Patterns in Fish Assemblage Structure in a Small Western Stream

Zachary S. Beard[1], Michael C. Quist[2], Ryan S. Hardy[3], and Tyler J. Ross[3]

Knowledge of how patterns in fish assemblages are spatially structured is important for guiding management and conservation actions. However, most studies have taken place in the eastern and midwestern U.S., resulting in a poor understanding of factors influencing western stream fishes. The objectives of this study were to evaluate habitat and species associations of fishes in Deep Creek, a small tributary of the Kootenai River in Idaho. Fishes and habitat were sampled from 58 reaches in Deep Creek. In total, 7,129 individual fishes representing 18 species were sampled. Patterns in species richness were largely a function of channel gradient and associated habitat characteristics. Species richness decreased with increased channel gradient. Species-specific habitat relationships for native and nonnative fishes in Deep Creek provided specific insights into the ecology of each species. Predicted probability of occurrence and relative abundance varied by species and were related to a broad suite of environmental characteristics. This study provides insight on patterns of fish assemblage structure, as well as important information on the ecology of native and nonnative fishes in a western stream system.

UNDERSTANDING spatial patterns in fish assemblage structure is important for the conservation and management of freshwater ecosystems (Bond and Lake, 2003; Rice, 2005; Sindt et al., 2012). Consequently, describing fish assemblage structure and the factors influencing the organization of fish assemblages has been a major focus of research in fish ecology. A large body of information has accumulated regarding the spatial distribution of fishes in lotic systems and a major observation is the presence of longitudinal gradients that structure fish assemblages (Angermeier and Schlosser, 1989; Matthews, 1998). In particular, species richness often increases in a downstream direction. Although such patterns may emerge for a variety of reasons, the two most prominent conceptual models for such patterns are faunal zonation and species addition. Faunal zonation occurs when ecologically similar species form unique assemblages in response to changes in habitat (Huet, 1959; Winemiller and Leslie, 1992; Kirchhofer, 1995; Quist et al., 2005). Excellent examples are those systems that transition from coldwater to warmwater habitats and (or) experience major changes in channel morphology (Rahel and Hubert, 1991). Transitions in habitat and assemblage structure are sometimes gradual, but can be abrupt, particularly in montane systems. Species can be added in a downstream progression (species addition; Matthews, 1998). Addition may occur without the loss and replacement of other species (e.g., Sheldon, 1968; Morin and Naiman, 1990), or species may be added while others disappear from the assemblage (e.g., Gard and Flitner, 1974; Matthews, 1998).

The majority of studies investigating spatial patterns in fish assemblage structure have been conducted in the eastern and midwestern U.S. (e.g., Kuehne, 1962; Harrel et al., 1967; Lotrich, 1973; Evans and Noble, 1979; Matthews, 1986). Because many changes in habitat, and thus fish assemblage structure, are gradual with little or no evidence of faunal zonation, zonation is often ignored as a major feature structuring fish assemblages in eastern and midwestern regions (Matthews, 1998). Streams in the western U.S. differ from those to the east in a number of important ways. In particular, thermal and elevational gradients are important longitudinal components of western streams and play a major role in structuring fish assemblages (Bozek and Hubert, 1992; Quist et al., 2004). Many streams in the western U.S. originate in mountainous regions and transition, often abruptly, to prairie, grassland, or desert habitats. A coldwater faunal zone is common in these stream systems, as is within-zone addition of species (e.g., Hughes and Gammon, 1987; Rahel and Hubert, 1991; Maret et al., 1997; Quist et al., 2004). Despite the social, economic, and ecological importance of western stream systems, the number of studies focused on evaluating spatial patterns in fish assemblage structure remains low. Furthermore, except for salmonids, little is known about the ecology (e.g., habitat use) of fishes inhabiting streams characteristic of western North America. Not only are more studies needed to contribute to our understanding of how fish assemblages are organized, but continued and new threats to native species highlight the importance of understanding factors influencing the occurrence and abundance of different fishes and how they are organized (Richter et al., 1997).

The purpose of our research was to examine patterns in fish assemblage structure and provide insight on the ecology of fishes in Deep Creek, a small tributary to the Kootenai River, Idaho. Specifically, we investigated spatial patterns in fish assemblage structure and modeled species-specific habitat relationships. Our findings contribute to the knowledge of the ecology of individual species and provide insight into mechanisms structuring fish assemblages in western stream systems.

MATERIALS AND METHODS

Study area.—Deep Creek is a 3rd-order stream that originates east of White Mountain, Idaho, with a watershed area of approximately 480 km^2. Deep Creek is impounded 10 km from its headwaters to form McArthur Lake (Fig. 1). Deep Creek flows 33 km north from McArthur Lake to its confluence with the Kootenai River 5 km west of Bonners Ferry, Idaho. Downstream of McArthur Lake, Deep Creek averages between 8 m and 12 m in bank-full channel width

[1] Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Dr. MS1141, Moscow, Idaho 83844; Present address: Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, Arizona, 85086; Email: zbeard@azgfd.gov. Send reprint requests to this address.

[2] U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Dr. MS1141, Moscow, Idaho 83844.

[3] Idaho Department of Fish and Game, 2885 West Kathleen Avenue, Coeur d'Alene, Idaho 83815.

Submitted: 21 November 2017. Accepted: 9 September 2018. Associate Editor: M. P. Davis.

 DOI: 10.1643/CE-17-712 Published online: 18 October 2018

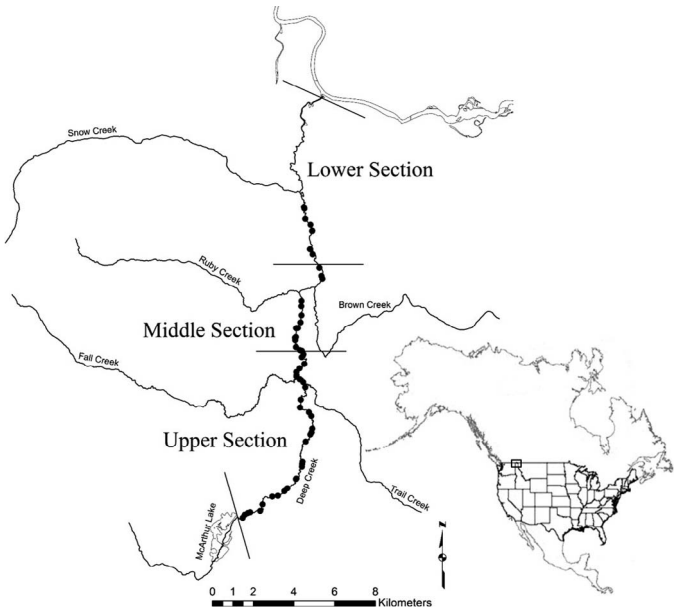

Fig. 1. Deep Creek watershed showing the main channel of Deep Creek, Deep Creek's five major tributaries (i.e., Trail, Fall, Ruby, Brown, and Snow creeks), and the Idaho portion of the Kootenai River. Circles represent the 58 stream reaches sampled on Deep Creek. Upper, middle, and lower sections of Deep Creek are also shown.

and is dominated by cobble and gravel substrates. However, directly downstream of the McArthur Lake Dam, Deep Creek is dominated by deep pools and fine substrates. The impoundment influences water quality in Deep Creek. Deep Creek is listed on the Idaho §303(d) list of impaired waters for excessive sediment and elevated temperatures (IDEQ, 2006). Deep Creek has five major tributaries (Brown, Fall, Ruby, Snow, and Trail creeks). Land ownership in the watershed is mixed. The U.S. Forest Service, Idaho Department of Lands, Forest Capital, and Stimson Lumber Capital all manage forest lands, mostly in the upper portions of the watershed. The lower portions of Deep Creek are generally privately owned and include areas of wetlands, agriculture, residential development, and forest (IDEQ, 2006).

