Fish assemblage structure and relations with environmental conditions in a Rocky Mountain watershed

Michael C. Quist, Wayne A. Hubert, and Daniel J. Isaak

Abstract: Fish and habitat were sampled from 110 reaches in the Salt River basin (Idaho and Wyoming) during 1996 and 1997 to assess patterns in fish assemblage structure across a Rocky Mountain watershed. We identified four distinct fish assemblages using cluster analysis: (1) allopatric cutthroat trout (*Oncorhynchus clarki* (Richardson, 1836)); (2) cutthroat trout – brook trout (*Salvelinus fontinalis* (Mitchell, 1814)) – Paiute sculpin (*Cottus beldingi* Eigenmann and Eigenmann, 1891); (3) cutthroat trout – brown trout (*Salmo trutta* L., 1758) – mottled sculpin (*Cottus bairdi* Girard, 1850); and (4) Cyprinidae–Catostomidae. The distribution of fish assemblages was explained by thermal characteristics, stream geomorphology, and local habitat features. Reaches with allopatric cutthroat trout and the cutthroat trout – brook trout – Paiute sculpin assemblage were located in high-elevation, high-gradient streams. The other two fish assemblages were generally located in low-elevation streams. Associations between habitat gradients, locations of reaches in the watershed, and occurrence of species were further examined using canonical correspondence analysis. The results suggest that stream geomorphology, thermal conditions, and local habitat characteristics influence fish assemblage structure across a Rocky Mountain watershed, and they provide information on the ecology of individual species that can guide conservation activities.

Résumé : Afin de déterminer les patterns dans la structure des communautés de poissons dans un bassin versant des montagnes Rocheuses, nous avons échantillonné les habitats et les poissons dans 110 sections de la rivière Salt (Idaho et Wyoming) en 1996 et 1997. Une analyse de groupement identifie quatre associations : (1) la truite fardée (*Oncorhynchus clarki* (Richardson, 1836)) allopatrique; (2) la truite fardée – l'omble de fontaine (*Salvelinus fontinalis* (Mitchell, 1814)) – le chabot paiute (*Cottus beldingi* Eigenmann et Eigenmann, 1891); (3) la truite fardée – la truite brune (*Salmo trutta* L., 1758) – le chabot tacheté (*Cottus bairdi* Girard, 1850) et (4) les cyprinidés – les catostomidés. La répartition des communautés de poissons s'explique par les caractéristiques thermiques, la géomorphologie des cours d'eau et les particularités locales de l'habitat. Les sections contenant l'association de la truite fardée allopatrique et celle de la truite fardée – omble de fontaine – chabot paiute se situent dans des cours d'eau de haute altitude à forte pente. Les deux autres associations se retrouvent généralement dans des cours d'eau de basse altitude. Une analyse des correspondances canoniques a permis d'explorer les relations entre les gradients de l'habitat, la position des sections dans le bassin versant et la présence des espèces. Les résultats indiquent que la géomorphologie du cours d'eau, les conditions thermiques et les particularités locales de l'habitat influencent la structure des associations de poissons dans ce bassin versant des Rocheuses et ils fournissent des renseignements sur l'écologie des espèces individuelles qui peuvent servir à orienter les efforts de conservation.

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Introduction

Community ecology has been defined as the study of the organization of ecological communities, including the number, identity, abundance, and ecological attributes of member species, the relationships among these species, and how the organization of species varies over space and through time (Gee and Giller 1987). Within this framework, the primary goals of community ecology are to identify patterns within and among communities and to determine mechanisms that affect patterns in community structure on the landscape (Strong et al. 1984). While these goals appear simple, the complexity of ecological communities and inherent variability among systems hinders the ability to make broad generalizations and commonly results in considerable controversy (Schoener 1987). Despite these difficulties, contributions of community ecologists have enhanced basic ecological concepts and provided practical knowledge for conservation ac-

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tivities. Research on ecological communities spans the range of ecosystems; however, a large portion of current knowledge comes from studies in aquatic systems (e.g., Matthews 1998; Marsh-Matthews and Matthews 2000; Jackson et al. 2001).

One of the primary goals of community ecology is to describe the organization of assemblages. Although descriptive studies of fish assemblage structure are insightful and valuable, determining the mechanisms responsible for differences in assemblage structure and understanding how assemblages vary across a landscape can contribute to basic ecological principles with application for conservation (Smith and Powell 1971; Lohr and Fausch 1997; Maret et al. 1997; Scott and Hall 1997). Consequently, describing assemblage structure and factors influencing the organization of assemblages has been an active research focus in fish ecology. For example, Tonn and Magnuson (1982) examined fish assemblage structure in small lakes of northern Wisconsin and found that assemblages were organized in discrete assemblage types. They also showed that the spatial distribution of fish assemblage types was due to winter oxygen concentrations, which interacted with the availability of refugia from detrimental physical environmental conditions and large piscivores. On a larger scale, Pflieger et al. (1982) investigated the compositions of fish assemblages across the state of Missouri and determined that they could be categorized into four large assemblage types based largely on historical constraints (e.g., zoogeography, geology) and stream geomorphology (e.g., stream size). Other studies have been conducted to elucidate factors associated with fish assemblage structure in natural lakes (Tonn and Magnuson 1982; Robinson and Tonn 1989), large rivers (Pegg and Pierce 2002; Stewart et al. 2002), and reservoirs (Gido et al. 2002), but most research has been conducted in small stream systems in eastern North America (e.g., Schlosser 1982; Hansen and Ramm 1994; Matthews and Robinson 1998).

Lotic systems in the Rocky Mountain region of North America differ from those to the east with regard to environmental conditions and fish assemblage complexity. Elevational gradients and thermal characteristics are especially important longitudinal components of stream systems in the West. Consequently, these gradients have been shown to have a substantial influence on the occurrence of both coldwater and warmwater species (e.g., Bozek and Hubert 1992; Quist et al. 2004). Western streams differ from many other systems in that fish assemblages are comparably depauperate and lack the complexity of assemblages found to the east (Lee et al. 1980). Most knowledge on the organization of fish assemblages has emerged from research conducted in eastern North America (e.g., Hawkes et al. 1986; Hansen and Ramm 1994; Matthews and Robinson 1998). In contrast, a paucity of information exists regarding the ecology of fish assemblages in western North America, particularly in the central Rocky Mountains.

The Salt River valley in the central Rocky Mountains on the border between the states of Idaho and Wyoming represents a unique system with regard to stream geomorphology and instream habitat (Isaak 2001). Elevations in the basin vary from 1700 m to over 3300 m and differences in topography, geology, and orographic events have resulted in diverse stream habitats across the basin. The eastern boundary of the watershed is formed by the rugged Salt River Range with elevations exceeding 3300 m and constrained valley forms. Consequently, these streams generally have high channel slopes and current velocities, large substrates, and low water temperatures (Isaak and Hubert 2001). The Caribou Range, Webster Range, and Gannett Hills form the western and southern boundaries of the basin, where the topography is less rugged, elevations do not exceed 2800 m, and valleys are unconstrained. Western and southern tributaries reflect these characteristics and generally have lower channel slopes, smaller substrate particle sizes, and warmer summer water temperatures than streams on the east side of the basin.

