Paiute Sculpin in a manner similar to that observed by Finger (1982) for Paiute Sculpin and Torrent Sculpin (*Cottus rhotheus*) where the two species segregate based on current velocity and availability of interstitial spaces.

Our results identify that large-scale factors (i.e., elevation and thermal characteristics), local habitat conditions (i.e., stream width and fine substrate), and abundance of an exotic piscivore (i.e., Brown Trout) influence the occurrence of allopatric and sympatric Paiute Sculpin and Mottled Sculpin across a watershed. Additionally, these observations indicate that human activities (i.e., enhancement of sediment deposition and introduction of Brown Trout) may have affected Paiute Sculpin distributions in the watershed. Management of these affects may be important to conservation of this species across its limited distribution.

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