Fish and habitat sampling.—Fishes and small-scale physical habitat characteristics were sampled from 58 stream reaches in Deep Creek (Fig. 1) during the summers (June–August) of 2014 and 2015. In 2014, 25 reaches were randomly selected from Deep Creek. In 2015, 29 reaches were randomly selected. As part of a larger study, four additional reaches were selected based on known Burbot (*Lota lota*) locations (Beard et al., 2017). Analyses were conducted with and without these four sites and results were consistent. As such, the four sites were retained in the analysis. Each reach was 35× mean stream width (Lyons, 1992; Simonson et al., 1994) up to a maximum length of 300 m, and was delineated into macrohabitats (i.e., pools, riffles, runs, and off-channel units; Quist et al., 2003; Sindt et al., 2012). Fishes were sampled in each reach using single-pass DC electrofishing (Model 15-C POW Backpack Electrofisher; Smith Root, Inc., Vancouver, Washington; Simonson and Lyons, 1995). For all electrofishing, one netter used a 6.4 mm mesh dip net to collect fish. Each macrohabitat was sampled separately. Seconds of electrofishing were recorded for each macrohabitat and used to calculate catch per unit effort (CPUE; fish/minute of electrofishing). All fishes were identified to species; fishes that could not be identified in the field were preserved and transported to the laboratory for identification.

Habitat was quantified by measuring physical habitat features in each macrohabitat. Total length of each macrohabitat was measured along the thalweg. If the macrohabitat was $\leq$30 m, two transects at 25% and 75% of the length were established perpendicular to the stream; if the macrohabitat was >30 m, transects were established at 25%, 50%, and 75% of the length (Quist et al., 2003). At each transect, the wetted stream width was measured perpendicular to the stream. Additionally, depth, current velocity, and substrate particle size were measured at four equidistant points and the midpoint (20%, 40%, 50%, 60%, and 80%; Platts, 1983). Both benthic and mean current velocities were taken with a portable velocity meter (Hach FH950 Handheld Flow Meter; Hach Company, Loveland, Colorado). Benthic velocity was measured at 0.03 m above the substrate. Mean current velocity was measured at 60% of the depth when depths were $\leq$0.75 m, and at 20% and 80% of the depth when depths were >0.75 m (Buchanan and Somers, 1969). Substrate was visually estimated at each point and classified as wood, clay (<0.004 mm), silt (0.004–0.063 mm), sand (0.064–2.000 mm), gravel (2.001–16.000 mm), coarse gravel (16.001–64.000 mm), cobble (64.001–256.000 mm), boulder (>256 mm), and bedrock (i.e., modified Wentworth scale; Cummins, 1962; Sindt et al., 2012). Canopy cover (%) was estimated at each transect using a concave densiometer facing each bank at the stream margin and facing upstream and downstream at the midpoint of the channel (Sindt et al., 2012). Distance from each bank to the nearest anthropogenic disturbance (e.g., agricultural fields, railroad tracks, road) was visually estimated at each transect (<10 m from the bank, $\geq$10 m from the bank, and no disturbance). Bank characteristics were visually estimated for both banks at each transect. Bank characteristics included the percent coverage of woody vegetation, nonwoody vegetation, roots, boulders, eroding ground, and bare ground. All instream cover at least 0.3 m in length was quantified by taking one length measurement, three width measurements, and three depth measurements. Instream cover was classified as undercut bank, overhanging vegetation, branch complex, log complex, root wad, boulder, aquatic vegetation, and other (Quist et al., 2003).

The area (m^2) of each macrohabitat was estimated by multiplying the thalweg length by the mean width. Mean depth, current velocity, canopy cover, and bank coverage percentages were calculated for each macrohabitat unit. The coefficient of variation (CV = 100 × [standard deviation/mean]) was also calculated for depth, wetted stream width, mean current velocity, and canopy cover. The proportions of each substrate, distance to anthropogenic disturbance category, and instream cover type were also quantified for each macrohabitat unit. Habitat characteristics were averaged across macrohabitats. Averaged values were weighted by the proportion of the total reach area represented by that macrohabitat (Sindt et al., 2012). Weighted values were summed to quantify habitat characteristics for the entire reach. Additional variables were created by summing two or more habitat variables (e.g., $Substrate_{Coarse}$; Table 1).

Fish assemblage.—An *a priori* investigation of the elevation profile of Deep Creek revealed three distinct sections with different average gradients: a lower section with low average gradient (mean ± SD; 0.12±6.82%), a middle section with high average gradient (0.71±6.04%), and an upper section with a moderate average gradient (0.26±8.59%). Species

Table 1. Mean and standard error (in parenthesis) of habitat variables measured from 58 reaches on Deep Creek, Idaho during 2014 and 2015. Habitat variables were averaged by section (upper, middle, lower) to highlight differences in habitat among the three sections.

Variable	Description	Section		
		Upper	Middle	Lower
Depth	Mean depth (m)	0.45 (0.13)	0.31 (0.12)	0.37 (0.09)
$Depth_{CV}$	Mean coefficient of variation (CV) of depth	42.9 (16.6)	41.4 (15.1)	52.7 (11.6)
Vel_{Mean}	Mean current velocity (m/s)	0.14 (0.09)	0.25 (0.13)	0.28 (0.07)
Vel_{cv}	Mean CV of current velocity	85.0 (30.2)	62.8 (23.2)	68.8 (9.0)
CanopyCover	Mean canopy cover (%)	17.0 (14.4)	12.9 (10.4)	4.8 (5.6)
$CanopyCover_{CV}$	Mean CV of canopy cover	151.6 (88.5)	149.8 (75.4)	93.1 (91.7)
$Substrate_{Coarse}$	Proportion of substrate that is coarse (coarse gravel, cobble, and boulder)	0.45 (0.33)	0.84 (0.25)	0.84 (0.13)
$Cover_{Woody}$	Proportion of reach area with branch complexes, log complexes, or root wads as cover	0.05 (0.05)	0.02 (0.02)	0.03 (0.03)
$Cover_{Veg}$	Proportion of reach area with aquatic macrophytes or overhanging vegetation as cover	0.25 (0.23)	0.05 (0.08)	0.01 (0.01)
DistAnt	Proportion of banks with no anthropogenic disturbance	0.45 (0.40)	0.27 (0.35)	0.20 (0.35)
$Width_{CV}$	Mean CV of wetted channel width	15.8 (8.3)	16.0 (9.5)	21.4 (6.7)
Pool	Percentage of reach area as pool	2.7 (5.8)	4.4 (5.6)	6.4 (8.5)

richness (i.e., the number of species sampled, *S*) was calculated for each sample reach. Species richness values were plotted against the stream elevation profile of Deep Creek to visualize longitudinal patterns in species richness associated with channel gradient and stream section. Mean species richness values and standard deviations were calculated for each section of Deep Creek. Differences in species richness were compared among the three sections using a one-way analysis of variance (Ott and Longnecker, 2010).