The Salt River originates in the Salt River Range, bisects the valley, and is a major tributary to the Snake River. Numerous spring streams emerge from the alluvium adjacent to the Salt River and flow a short distance before joining the river. The magnitude of anthropogenic disturbances varies within and among streams. Downstream segments of mountain tributaries are privately owned and the dominant land use is agriculture. Although small water-diversion structures (i.e., for irrigation withdrawals) have been built throughout the valley, large structures (>1 m high) occur on the eastern tributaries, resulting in seasonal intermittence or dewatering of the lower portions of those tributaries. The headwaters of mountain tributaries are publicly owned and the dominant anthropogenic disturbance is livestock grazing. Thus, streams in the Salt River basin are highly variable with regard to stream geomorphology, thermal characteristics, instream habitat, and anthropogenic disturbances. Consequently, the Salt River basin provides an excellent system in which to investigate the role of varying environmental characteristics in fish assemblage structure.

The fish assemblage of the Salt River basin contains 11 native and 3 nonnative species. The native species are mountain whitefish (*Prosopium williamsoni* (Girard, 1856)), Utah sucker (*Catostomus ardens* Jordan and Gilbert, 1881), mountain sucker (*Catostomus platyrhynchus* (Cope, 1874)), longnose dace (*Rhinichthys cataractae* (Valenciennes, 1842)), speckled dace (*Rhinichthys osculus* (Girard, 1856)), Utah chub (*Gila atraria* (Girard, 1856)), leatherside chub (*Sniderichthys copei* (Jordan and Gilbert, 1881)), redside shiner (*Richardsonius balteatus* (Richardson, 1836)), mottled sculpin (*Cottus bairdi* Girard, 1850), Paiute sculpin (*Cottus beldingi* Eigenmann and Eigenmann, 1891), and cutthroat trout (*Oncorhynchus clarki* (Richardson, 1836)) (Baxter and Stone 1995). The naturalized nonnative species are rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), brook trout (*Salvelinus fontinalis* (Mitchell, 1814)), and brown trout (*Salmo trutta* L., 1758). Declining species of immediate conservation concern include leatherside chub and cutthroat trout. Although the ecology of nonnative salmonids is well understood (Behnke 2002), little is known about the ecology of the native fishes in the basin and even less is known about species associations and the structure of fish assemblages.

Our objective was to describe fish assemblages and identify factors related to their composition in the Salt River watershed. Specifically, we sought to identify whether fish assemblage structure varied among different regions of the watershed (e.g., eastern versus western tributaries) and to determine how patterns in fish assemblage structure and the occurrence of species were related to abiotic habitat features. Our findings enhance knowledge of the ecology of individual species and provide insight into mechanisms structuring fish assemblages in Rocky Mountain stream systems. Such information not only contributes to knowledge of the ecological processes structuring aquatic communities, but also helps direct conservation and management activities.

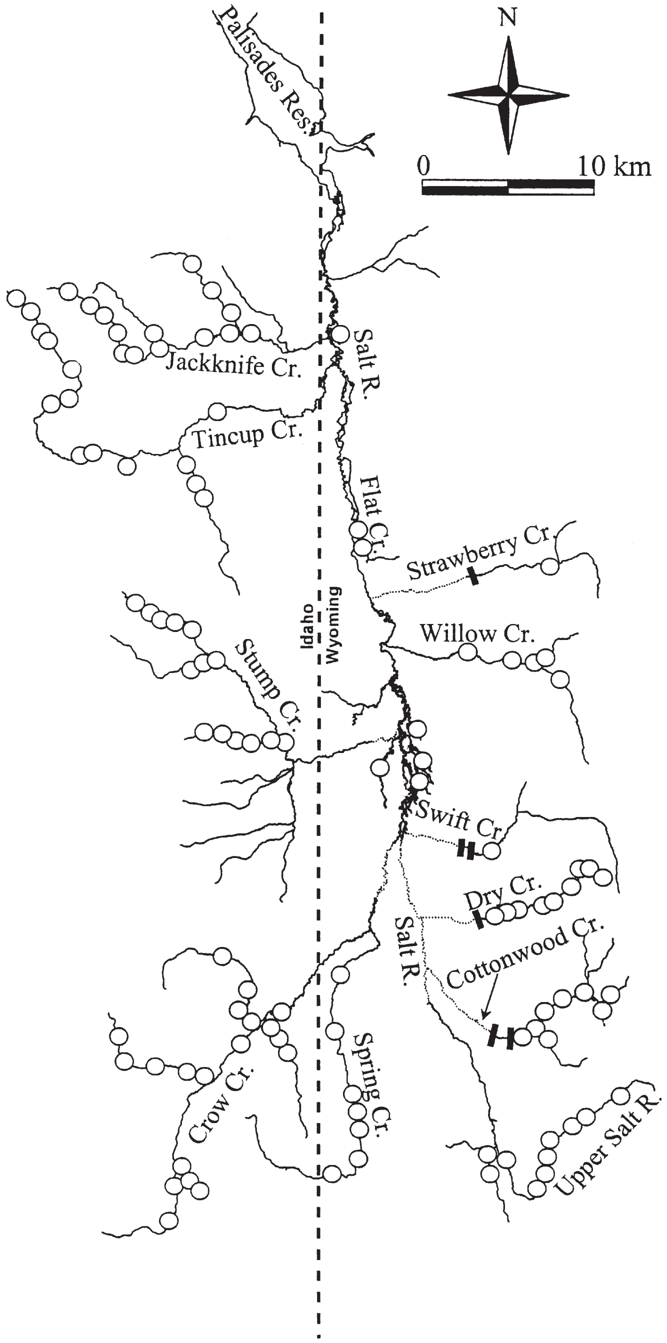
Materials and methods

Fish and habitat sampling

Fish assemblages were sampled from 110 reaches throughout the Salt River watershed during 1996 and 1997 (Fig. 1). Sampling began in July after spring runoff and continued until mid-September of each year. A backpack electrofishing unit (Model 15-C, Smith-Root, Vancouver, Washington) was used to sample fishes from stream reaches that averaged 194.2 m in length (SE = 8.9 m). Multiple electrofishing passes (i.e., at least three passes) were conducted at 76% of the reaches, and one pass was conducted at each of the remaining reaches. All fish were identified to the species level in the field, and species were noted as either present or absent in reaches. A detailed description of the fish sampling methodology is provided by Isaak (2001).