Fish assemblage relationships were investigated using non-metric multidimensional scaling (NMDS). Non-metric multidimensional scaling is an ordination technique that is widely used to describe fish assemblage patterns (e.g., Helms et al., 2005; Ruetz et al., 2007; Smith et al., 2016). Ordination stress was used to evaluate fit; final stress values less than 20.0 indicated a good fit of the ordination to the data (McCune and Grace, 2002). All ordinations used a Bray-Curtis distance measure. Two separate NMDS ordinations were used to evaluate patterns in the fish assemblage. The first ordination used reach-specific presence-absence data and the second used reach-specific CPUE data. Differences in fish assemblage structure among stream sections (i.e., lower, middle, upper) were evaluated with a permutational multivariate analysis of variance (PERMANOVA). If a significant difference ($P \leq 0.05$) among stream sections was observed, habitat vectors were fit onto the NMDS ordination with rotational vector fitting (Faith and Norris, 1989). Spearman's correlation coefficient was used to test for significant correlations between NMDS axis scores for fish presence-absence and fish CPUE and stream habitat characteristics. A Bonferroni correction was used to maintain the family-wise error rate (Benjamini and Hochberg, 1995); habitat variables that were significant ($P \leq 0.002$) with at least one ordination axis were displayed on the ordination. Additionally, if a significant difference ($P \leq 0.05$) in fish assemblage structure was observed from the PERMANOVA, a pairwise PERMANOVA was used to assess differences between individual stream sections. A Bonferroni correction was used to adjust *P*-values from pairwise PERMANOVAs to maintain the family-wise error rate. Ordinations were constructed using metaMDS in the vegan package in R (Oksanen et al., 2015). Permutational multivariate analysis of variance tests were performed separately for presence-absence and relative abundance ordinations using the ADONIS function in the vegan package in R. Pairwise PERMANOVAs were performed separately for presence-absence and relative abundance ordinations using the PAIRWISE.PERM.MANOVA function in the RVAideMemoire package in R (Hervé, 2018).

Species-specific habitat relationship.—In addition to investigations of fish assemblage structure, species-specific habitat relationships with presence-absence data and CPUE data were evaluated using a hurdle regression modeling approach (Martin et al., 2005; Smith et al., 2016). Hurdle models consisted of two submodels. One submodel used logistic regression to predict the probability of species presence for all reaches. The other submodel investigated relationships among species-specific CPUE and habitat characteristics (negative binomial error distribution) for reaches with at least one individual of the focal species (Maunder and Punt, 2004; Martin et al., 2005).

Hurdle submodels were constructed using the glm (R Development Core Team, 2008) and zerotrunc (Zeileis and Kleiber, 2015) functions in program R. Species-specific models were created for all species found in at least 10% of the stream reaches (Watkins et al., 2015; Smith et al., 2016). Model fit was assessed using McFadden's pseudo R^2 (McFadden, 1974; Hosmer and Lemeshow, 1989). McFadden's pseudo R^2 was calculated as one minus the difference in the log likelihood of a model with an intercept plus explanatory variables and the log likelihood of an intercept-only model (McFadden, 1974). McFadden's pseudo R^2 values vary from 0.0 to 1.0 with values greater than 0.20 indicating good fit (Hox, 2010; Mujalli and de Ona, 2013).

Spearman's correlation coefficient was used to investigate relationships among habitat characteristics to reduce the risk of multicollinearity. Variables with a correlation coefficient $\geq$ 0.70 were considered highly correlated. When two variables were highly correlated, the most ecologically important or interpretable variable was retained for consideration in *a priori* candidate models (Sindt et al., 2012; Smith et al., 2016). For example, mean current velocity was highly correlated ($r \geq 0.70$) with mean benthic velocity, the proportion of riffle macrohabitat, and the proportion of run macrohabitat. Mean

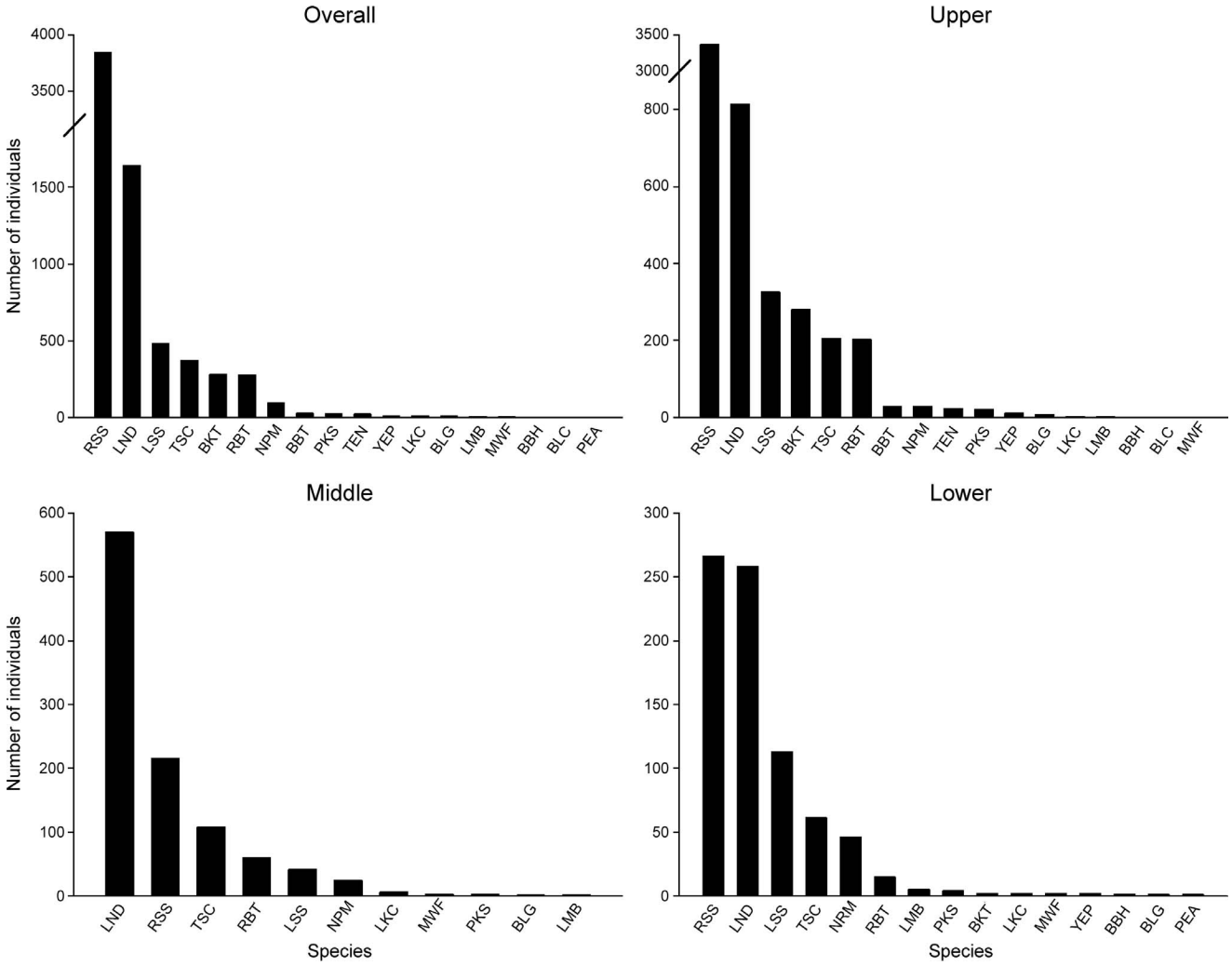

Fig. 2. Total number of individuals of each species sampled from Deep Creek and each individual section (i.e., upper, middle, and lower) during the summers of 2014 and 2015. Taxa include Brown Bullhead (BBH), Burbot (BBT), Brook Trout (BKT), Black Crappie (BLC), Bluegill (BLG), Lake Chub (LKC), Largemouth Bass (LMB), Longnose Dace (LND), Largescale Sucker (LSS), Mountain Whitefish (MWF), Northern Pikeminnow (NPM), Peamouth (PEA), Pumpkinseed (PKS), Rainbow Trout (RBT), Redside Shiner (RSS), Tench (TEN), Torrent Sculpin (TSC), and Yellow Perch (YEP).

current velocity was deemed the most ecologically important variable and retained in candidate models; the other variables were removed. Five to fifteen candidate models were generated *a priori* for each submodel. Candidate models were ranked using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson, 2002). Models within two AIC_c values were considered to have equal support and retained for interpretation.

RESULTS

In total, 7,127 individual fishes representing 18 species and 7 families were sampled from 58 reaches (249 separate macrohabitats). Redside Shiner (*Richardsonius balteatus*) was the most abundant species followed by Longnose Dace (*Rhinichthys cataractae*), Largescale Sucker (*Catostomus macrocheilus*), Torrent Sculpin (*Cottus rhotheus*), Brook Trout (*Salvelinus fontinalis*), and Rainbow Trout (*Onchorhynchus mykiss*; Fig. 2). In both the upper and lower sections, Redside Shiner was the most numerous species followed by Longnose Dace and Largescale Sucker. In the middle section, Longnose Dace was the most abundant species followed by Redside Shiner and Torrent Sculpin. Species richness varied significantly ($F_{2,55} = 4.8$, $P = 0.01$) among stream sections with the lowest richness in the middle section (mean richness ± SE; 5.5±0.5) followed by the upper (6.7±0.2) and lower sections (7.7±0.5; Fig. 3).

A stable NMDS ordination was fit to the species occurrence data (stress = 13.8; Fig. 4). Permutational multivariate analysis of variance indicated that fish assemblage composition differed among stream sections with regard to species occurrence ($F_{2,55} = 10.7$, $P < 0.01$). Pairwise PERMANOVAs indicated that fish assemblage composition differed significantly between the lower and upper sections ($P < 0.01$), and the middle and upper sections ($P < 0.01$). Fish assemblage composition did not vary significantly between the lower and middle sections ($P = 0.06$) with regard to species occurrence. Based on occurrence, Northern Pikeminnow (*Ptychocheilus oregonensis*), Largemouth Bass (*Micropterus salmoides*), Black Bullhead (*Ameiurus melas*), and Bluegill (*Lepomis macrochirus*) were most closely associated with the lower section (Fig. 4). Mountain Whitefish (*Prosopium williamsoni*) and Torrent Sculpin most commonly occurred in the middle section, and Tench (*Tinca tinca*) and Brook Trout most commonly occurred in the upper section (Fig. 4). Several habitat characteristics were significantly correlated with NMDS axis scores (Table 2). Mean depth, proportion of coarse substrate, proportion of instream woody cover, and

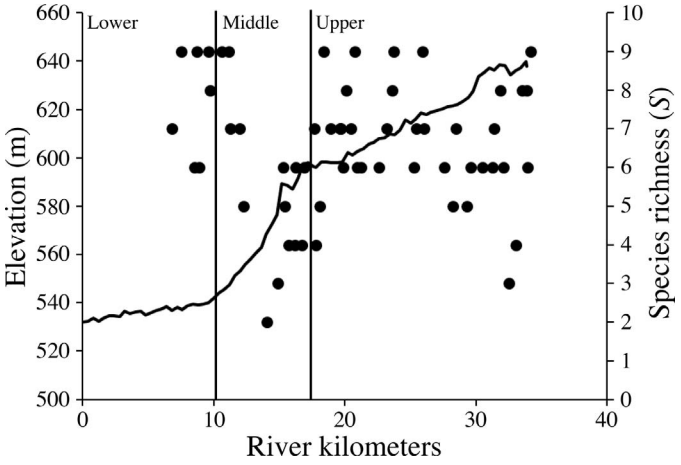

Fig. 3. A stream elevation (m) profile of Deep Creek from the McArthur Lake impoundment to its confluence with the Kootenai River (river kilometer 0). Vertical bars represent the breaks between the lower, middle, and upper sections of Deep Creek. Circles represent the species richness value for each of the 58 sampled reaches in Deep Creek.

proportion of instream vegetative cover were all significantly correlated with at least one axis of the fish presence-absence ordination (Table 2; Fig. 4). Mean depth, proportion of instream woody cover, and proportion of instream vegetative cover were higher in reaches in the upper section, and the proportion of coarse substrate was highest in reaches in the middle section of Deep Creek (Fig. 4).

Logistic regression models indicated that the relationship between probability of occurrence and habitat characteristics varied by species (Table 3). Moreover, the results corroborated patterns observed with the NMDS analysis. In general, logistic models appeared to have good fit and predict species occurrence for most species. The presence of Largescale Sucker, Pumpkinseed (*Lepomis gibbosus*), Redside Shiner, and Brook Trout was positively related to mean depth. The proportion of instream woody cover was positively related to the presence of Pumpkinseed and Brook Trout, but negatively related to the presence of Rainbow Trout and Torrent Sculpin. The proportion of instream vegetative cover was positively related to the presence of Tench and negatively associated with the presence of Lake Chub (*Couesius plumbeus*). The presence of Torrent Sculpin and Lake Chub was positively associated with the proportion of coarse substrate. Brook Trout occurrence was negatively related to the proportion of coarse substrate.

A stable NMDS was fit to the CPUE data (stress = 10.8; Fig. 5) and patterns were similar to those observed in the presence-absence ordination. Permutational multivariate analysis of variance indicated that assemblage composition differed among sections with regard to relative abundance ($F_{2,55} = 7.2$, $P < 0.01$). Pairwise PERMANOVAs indicated that fish assemblage composition differed significantly between the middle and upper sections ($P < 0.01$) with regard to relative abundance. Fish assemblage composition did not vary significantly between the lower and middle sections ($P = 0.06$) and lower and upper sections ($P = 0.08$). Ordinations of relative abundances indicated that Northern Pikeminnow were most abundant in the lower section (Fig. 5). Longnose Dace and Torrent Sculpin were most abundant in the middle section, whereas Redside Shiner, Largescale Sucker, and Brook Trout were most abundant in the upper section. Habitat variables that were significantly correlated with at least one