A variety of habitat characteristics were measured to represent stream geomorphology, water-quality characteristics, and instream cover (Table 1). Elevation (metres above mean sea level) of the study reaches was determined from US Geological Survey topographic maps (1 : 24 000). Water temperatures (°C) were recorded every 30 min using digital thermographs (model WTA32, Onset Computer Corporation, Pocasset, Massachusetts) deployed at opposite extremities of each study stream. Stream temperatures were summarized by calculating the mean temperature for July and August in 26 reaches that contained thermographs. Mean temperatures for reaches without thermographs were interpolated based on stream-specific rates of water temperature change calculated by dividing the difference in mean water temperature between upstream and downstream thermographs by the difference in elevation at those sites. Although the interpolation of some stream temperatures may have added variation to the data set, independent analyses indicate that the method provided accurate predictions of water temperature at reaches lacking thermographs. Channel slope (%) was estimated using an Abney level, following methods in Isaak and Hubert (1999). Wetted width was measured to the nearest centimetre along transects perpendicular to the streamflow. Transects were spaced at 10-m intervals along the length of the reach. Depth was measured to the nearest centimetre and substrate characteristics were identified at points spaced at 25%, 50%, and 75% of the transect length. Substrate categories were modified from Platts et al. (1983) and included fine (<2 mm diameter), gravel (2–64 mm), cobble (65–256 mm), and boulder (>256 mm) substrates. Wetted width, depth, and substrate composition were indexed as the mean of each variable across all transects. Length and width were measured for all cover patches within 1 m of each transect. Cover was defined as woody debris and aquatic vegetation in water at least 15 cm deep. Similarly, deep-pool habitat was considered pools with depths greater than 45 cm. The amount of aquatic vegetation and woody debris was estimated as the proportion of the sampled surface area of the reach with cover, and the amount of deep-pool habitat was estimated as the proportion of the sampled surface area of the reach comprising deep-pool habitat.

Fig. 1. Map showing the locations of reaches (N = 110) sampled in the Salt River watershed of Wyoming and Idaho, 1996–1997. Open symbols represent sampled reaches and dark bars represent large (> 1 m high), permanent water-diversion structures. Stream segments represented as dotted lines are segments where reaches are seasonally intermittent or dewatered.



Data analysis

We used a variety of multivariate statistical techniques to

Table 1. Habitat characteristics of reaches (N = 110) sampled in the Salt River drainage of Wyoming and Idaho, 1996–1997.

Characteristic	Mean	Standard error	Minimum	Maximum
Stream geomorphology				
Elevation (metres above mean sea level)	2060.9	14.6	1736.2	2500.9
Channel slope (%)	2.4	0.2	0.1	10
Wetted width (m)	4.6	0.2	1.3	14.8
Depth (cm)	20.4	1.1	7.3	71.4
Proportion of reach with deep-pool habitat (%)	9.4	1.5	0	73.6
Water quality				
Alkalinity (mg/L)	191.7	4.6	88.4	285.6
Summer (Jul.–Aug.) water temperature (°C)	10.9	0.3	5.2	17.9
Instream cover				
Boulder substrate (%)	6	0.8	0	36
Cobble substrate (%)	48.8	2.7	0	98
Gravel substrate (%)	34.8	2.2	0	89
Fine substrate (%)	10.6	1.7	0	87
Aquatic vegetation (%)	0.8	0.1	0	7
Woody debris (%)	0.1	0.1	0	2
Total cover (%)	1.8	1.7	0	8.6

assess patterns in fish assemblage structure and relations of fish assemblages with environmental features in the watershed. Because reaches within the same stream were highly variable with regard to stream geomorphology, instream habitat, and fish assemblage structure, and because one of the primary objectives of the study was to evaluate patterns of fish assemblage structure among reaches, reaches were treated as the experimental unit in the analyses. Similarities in fish assemblages among reaches were evaluated using Jaccard's index of assemblage similarity (Jongman et al. 1995). The matrix of similarity indices was then clustered using the unweighted pair-group method (Jongman et al. 1995) to produce a dendrogram depicting clusters of reaches with similar fish assemblages. Examination of the cluster dendrogram was the primary method for identifying fish assemblage types. Jaccard index values near 0.60 are generally considered to be biologically significant (Gauch 1982; Matthews 1998), and this criterion was an additional consideration when delineating fish assemblage types. Similar approaches have been used to describe the organization of fish assemblages (e.g., Cairns and Kaesler 1971; Maret et al. 1997; Matthews and Robinson 1998). The location of each assemblage type was plotted on a map to illustrate large-scale patterns in the distribution of individual species and fish assemblages across the watershed. Calculation of similarity indices and cluster analysis were conducted using NTSYSpc version 2.1 (Exeter Software, Setauket, New York).

Relations between the organization of fish assemblages and environmental features were examined using multivariate analysis of variance (MANOVA; Johnson 1998). The MANOVA allowed for testing of differences among assemblage types without incurring excessive likelihood of type I error. When a difference was detected with MANOVA, one-way analysis of variance (ANOVA) and pairwise comparisons of least squares means (Milliken and Johnson 1992) were conducted. Multivariate analysis of variance, ANOVA, and pairwise comparisons were conducted using SAS (SAS Institute Inc. 1996), and $\alpha = 0.05$.

Canonical correspondence analysis (CCA) was used to examine relationships between habitat characteristics, fish assemblage types, and the location of sampled reaches in the watershed using the program CANOCO version 4.5 (ter Braak and Smilauer 2002). Canonical correspondence analysis is a direct gradient analysis technique, meaning that the ordination axes are linear combinations of environmental variables. Ordination axes are determined using reciprocal averaging (i.e., an eigen analysis) and linear least-squares regression. The CCA plots samples (i.e., reaches) and species in an ordination diagram with environmental variables depicted as vectors. The location of a sample in the ordination diagram is based on the species that constitute the sample. Thus, samples with the most similar fish assemblages are located closest to each other in the diagram, and the likelihood of species occurrence decreases with distance from individual samples in the diagram. The location of a species in the diagram is determined by assuming that species exhibit a Gaussian-type response to environmental gradients, where species occur across a range of values for each environmental variable and have their peak occurrence at some optimum value within the range of environmental conditions. The directions and lengths of environmental vectors indicate the magnitude and influence of environmental variables on the fish assemblage. Prior to analysis, species that occurred at fewer than five reaches (i.e., leatherside chub and rainbow trout) were considered passive in the analysis so that they did not influence the ordination (Jongman et al. 1995; ter Braak and Smilauer 2002).

The CANOCO program provides several diagnostic tools when conducting the CCA (ter Braak and Smilauer 2002). One diagnostic is the use of variation inflation factors. Inflation factors suggest the degree to which a variable independently contributes to explaining variation in the species data. Inflation factors greater than 20 indicate that a variable is highly correlated with other variables in the analysis and does not contribute unique information in the regression. Environmental variables remaining after consideration of inflation factors and those with Pearson's correlation coefficients less than |0.60| were subjected to a forward-selection procedure. A Monte Carlo permutation test with 499 permutations computed the significance of each variable as it was added to the analysis. Only variables with $P < 0.05$ were retained in the analysis. In addition, canonical coefficients, which are analogous to regression coefficients, were examined to illustrate the composition (i.e., environmental characteristics) of the canonical axes (ter Braak and Smilauer 2002).

Results

The three nonnative salmonids and all native species except Utah chub were sampled in the watershed. The most common species was cutthroat trout (frequency of occurrence in reaches = 76%), followed by two native species, Paiute sculpin (63%) and mottled sculpin (32%), and two nonnative species, brown trout (25%) and brook trout (24%). Mountain sucker (20%), longnose dace (15%), and speckled dace (13%) were also relatively common, while the remaining species occurred in less than 10% of the reaches. Rainbow trout and leatherside chub were each collected from only three reaches.

Species richness varied from 0 to 10 species among reaches. Jaccard index values varied from 0.07 to 1.0, indicating that some reaches had almost no species in common while other reaches were identical (Fig. 2). Based on the cluster analysis, we identified four distinct fish assemblages and one group of reaches that had little in common with the other reaches. Reaches within major clusters (i.e., with the same assemblage type) had similarity index values of 0.60 or more. One assemblage was relatively diverse, consisting primarily of cutthroat trout, brown trout, and mottled sculpin (Fig. 1, Table 2; hereafter the CUT–BNT–MSC assemblage). Paiute sculpin had a high frequency of occurrence in the CUT–BNT–MSC assemblage (Table 2) but was most common in the second assemblage. The second assemblage was dominated by cutthroat trout, brook trout, and Paiute sculpin (CUT–BKT–PSC assemblage), and a third assemblage comprised allopatric cutthroat trout. Similar to the CUT–BNT–MSC assemblage, a fourth assemblage was relatively diverse but was dominated by cyprinids and catostomids. The cyprinid–catostomid assemblage was the only assemblage that included leatherside chub. The last group exhibited no clear trends in assemblage organization and included a mixture of salmonids, Utah sucker, and cottids (Fig. 2).

Using these broad categories of fish assemblage structure, several patterns emerged relative to the locations of reaches in the watershed. Reaches in nearly all of the eastern tributaries were classified as having the CUT–BKT–PSC assemblage or the allopatric cutthroat trout assemblage (Figs. 2 and 3). Spring streams had relatively diverse fish assemblages, and most reaches were categorized as having the CUT–BNT–MSC assemblage. Reaches in the Salt River generally had either the CUT–BKT–PSC assemblage or the allopatric cutthroat trout assemblage. Western streams were more variable with regard to fish assemblage structure and had reaches with each of the four assemblage types.

Examination of the spatial distribution of each assemblage type corroborated patterns observed in the cluster dendrogram and illustrated longitudinal patterns in fish assemblage structure (Fig. 3). For instance, allopatric cutthroat trout were in the uppermost reaches of all tributaries. The two most diverse assemblage types (i.e., CUT–BNT–MSC and cyprinid–catostomid assemblages) were in the downstream reaches of mountain tributaries or in spring streams.

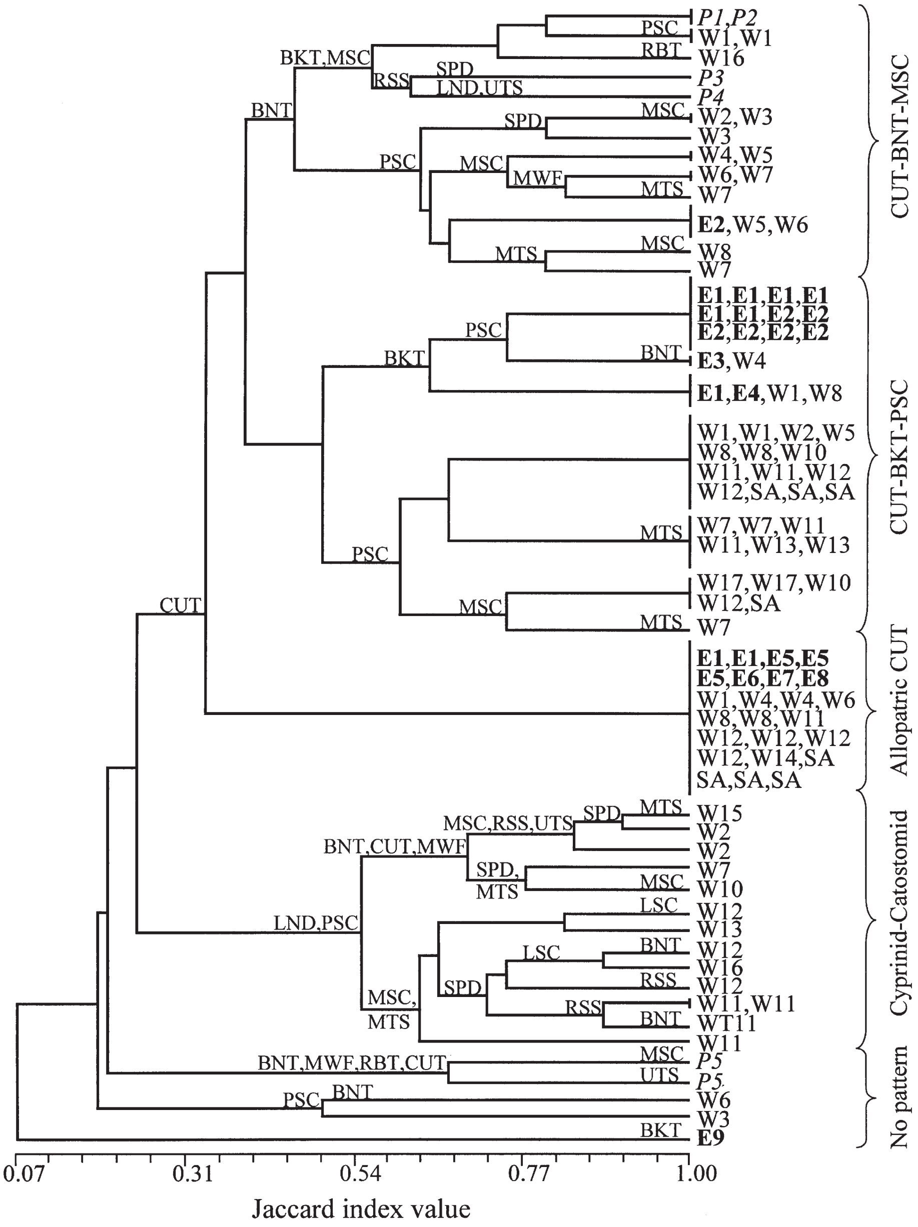
Multivariate analysis of variance indicated that habitat characteristics differed among the four assemblage types ($F_{[42,236]} = 4.53$, $P = 0.0001$). Reaches with no discernible assemblage structure were excluded from the analysis. Therefore, one-way ANOVA was conducted for each variable (Table 3) to clarify differences in habitat associations among assemblages. Reaches characterized by the allopatric cutthroat trout or CUT–BKT–PSC assemblages were at high elevations and had high channel slopes, shallow depths, few deep pools, low alkalinity, low mean summer water temperatures, and large substrates (Table 3). Reaches with the CUT–BNT–MSC assemblage or the cyprinid–catostomid assemblage were in low-elevation stream segments with low channel slopes and abundant deep-pool habitat. However, reaches with the cyprinid–catostomid assemblage typically had warmer summer water temperatures and larger substrates than reaches with the CUT–BNT–MSC assemblage. Mean wetted widths and the proportions of aquatic vegetation and woody debris did not differ significantly among assemblage types.