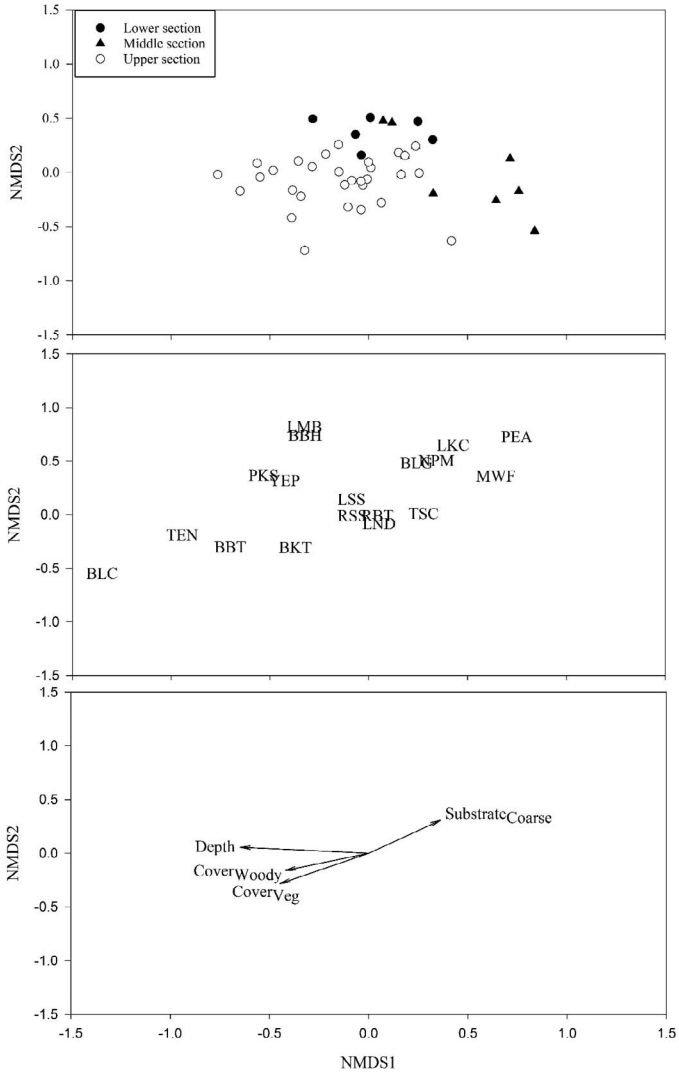

Fig. 4. Non-metric multidimensional scaling ordination (stress = 13.8) of reach-specific ($n = 58$) fish assemblage presence-absence data from Deep Creek organized by section (upper, middle, lower). Species scores are displayed in the middle figure, and taxa include Brown Bullhead (BBH), Burbot (BBT), Brook Trout (BKT), Black Crappie (BLC), Bluegill (BLG), Lake Chub (LKC), Largemouth Bass (LMB), Longnose Dace (LND), Largescale Sucker (LSS), Mountain Whitefish (MWF), Northern Pikeminnow (NPM), Peamouth (PEA), Pumpkinseed (PKS), Rainbow Trout (RBT), Redside Shiner (RSS), Tench (TEN), Torrent Sculpin (TSC), and Yellow Perch (YEP). Significant ($P < 0.002$) habitat vectors were fit to the ordination and include the proportion of coarse substrate, mean depth, the proportion of instream woody cover, and the proportion of instream vegetative cover. The closer species or reach scores are located to one another on the ordination, the more closely the presence of those species and (or) reaches are associated with one another. Habitat vectors are in the direction of the increasing values of the habitat variable.

axis of the fish CPUE NMDS ordination included mean depth, mean current velocity, the proportion of coarse substrate, and the proportion of instream vegetative cover (Table 2; Fig. 5). Both mean current velocity and the proportion of coarse substrate were highest in the middle section of Deep Creek. In addition, the relative abundance of Longnose Dace and Torrent Sculpin was most closely associated with mean current velocity and coarse substrate (Fig. 5). Mean depth and the proportion of instream vegetative cover were highest in the upper section of Deep

Table 2. Spearman's correlation coefficients (ordination *P*-values in parenthesis) between stream habitat characteristics and non-metric multidimensional scaling (NMDS) axis scores for fishes sampled in Deep Creek, Idaho during 2014 and 2015. The NMDS analyses were conducted using fish presence-absence (P-A) and fish catch per unit effort (CPUE; fish/minute of electrofishing). Values in bold were significant using a Bonferroni correction (i.e., $P \leq 0.002$).

	Fish P-A		Fish CPUE	
Variable	NMDS1	NMDS2	NMDS1	NMDS2
Depth	**−0.62 (<0.01)**	0.06 (0.67)	−0.39 (<0.01)	**−0.44 (<0.01)**
$Depth_{CV}$	−0.01 (0.95)	0.21 (0.11)	0.01 (0.98)	0.34 (0.01)
Vel_{Mean}	0.38 (<0.01)	0.23 (0.09)	**0.63 (<0.01)**	0.19 (0.15)
Vel_{CV}	−0.35 (0.01)	−0.04 (0.77)	−0.37 (<0.01)	0.09 (0.50)
CanopyCover	−0.22 (0.10)	−0.21 (0.11)	−0.03 (0.84)	0.07 (0.58)
$CanopyCover_{CV}$	−0.04 (0.74)	0.08 (0.56)	0.16 (0.24)	−0.17 (0.21)
$Substrate_{Coarse}$	**0.41 (<0.01)**	0.29 (0.03)	**0.59 (<0.01)**	0.18 (0.18)
$Cover_{Woody}$	**−0.42 (<0.01)**	−0.07 (0.58)	−0.36 (0.01)	−0.03 (0.80)
$Cover_{Veg}$	**−0.52 (<0.01)**	−0.31 (0.02)	**−0.59 (<0.01)**	−0.28 (0.03)
DistAnt	−0.30 (0.02)	−0.15 (0.26)	0.07 (0.58)	−0.35 (0.01)
$Width_{CV}$	−0.09 (0.52)	0.01 (0.97)	−0.06 (0.65)	0.22 (0.09)
Pool	0.04 (0.74)	0.33 (0.01)	0.36 (0.01)	−0.26 (0.05)

Table 3. Top models from the candidate sets investigating species occurrence among stream reaches ($n = 58$) sampled in Deep Creek, Idaho during 2014 and 2015. Akaike's Information Criterion (AIC_c) adjusted for small sample size ranked the candidate models. Delta AIC_c (ΔAIC_c) is the difference between the AIC_c of a given model and the AIC_c of the top model. The total number of parameters (K), model weight (w_i), and McFadden's pseudo R^2 are included. Direction of effect for each habitat covariate is indicated (positive [+], negative [−]).