Several environmental variables were correlated to other variables, as indicated by Pearson's correlation coefficients (r) ≥|0.60| and variance inflation factors >20. All measures of substrate composition were related to the proportion of cobble substrate, and the proportion of fine substrate was also related to the amount of deep-pool habitat. Similarly, measures of stream width, depth, and channel slope were related to deep-pool habitat. Thus, they were removed from the CCA. Aquatic vegetation and woody debris were redundant with total cover, so they were removed from the analysis. Consequently, the environmental variables used in the CCA were elevation, summer water temperature, deep-pool habitat, cobble substrate, alkalinity, and total cover.

The first two canonical axes explained over 85% of the total variance in the occurrence of species and associated habitat variables (Fig. 4). The environmental habitat vectors on the CCA ordination diagram represent the relationships between reaches, species, and habitat variables (e.g., Fig. 4A). The perpendicular projection of a species score to an environmental vector represents the center of that species distribution along the vector. Although the vectors are drawn in only one direction, they also extend in the opposite direction, which indicates low values of the habitat variables. Elevation, temperature, deep-pool habitat, and cobble substrate were identified as significant ($P < 0.002$ for all variables) in the ordination of the species data, as was the final model that included all four variables ($P = 0.012$).

The first canonical axis was highly correlated with elevation (canonical coefficient, $r^* = 0.83$) and cobble substrate ($r^* = 0.61$), while the second axis was highly correlated with summer water temperature ($r^* = -0.66$) and the amount of deep-pool habitat ($r^* = 0.95$). Based on this outcome, cutthroat trout, brook trout, and Paiute sculpin generally oc-

Fig. 2. Dendrogram depicting fish assemblage similarity among reaches sampled in the Salt River watershed of Idaho and Wyoming, 1996–1997. Reach labels indicate whether the reach was located on the east (E, in bold to illustrate patterns) or west (W) side of the basin or whether the reach was located in the upper Salt River (SA) or in spring streams (P, in italics to illustrate patterns). Reaches with the same letter and number are from the same stream. Species are provided to illustrate the composition of the assemblage in each reach. Where species are located at a branch, all subsequent reaches contain the species. Species are as follows: MWF, mountain whitefish (*Prosopium williamsoni*); UTS, Utah sucker (*Catostomus ardens*); MTS, mountain sucker (*Catostomus platyrhynchus*); LND, longnose dace (*Rhinichthys cataractae*); SPD, speckled dace (*Rhinichthys osculus*); LSC, leatherside chub (*Sniderichthys copei*); RSS, redside shiner (*Richardsonius balteatus*); MSC, mottled sculpin (*Cottus bairdi*); PSC, Paiute sculpin (*Cottus beldingi*); CUT, cutthroat trout (*Oncorhynchus clarki*); RBT, rainbow trout (*Oncorhynchus mykiss*); BKT, brook trout (*Salvelinus fontinalis*); and BNT, brown trout (*Salmo trutta*).



curred in high-elevation streams compared with other species in the basin (Fig. 4A), but their occurrence varied relative to other habitat characteristics (e.g., deep-pool habitat, temperature). Several species (e.g., rainbow trout, Utah sucker, redside shiner, mountain whitefish, brook trout, brown trout, and mottled sculpin) were most common in streams with a high proportion of deep-pool habitat, while other species (e.g., mountain sucker, Paiute sculpin, and cutthroat trout) occurred in reaches with little deep-pool habitat. Cyprinids and catostomids were most frequently found in reaches with high summer water temperatures, whereas brook trout were found in reaches with the lowest summer temperatures.

Sample scores provide additional insight regarding the dynamics of fish assemblage structure in the watershed (Fig. 4B). Reaches on the east side of the drainage and the

Table 2. Frequency of reaches (%) in which each species was sampled for each fish assemblage type (1, cutthroat trout – brown trout – mottled sculpin; 2, cutthroat trout – brook trout – Paiute sculpin; 3, allopatric cutthroat trout; 4 Cyprinidae–Catostomidae; 5, no distinct fish assemblage pattern observed) in the Salt River watershed of Idaho and Wyoming, 1996–1997.

	Fish assemblage				
Species	1	2	3	4	5
Salmonidae					
Cutthroat trout (*Oncorhynchus clarki*)	100 (20)	100 (44)	100 (24)	35.7 (5)	40.0 (2)
Rainbow trout (*Oncorhynchus mykiss*)	5.0 (1)	0	0	0	40.0 (2)
Mountain whitefish (*Prosopium williamsoni*)	15.0 (3)	0	0	35.7 (5)	40.0 (2)
Brown trout (*Salmo trutta*)	100 (20)	4.5 (2)	0	14.3 (2)	60.0 (3)
Brook trout (*Salvelinus fontinalis*)	35.0 (7)	40.9 (18)	0	0	20.0 (1)
Cyprinidae					
Leatherside chub (*Sniderichthys copei*)	0	0	0	21.4 (3)	0
Longnose dace (*Rhinichthys cataractae*)	10.0 (2)	0	0	100 (14)	0
Speckled dace (*Rhinichthys osculus*)	20.0 (4)	0	0	71.4 (10)	0
Redside shiner (*Richardsonius balteatus*)	10.0 (2)	0	0	42.8 (6)	0
Catostomidae					
Utah sucker (*Catostomus ardens*)	5.0 (1)	0	0	21.4 (3)	20.0 (1)
Mountain sucker (*Catostomus platyrhynchus*)	15.0 (3)	15.9 (7)	0	85.7 (12)	0
Cottidae					
Mottled sculpin (*Cottus bairdi*)	80.0 (16)	13.6 (6)	0	85.7 (12)	20.0 (1)
Paiute sculpin (*Cottus beldingi*)	70.0 (15)	86.3 (38)	0	100 (14)	40.0 (2)

Note: Number in parentheses is the number of reaches where a species was sampled.