Taxon	Model name	AIC_c	ΔAIC_c	K	w_i	R^2
Catostomidae						
Largescale Sucker	+ Depth	62.35	0.00	2	0.24	0.06
	+ Pool	64.06	1.57	2	0.10	0.03
	+ Depth + $Substrate_{Coarse}$	64.33	1.98	3	0.09	0.06
Centrarchidae						
Pumpkinseed	+ Depth	68.50	0.00	2	0.31	0.06
	+ DistAnt	69.44	0.94	2	0.20	0.05
	+ $Cover_{Woody}$	69.94	1.44	2	0.15	0.04
Cottidae						
Torrent Sculpin	− Depth + $Substrate_{Coarse}$	39.61	0.00	3	0.23	0.38
	− Depth − $Cover_{Woody}$	39.75	0.14	3	0.21	0.38
	+ Vel_{Mean}	39.84	0.23	2	0.20	0.33
	− Depth	40.69	1.08	2	0.13	0.32
Cyprinidae						
Lake Chub	+ $Substrate_{Coarse}$	42.50	0.00	2	0.35	0.10
	− $Cover_{Veg}$	42.75	0.25	2	0.31	0.10
	− Vel_{Mean} + $Substrate_{Coarse}$	44.19	1.69	3	0.15	0.12
Northern Pikeminnow	+ Vel_{Mean}	76.39	0.00	2	0.23	0.06
	+ Pool + $Substrate_{Coarse}$	76.87	0.48	3	0.18	0.09
	− $Cover_{Woody}$	77.41	1.02	2	0.14	0.05
	+ Pool + Depth + $Substrate_{Coarse}$	78.28	1.90	4	0.09	0.10
Redside Shiner	+ Vel_{CV}	28.81	0.00	2	0.45	0.28
	+ Depth	30.05	1.25	2	0.24	0.24
Tench	+ $Cover_{Veg}$	46.15	0.00	2	0.40	0.21
	− Vel_{Mean} + $Cover_{Veg}$	47.98	1.82	3	0.16	0.22
	− CanopyCover + $Cover_{Veg}$	48.01	1.86	3	0.16	0.22
Percidae						
Yellow Perch	+ Depth	37.77	0.00	2	0.42	0.13
	+ $Cover_{Woody}$	38.48	0.71	2	0.30	0.11
Salmonidae						
Brook Trout	+ Depth − $Substrate_{Coarse}$ + $Cover_{Woody}$	53.94	0.00	4	0.67	0.43
	+ Depth + $Cover_{Woody}$	55.72	1.78	3	0.28	0.37
Rainbow Trout	− $Width_{CV}$	40.22	0.00	2	0.26	0.07
	− $Cover_{Woody}$	41.89	1.66	2	0.11	0.02

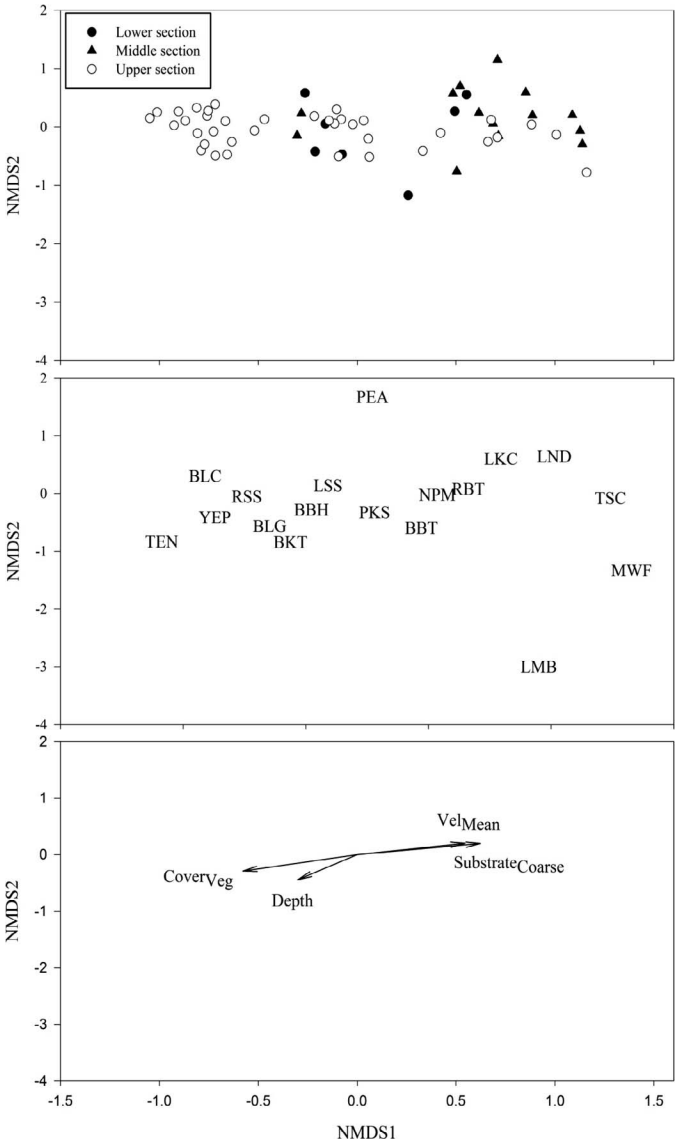

Fig. 5. Non-metric multidimensional scaling ordination (stress = 13.8) of reach-specific ($n = 58$) fish assemblage relative abundance data from Deep Creek organized by section (upper, middle, lower). Species scores are displayed in the middle figure, and taxa include Brown Bullhead (BBH), Burbot (BBT), Brook Trout (BKT), Black Crappie (BLC), Bluegill (BLG), Lake Chub (LKC), Largemouth Bass (LMB), Longnose Dace (LND), Largescale Sucker (LSS), Mountain Whitefish (MWF), Northern Pikeminnow (NPM), Peamouth (PEA), Pumpkinseed (PKS), Rainbow Trout (RBT), Redside Shiner (RSS), Tench (TEN), Torrent Sculpin (TSC), and Yellow Perch (YEP). Significant ($P < 0.002$) habitat vectors were fit to the ordination and include the proportion of coarse substrate, mean current velocity, mean depth, and the proportion of instream vegetative cover. The closer species or reach scores are located to one another on the ordination, the more closely the relative abundance of those species and (or) reaches are associated with one another. Habitat vectors point in the direction of the increasing gradient of the habitat variable (e.g., increasing mean water velocity) on the ordination.

Creek. The relative abundance of species such as Tench and Redside Shiner was most closely associated with deep habitats that contained vegetative cover (Fig. 5).

The second stage of the hurdle regressions (i.e., CPUE) indicated that relationships with habitat characteristics varied among species (Table 4). Moreover, results corroborated relationships observed with the NMDS ordination. The relative abundance of Largescale Sucker, Pumpkinseed, Lake Chub, Redside Shiner, Tench, and Brook Trout was negatively associated with mean current velocity (Table 4). Instream vegetative cover was negatively associated with catch rates of Lake Chub, Longnose Dace, and Rainbow Trout, whereas the relative abundance of Largescale Sucker, Pumpkinseed, Redside Shiner, and Tench was positively associated with instream vegetative cover. Torrent Sculpin, Longnose Dace, and Rainbow Trout catch rates were positively related to coarse substrate (Table 4).

DISCUSSION

Both biotic (e.g., piscivores) and abiotic (e.g., gradient, temperature) characteristics influence fish assemblage structure and create discernible patterns in lotic systems (Rahel and Hubert, 1991; Quist et al., 2005). A common and consistently reported pattern is the gradual addition of species from upstream to downstream areas (Kuehne, 1962; Harrel et al., 1967; Evans and Noble, 1979; Rahel and Hubert, 1991; Quist et al., 2004). However, in the current study, we observed a different pattern with high species richness in the upper and lower sections, and low species richness in the middle section of the system. Low species richness in the middle section was most likely due to the high channel gradient and related habitat characteristics. Patterns in fish assemblage structure associated with stream gradient have been commonly reported in lotic systems. For example, Paller (1994) found that high species richness in headwater streams was related to a lack of steep elevations in coastal plain streams of South Carolina. Lyons (1996) found similar results where high-gradient streams in the Driftless Area of Wisconsin had many riffle-dwelling species, whereas species-rich, low-gradient streams in the Southeastern Wisconsin Till Plains had more pool-dwelling species. Maret et al. (1997) reported stream gradient as one of the landscape characteristics that was important for structuring the fish assemblages in the upper Snake River basin, Idaho and Wyoming. Waite and Carpenter (2000) found that fish assemblages were primarily structured by stream gradient and that gradient-related patterns superseded patterns that were ecoregion-specific for streams in the Willamette Basin, Oregon. Quist et al. (2004) also found patterns in fish assemblage structure associated with gradient in the Salt River basin, Idaho and Wyoming. Stream reaches in the Salt River with high channel slopes had very low species richness; the only species present at high-gradient sites were often just Cutthroat Trout (*Oncorhynchus clarkii*) and (or) Paiute Sculpin (*Cottus beldingii*). In contrast, stream reaches in the Salt River with low gradient had highly diverse and speciose fish assemblages. The middle section of Deep Creek had high channel gradient and low habitat diversity (e.g., instream cover) in comparison to lower and upper sections and likely explained the low species richness observed in middle sections. In addition to the broad spatial patterns observed in this study, species-specific analyses provided important insight on the ecology of fishes in the system.

While a pattern in fish assemblage structure associated with gradient was obvious, pairwise PERMANOVAs did not indicate statistically significant differences between all stream sections with regard to species occurrence and relative abundance. The mostly likely reason for the lack of statistically significant differences between stream sections was the small number of reaches that were located in the lower section ($n = 7$). Additionally, several sites from both the lower and middle section were located close to the boundary

Table 4. Top models from the candidate sets investigating relative abundance of species in relation to habitat characteristics sampled from reaches ($n = 58$) in Deep Creek, Idaho during 2014 and 2015. Akaike's Information Criterion (AIC_c) adjusted for small sample size ranked the candidate models. Delta AIC_c (ΔAIC_c) is the difference between the AIC_c of a given model and the AIC_c of the top model. The total number of parameters (K), model weight (w_i), and McFadden's pseudo R^2 are included. Direction of effect for each habitat covariate is indicated (positive [+], negative [–]).

Taxon	Model name	AIC_c	ΔAIC_c	K	w_i	R^2
Catostomidae						
Largescale Sucker	– Pool	302.90	0.00	3	0.19	0.01
	+ $Width_{CV}$	303.62	0.72	3	0.13	0.01
	– Vel_{Mean}	304.25	1.35	3	0.10	0.01
	– $Cover_{Woody}$	304.50	1.60	3	0.09	0.01
	– $Cover_{Woody}$ + $Width_{CV}$	304.56	1.66	4	0.08	0.01
Centrarchidae						
Pumpkinseed	+ $Cover_{Veg}$	40.60	0.00	3	0.18	0.06
	+ CanopyCover	40.73	0.13	3	0.17	0.06
	– Vel_{Mean}	41.58	0.98	3	0.11	0.03
	+ Depth	41.61	1.01	3	0.11	0.03
	+ $Cover_{Woody}$	41.61	1.01	3	0.11	0.03
	+ $Velocity_{CV}$	41.73	1.13	3	0.10	0.03
	+ DistAnt	42.58	1.98	3	0.07	0.01
Cottidae						
Torrent Sculpin	+ $Substrate_{Coarse}$ – Vel_{CV}	287.10	0.00	4	0.29	0.03
	+ $Substrate_{Coarse}$	288.34	1.34	3	0.15	0.02
Cyprinidae						
Lake Chub	– Vel_{Mean}	25.80	0.00	3	0.46	0.10
	– $Cover_{Veg}$	26.69	0.89	3	0.29	0.03
	– $Substrate_{Coarse}$	27.04	1.24	3	0.25	0.01
Longnose Dace	– $Cover_{Veg}$	476.60	0.00	3	0.26	0.06
	– Depth – $Cover_{Veg}$	476.94	0.34	4	0.22	0.06
	– Depth + $Substrate_{Coarse}$	477.65	1.05	4	0.16	0.06
	– Depth + Vel_{Mean} – $Cover_{Veg}$ + $Substrate_{Coarse}$ + CanopyCover + $Width_{CV}$ + Vel_{CV} – Pool	477.71	1.11	10	0.15	0.09
Northern Pikeminnow	– CanopyCover	109.20	0.00	3	0.27	0.03
	+ Vel_{Mean}	110.44	1.24	3	0.15	0.02
Redside Shiner	+ $Cover_{Veg}$ – $Substrate_{Coarse}$	547.70	0.00	4	0.37	0.04
	– Vel_{Mean} + $Cover_{Veg}$	548.48	0.78	4	0.25	0.04
Tench	– Vel_{Mean}	38.30	0.00	3	0.48	0.09
Percidae						
Yellow Perch	– Depth	29.40	0.00	3	0.53	0.32
Salmonidae						
Brook Trout	– Vel_{Mean}	105.80	0.00	3	0.58	0.08
	– Vel_{Mean} + $Substrate_{Coarse}$	107.14	1.34	4	0.30	0.10
Rainbow Trout	+ $Substrate_{Coarse}$	265.00	0.00	3	0.17	0.01
	– $Cover_{Veg}$	265.48	0.48	3	0.13	0.01
	+ $Width_{CV}$	265.79	0.79	3	0.12	0.01
	+ Depth – $Cover_{Veg}$	266.63	1.63	4	0.08	0.01
	+ Depth + $Substrate_{Coarse}$	266.69	1.69	4	0.07	0.01
	– Vel_{Mean} +$Substrate_{Coarse}$	266.80	1.80	4	0.07	0.01

between the two sections (Fig. 1). This area represented a transition zone, where the gradient transitions from high to low. The reaches near the boundary between the two sections were generally characterized by stream characteristics that were intermediate to those of the lower and middle sections. The presence of the stream reaches located in the transition zone between high to low gradient and the small sample size probably affected the ability of the statistical analysis to distinguish differences in fish assemblage composition between the sections.

Patterns of species occurrence in different sections of Deep Creek typically reflected what is known about the ecology of individual species. Species that occurred most frequently in the middle section of Deep Creek included Mountain Whitefish and Torrent Sculpin. These species are generally considered fast-water species (Wallace and Zaroban, 2013), and the middle section of Deep Creek was characterized by a high gradient, fast-current velocities, and large substrate (i.e., riffles). In contrast, some native (i.e., Northern Pikeminnow and Redside Shiner) and nonnative (Tench, Largemouth Bass, Yellow Perch, Pumpkinseed) species are generally more common in lentic systems or in low-velocity habitats in lotic systems (Becker, 1983; Zarkami et al., 2010; Wallace and Zaroban, 2013). These species occurred most frequently either directly downstream of the McArthur Lake impoundment (i.e., upper section) or in the lower section of Deep Creek—areas characterized by low-velocity habitats. Brook Trout were most common in the upper section of Deep Creek, which was characterized by an intermediate gradient, deep habitats, fine substrates, and high proportions of instream vegetation. Although Brook Trout are often associated with high-gradient, cold streams (Maret et al., 1997;

Walrath et al., 2016), this finding is not consistent across all Brook Trout populations. In many streams, Brook Trout are often associated with habitats that have deep pools and an abundance of instream cover (Butler and Hawthorne, 1968; Enk, 1977; Josephson, 1983; Riley et al., 1992). For instance, Shepard (2004) found that Brook Trout densities were highest in areas with abundant instream cover, a high proportion of pool habitats, and substrates dominated by fine particles. Additionally, the upper section of Deep Creek contained many Beaver (*Castor canadensis*) pools which have been shown to provide excellent habitat for Brook Trout in other systems (Kozel and Hubert, 1989; Behnke et al., 2002).