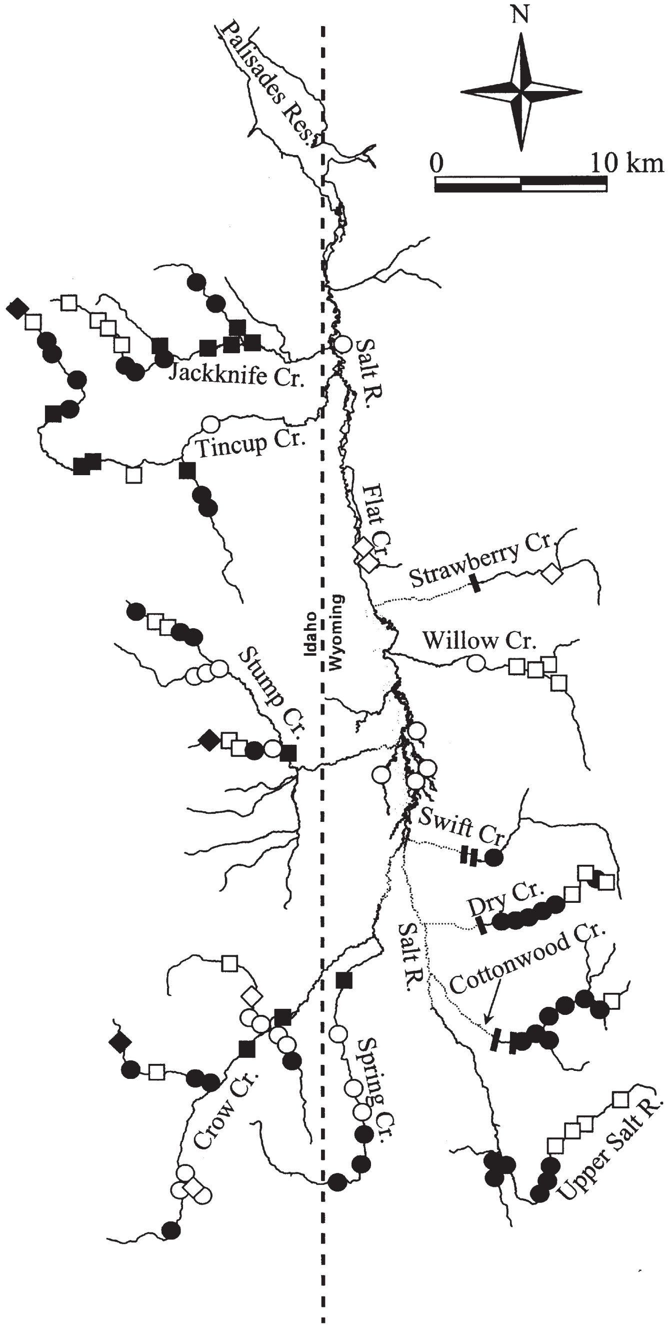
upper Salt River varied in elevation, channel morphology, and substrate composition, but nearly all of the reaches had low mean summer water temperatures. Reaches on the western side of the drainage were highly variable with regard to habitat characteristics. For instance, some high-elevation reaches had low water temperatures and large substrates, and other high-elevation reaches had warmer water temperatures and little large substrate. Spring streams were exclusively at low elevations and had intermediate summer water temperatures, low proportions of cobble substrate, and an abundance of deep-pool habitat. Fish assemblages reflected these environmental gradients and supported the results from the cluster and MANOVA and ANOVA analyses. Fish assemblages in streams on the eastern side of the drainage and the upper Salt River consisted of cutthroat trout, brook trout, and Paiute sculpin (Fig. 4C), corresponding to the CUT–BKT–PSC and allopatric cutthroat trout assemblages identified using the cluster analysis (Figs. 2 and 3). Similarly, reaches characterized by the cyprinid–catostomid assemblage were found exclusively on the western side of the drainage.

Discussion

Four distinct fish assemblages were identified in the Salt River watershed, each representing unique species associations, habitat characteristics, and spatial distributions. Reaches with the allopatric cutthroat trout or CUT–BKT–PSC assemblages were generally in high-elevation stream segments with high channel slopes, low alkalinity (e.g., a measure of biological productivity; Allan 1995), shallow depths, little deep-pool habitat, and low mean summer water temperatures. Cutthroat trout occurred throughout the watershed, illustrating their relatively high ecological plasticity. However, allopatric cutthroat trout were found only in reaches at the highest elevations. Bozek and Hubert (1992) observed that allopatric cutthroat trout were in small, high-gradient, high-elevation streams in Wyoming. Similar results have been reported throughout the Rocky Mountain region (e.g., Kruse et al. 1997; Shepard et al. 1997; Harig et al. 2000), an observation that is guiding cutthroat trout conservation activities (Kruse et al. 2001; Novinger and Rahel 2003). In our study, the CUT–BKT–PSC assemblage was also in high-elevation streams, but the more detailed CCA indicated that although brook trout were common in high-elevation reaches, they were more common than either cutthroat trout or Paiute sculpin in reaches with more deep-pool habitat and lower water temperatures. Many of these reaches were associated with beaver (*Castor canadensis* Kuhl, 1820) ponds, which have been shown to provide excellent habitat for brook trout (Kozel and Hubert 1989; Behnke 2002). Paiute sculpin were also common in the watershed and occurred in a variety of habitats. However, they were most common in high-elevation streams with large substrates and little deep-pool habitat. These observations are consistent with previous studies that have shown an affinity of Paiute sculpin for fast-water habitats, particularly riffles with large substrates (Jones 1972; Johnson 1985; Moyle and Vondracek 1985). Nearly all of the remaining species and assemblages occurred in low-elevation reaches, but their occurrence varied with regard to the other habitat gradients.

Two distinct fish assemblages in the Salt River basin, the CUT–BNT–MSC and cyprinid–catostomid assemblages, were relatively diverse and often contained up to 10 different species. These assemblages were in low-elevation, low-gradient reaches that had warmer water temperatures and higher proportions of deep-pool habitat than reaches with

Fig. 3. Map showing the locations of different fish assemblages in the Salt River watershed of Wyoming and Idaho, 1996–1997. Note that the symbols represent different assemblage types, not necessarily the locations of individual species. ○, cutthroat trout – brown trout – mottled sculpin; ●, cutthroat trout – brook trout – Paiute sculpin; □, allopatric cutthroat trout; ■, Cyprinidae–Catostomidae; ◇, no pattern; ◆, no fish.



allopatric cutthroat trout or the CUT–BKT–PSC assemblage. Although the CUT–BNT–MSC and cyprinid–catostomid assemblages generally occurred in the same types of habitat (i.e., low-elevation, low-gradient streams), several differences were apparent. The CUT–BNT–MSC assemblage was found in reaches with the highest mean depths, proportions of deep-pool habitat, and proportions of fine substrate. Many of these reaches were in spring streams and the lower segments of western tributaries. Pool habitat has been shown to be an important factor influencing the abundance of brown trout (Larscheid and Hubert 1992; Behnke 2002) and mottled sculpin (Brown and Downhower 1982), both of which were common in spring streams. These patterns were further illustrated by the CCA, where both mottled sculpin and brown trout were most common in reaches with abundant deep-pool habitat.

Similar to reaches with the CUT–BNT–MSC assemblage, reaches with the cyprinid–catostomid assemblage occurred in low-elevation, low-gradient streams. However, reaches with the cyprinid–catostomid assemblage had the highest mean summer water temperatures and little deep-pool habitat, and were dominated by rocky substrate. Even though this trend was observed for the assemblage as a whole, high variation in habitat associations among species within the assemblage was apparent. For instance, speckled dace, longnose dace, and mountain sucker were common in reaches with the highest summer water temperatures, whereas Utah sucker, redside shiner, and mountain whitefish were common in reaches with lower water temperatures. Longnose dace, speckled dace, and mountain sucker were also more common than other species in reaches with little deep-pool habitat, likely reflecting their affinity for riffle and run habitats (Hauser 1969; Johnson 1985; Hubert and Rahel 1989). Interestingly, the cyprinid–catostomid assemblage was the only assemblage that contained leatherside chub. Leatherside chub is a species of concern in the Rocky Mountain region and little is known about its ecology (Wilson and Belk 2001). However, our results suggest that it typically occurs in low-elevation streams with high summer water temperatures, little deep-pool habitat, and high proportions of large, rocky substrate.

One of the prominent concepts in stream ecology is that longitudinal gradients in habitat characteristics structure the composition of fish assemblages (Sheldon 1968; Schlosser 1982; Hughes and Gammon 1987). Longitudinal changes in fish assemblage structure are thought to arise through two different processes, species addition or biotic zonation. Species addition is the continual addition of species to downstream reaches (Sheldon 1968; Williams et al. 1996; Jackson et al. 2001), whereas biotic zonation results from the segregation of ecologically similar species into discrete faunal zones (e.g., cold-water versus warmwater zones) in response to abrupt changes in stream geomorphology or thermal characteristics (Huet 1959; Matthews 1998). Rahel and Hubert (1991) studied fish assemblage structure in a stream that spanned the Rocky Mountain – Great Plains interface in southeastern Wyoming and found two distinct faunal zones. Montane headwater reaches were characterized by a cold-water faunal zone comprising introduced salmonids, and downstream reaches were characterized by a warmwater zone dominated by cyprinids and catostomids native to the Great Plains. Within the warmwater faunal zone, increased species richness with downstream progression was due to within-zone addition of species. Thus, in isolation, neither biotic zonation nor species addition could explain the organization of fish assemblages. Similar results were reported by Hughes and Gammon (1987), who found different biotic zones (cold-water versus warmwater) in the Willamette River system in Oregon. These authors described distinct

Table 3. Habitat characteristics of reaches sampled in the Salt River drainage of Wyoming and Idaho, 1996–1997, by fish assemblage type (1, cutthroat trout – brown trout – mottled sculpin; 2, cutthroat trout – brook trout – Paiute sculpin; 3, allopatric cutthroat trout; and 4, Cyprinidae–Catostomidae).

		Fish assemblage			
Variable	Statistics	1	2	3	4
Stream geomorphology					
Elevation (metres above mean sea level)	$F_{[3,98]} = 23.8$, $P = 0.0001$	1956.7 (105.3)a	2098.5 (108.4)b	2173.7 (150.9)c	1896.5 (79.3)a
Channel slope (%)	$F_{[3,98]} = 20.9$, $P = 0.0001$	1.1 (0.9)a	2.5 (1.4)b	3.9 (1.5)c	1.2 (0.9)a
Wetted width (m)	$F_{[3,97]} = 2.6$, $P = 0.06$	4.9 (2.3)	4.5 (1.5)	3.9 (1.5)	5.5 (1.6)
Depth (cm)	$F_{[3,97]} = 11.9$, $P = 0.0001$	29.7 (18.1)a	17.7 (5.0)c	14.4 (4.1)c	22.9 (6.5)b
Proportion of reach with deep-pool habitat (%)	$F_{[3,92]} = 10.6$, $P = 0.0001$	22.3 (25.5)a	5.5 (5.5)b	2.4 (4.8)b	14.3 (11.1)a
Water quality					
Alkalinity (mg/L)	$F_{[3,98]} = 12.4$, $P = 0.0001$	224.1 (25.1)a	181.3 (48.9)b	164.3 (35.3)b	224.6 (28.9)a
Summer (Jul.–Aug.) water temperature (°C)	$F_{[3,97]} = 34.8$, $P = 0.0001$	12.9 (1.7)d	10.3 (2.9)a	8.0 (1.9)b	15.1 (0.9)c
Instream cover					
Boulder substrate (%)	$F_{[3,97]} = 2.0$, $P = 0.12$	2.4 (5.6)	7.0 (9.4)	7.9 (7.3)	5.0 (9.3)
Cobble substrate (%)	$F_{[3,97]} = 7.8$, $P = 0.0001$	25.6 (27.6)a	57.1 (25.6)b	56.7 (20.1)b	49.7 (29.9)b
Gravel substrate (%)	$F_{[3,97]} = 2.8$, $P = 0.04$	47.3 (25.9)a	29.5 (23.7)b	31.6 (20.1)b	31.9 (24.6)ab
Fine substrate (%)	$F_{[3,97]} = 8.3$, $P = 0.0001$	24.8 (28.9)a	6.3 (11.6)b	3.6 (4.1)b	13.3 (11.2)b
Aquatic vegetation (%)	$F_{[3,93]} = 0.2$, $P = 0.87$	1.0 (1.6)	0.8 (1.1)	0.9 (1.3)	0.7 (0.8)
Woody debris (%)	$F_{[3,93]} = 0.8$, $P = 0.49$	0.1 (0.2)	0.2 (0.4)	0.2 (0.2)	0.1 (0.2)
Total cover (%)	$F_{[3,93]} = 0.45$, $P = 0.72$	2.2 (1.8)	1.6 (1.7)	1.8 (1.9)	1.7 (1.1)

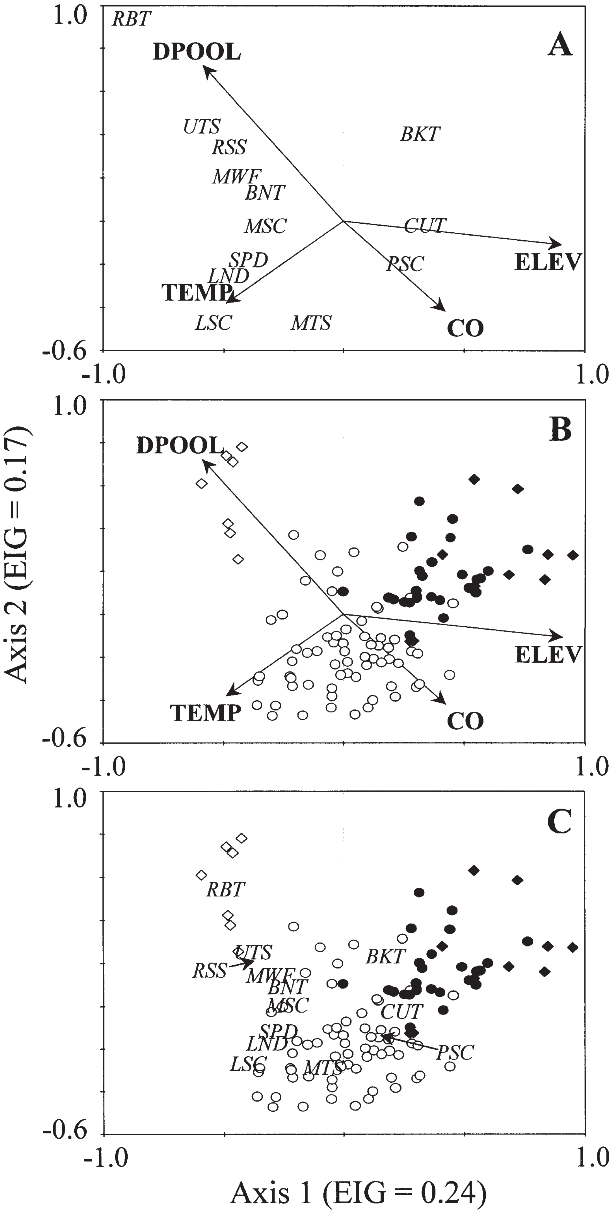
Note: Values are means; numbers in parentheses are standard errors. Test statistics represent the results of one-way analysis of variance. Mean values followed by the same letter are not significantly different (i.e., using least-squares means comparison) among fish assemblage types.

faunal zones, but most patterns were attributed to the addition of nonnative, warmwater species (e.g., bluegill (*Lepomis macrochirus* Rafinesque, 1819), largemouth bass (*Micropterus salmoides* (Lacepede, 1802)), and white crappie (*Pomoxis annularis* Rafinesque, 1818)). While biotic zonation has been illustrated in a variety of systems (e.g., Edds 1993; Kirchhofer 1995), zonation is usually observed only at large spatial scales or in areas with dramatic changes in habitat (Matthews 1998). Distinct assemblages are often present in stream systems, but their transitions are gradual (e.g., Matthews 1986; Williams et al. 1996), leading to the conclusion that the addition of species is the dominant process explaining longitudinal patterns in assemblage structure (Matthews 1998; Jackson et al. 2001). Despite the large number of studies investigating these processes, few have illustrated these trends in cold-water systems.

We observed and defined distinct fish assemblages in the Salt River system. However, the overall assemblage would be categorized as belonging to a cold-water faunal zone. Like Rahel and Hubert (1991), we found that increased fish assemblage complexity in downstream reaches was the result of within-zone additions of species to the Salt River watershed. An illustration of this process is provided by Jackknife Creek, on the western side of the basin. The four most upstream reaches contained allopatric cutthroat trout; Paiute sculpin was added to the assemblage in the next two downstream reaches; and mottled sculpin was added in the next downstream reach. The next reach downstream contained cutthroat trout, Paiute sculpin, and mottled sculpin, but also included longnose dace, mountain sucker, and leatherside chub. The second lowest reach contained all six species found in upstream reaches as well as speckled dace and brown trout. The lowermost reach included the six upstream species and speckled dace, but instead of brown trout, redside shiner and Utah sucker were added to the assemblage. This pattern was generally consistent among western tributaries, indicating that the addition of species was the dominant process explaining longitudinal changes in fish assemblage structure.

Biotic zonation and the addition of species are important processes that describe patterns in fish assemblage structure, but neither one is suggestive of underlying mechanisms. Longitudinal increases in species richness may be due to a variety of mechanisms, including increased habitat volume and heterogeneity (Gorman and Karr 1978; Schlosser 1982) or the addition of species from different faunal zones to downstream reaches (e.g., large-river species present in downstream reaches of small tributaries; Rahel and Hubert 1991). In the Salt River watershed, high-elevation reaches generally contained only one or two species, whereas downstream reaches were characterized by increasing species richness. Elevation is often considered a surrogate measure of water temperature (e.g., Bozek and Hubert 1992; Quist et al. 2004). Because fish are poikilothermic and have physiological constraints related to water temperature, thermal constraints may explain many of the patterns observed in our study, regardless of potential increases in habitat volume or heterogeneity. Although the relationship between elevation

Fig. 4. Canonical correspondence analysis biplots of fish assemblages and associated habitat variables in the Salt River watershed of Idaho and Wyoming, 1996–1997. Habitat variables include elevation (metres above mean sea level; ELEV), the percentage of cobble substrate (CO), mean summer (July–August) water temperature (°C; TEMP), and the percentage of the total water surface area consisting of deep-pool habitat (DPOOL). Species are as follows: BKT, brook trout; BNT, brown trout; CUT, cutthroat trout; LND, longnose dace; LSC, leatherside chub; MSC, mottled sculpin; MTS, mountain sucker; MWF, mountain whitefish; PSC, Paiute sculpin; RBT, rainbow trout; RSS, redside shiner; SPD, speckled dace; and UTS, Utah sucker. Panel (A) shows habitat variables and species scores; panel (B) shows habitat variables and sample (i.e., reach) scores; and panel (C) shows sample and species scores. ●, eastern reaches; ○, western reaches; ◆, southern reaches; ◇, spring reaches. Numbers in parentheses represent eigenvalues (EIG) for each axis.



and temperature may be strong in many systems of the Rocky Mountains, we included both variables in our analysis because mean water temperature varied among reaches of similar elevations in the Salt River watershed. A large reason for this variation across the watershed is that the eastern tributaries have lower mean summer water temperatures than reaches of comparable elevations in other areas of the basin (Isaak and Hubert 2001). Both eastern tributaries and high-elevation reaches in western tributaries were dominated by cutthroat trout, Paiute sculpin, and brook trout. This assemblage remained longitudinally static in eastern tributaries, but species were continually added to the assemblage in western tributaries.

Eastern tributaries and the upper Salt River originate in the Salt River Range, where reaches generally have high channel gradients and current velocities, narrow channels, and large substrates (Isaak and Hubert 2001). Further, streams have lower summer water temperatures on the east side of the basin (i.e., up to 9 °C lower) compared with other streams in the watershed at similar elevations. In addition to differences in physicochemical habitat, large water-diversion structures (> 1 m high) are present on the lower segments of eastern tributaries. Instream movement barriers fragment populations and can have a negative influence on native species (e.g., Luttrell et al. 1999). However, it is unlikely that any of the tributaries on the east side of the basin ever contained diverse fish assemblages. An example is provided by Willow Creek, which lacked downstream barriers and had a fish assemblage comprising cutthroat trout, Paiute sculpin, and brown trout. Thus, the most likely reasons for the lack of longitudinal species additions on the east side of the drainage are the inability of species to persist given their physiological thermal limitations and the relatively harsh environmental conditions that characterize eastern tributaries.

Our results provide insight regarding the organization of species and suggest that stream geomorphology, thermal conditions, and local habitat characteristics influence fish assemblage structure across the Salt River watershed. Because the Salt River basin is representative of many watersheds in the central Rocky Mountains, our results likely apply to other systems in the region. The results also provide information on the ecology of individual species and their associations with other species that can be used to guide conservation activities.

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