Patterns in relative abundance and species occurrence were generally similar. For example, results of the NMDS ordination showed that species such as Torrent Sculpin and Longnose Dace were most abundant in the middle section of Deep Creek. These species are generally considered fast-water species (Wallace and Zaroban, 2013), which likely explains their higher abundance in the middle section of Deep Creek. Species such as Redside Shiner, Largescale Sucker, Pumpkinseed, and Tench were most abundant in the upper section of Deep Creek; a section characterized by deep habitats, fine substrate, aquatic vegetation, and low water velocities. These observations are concurrent with the results of other studies and contribute to our knowledge of the ecology of the species (Scott and Crossman, 1973; Zarkami et al., 2010; Wallace and Zaroban, 2013).

An important consideration of this study is that we used CPUE data from a single sampling event of each reach in the ordination and species-specific habitat relationship analyses. Capture efficiencies from backpack electrofishing vary among species and are often related to habitat characteristics (Price and Peterson, 2010; Meyer and High, 2011). Failure to account for the different capture efficiencies may have biased our CPUE data, as well as resulted in an overestimation or underestimation of the strength of our species-specific habitat relationships (Meyer and High, 2011). However, stream characteristics were generally conducive for backpack electrofishing (i.e., depths <0.5 m, little instream cover). As such, we argue that bias was likely consistent throughout the study and that the data are adequate for evaluating general patterns in relative abundance and species-specific habitat relationships.

The presence of the McArthur Lake impoundment is also important to consider within the context of fish assemblage structure in Deep Creek. Ward and Stanford (1983) introduced the serial discontinuity concept (SDC) which suggests that dams reset river continua. McArthur Lake alters the habitat and fish assemblage composition immediately downstream by allowing the passage of nonnative species such as Tench, Largemouth Bass, and Pumpkinseed, from the reservoir to Deep Creek. This is opposite of what would be predicted under the SDC, where the impoundment would be predicted to reset the assemblage to that characteristic of a lower stream order (i.e., lower species richness). One likely reason for this discrepancy is that the McArthur Lake impoundment has an unregulated top-water discharge that releases warmer water from the reservoir. Also, the morphology of the system directly downstream of McArthur Lake is such that water velocities are low.

The results of this study provide unique insights into the environmental factors that structure fish assemblages in the western U.S. but are not well documented in studies of fish assemblage structure in the eastern and midwestern U.S. For example, an elevational gradient was obvious in Deep Creek and played an important role in structuring the fish assemblage. This elevational gradient resulted in a distinct faunal zone in the middle reach of Deep Creek, which had lower species richness and was characterized by the presence of species such as Longnose Dace and Torrent Sculpin. In addition to patterns in assemblage structure, this study provides new insights into the habitat associations of species that are common in streams in the intermountain west (e.g., Redside Shiner, Largescale Sucker, Torrent Sculpin), but little is known regarding their ecology (e.g., habitat use).

Our research illustrated differences in fish assemblage structure among sections of Deep Creek. These differences appeared to be related to changes in stream gradient and associated habitat characteristics. A clear pattern of decreased species richness with increased gradient was apparent, with the lowest species richness observed in the middle section and the highest richness in the lower section of Deep Creek. The McArthur Lake impoundment also played a role in structuring fish assemblage structure by introducing nonnative species and altering habitats downstream of the impoundment. In addition, species-specific habitat relationships indicated that habitat use varied by species, thereby suggesting that fish assemblage structure in Deep Creek is influenced by a diversity of abiotic characteristics.

DATA ACCESSIBILITY

Supplemental material is available at https://www.copeiajournal.org/ce-17-712.

ACKNOWLEDGMENTS

We thank J. Johnson, L. Schofield, L. Terraberry, G. Peck, V. Oliveras, M. Briggs, V. B. Nunez, A. Miera, K. Bush, and numerous Idaho Department of Fish and Game employees, particularly C. Gidley, for assistance with fieldwork. Helpful comments on a previous version of this manuscript were provided by D. Schill, C. Caudill, T. Johnson, and B. Shepard. Funding for this project was provided by the Idaho Department of Fish and Game. Additional support was provided by the U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the U.S. Geological Survey, University of Idaho, the Idaho Department of Fish and Game, and Wildlife Management Institute. This project was conducted under the University of Idaho Institutional Animal Care and Use Committee Protocol 2014-8. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Angermeier, P. L., and I. J. Schlosser. 1989. Species-area relationships for stream fishes. Ecology 70:1450–1462.

Beard, Z. S., M. C. Quist, R. S. Hardy, and T. J. Ross. 2017. Habitat associations of juvenile Burbot in a tributary of the Kootenai River. Transactions of the American Fisheries Society 146:1008–1015.

Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

Behnke, R. J., J. Tomelleri, and D. S. Proebstel. 2002. Trout and Salmon of North America. The Free Press, New York.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B (Methodological) 57:289–300.

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

Bozek, M. A., and W. A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. Canadian Journal of Zoology 70:886–890.

Buchanan, T. J., and W. P. Somers. 1969. Discharge measurements at gaging stations. Techniques of water-resource investigations, Book 3. U.S. Geological Survey, Washington, D.C.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second edition. Springer-Verlag, New York.

Butler, R. L., and V. M. Hawthorne. 1968. The reactions of dominant trout to changes in overhead artificial cover. Transactions of the American Fisheries Society 97:37–41.

Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. American Midland Naturalist 67: 477–504.

Enk, M. D. 1977. Instream overhead bank cover and abundance in two Michigan streams. Unpubl. master's thesis, Michigan State University, East Lansing, Michigan.

Evans, J. W., and R. L. Noble. 1979. The longitudinal distribution of fishes in an east Texas stream. American Midland Naturalist 101:333–343.

Faith, D. P., and R. H. Norris. 1989. Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. Biological Conservation 50:77–98.

Gard, R., and G. A. Flitner. 1974. Distribution and abundance of fishes in Sagehen Creek, California. Journal of Wildlife Management 38:347–358.

Harrel, R. C., B. J. Davis, and T. C. Dorris. 1967. Stream order and species diversity of fish in an intermittent Oklahoma stream. American Midland Naturalist 78:428–436.

Helms, B. S., J. W. Feminella, and S. Pan. 2005. Detection of biotic responses to urbanization using fish assemblages from small streams of western Georgia, USA. Urban Ecosystems 8:39–57.

Hervé, M. 2018. RVAideMemoire: testing and plotting procedures for biostatistics package. R package version 0.9-69-3. https://cran.r-project.org/web/packages/ordinal/index.html

Hosmer, D. W., and S. Lemeshow. 1989. Applied Regression Analysis. John Wiley, New York.

Hox, J. J. 2010. Multilevel Analysis: Techniques and Applications. Second edition. Routledge, New York.

Huet, M. 1959. Profiles and biology of European streams as related to fish management. Transactions of the American Fisheries Society 88:155–163.

Hughes, R. M., and J. R. Gammon. 1987. Longitudinal changes in fish assemblages and water quality in the Willamette River, Oregon. Transactions of the American Fisheries Society 116:196–209.

IDEQ (Idaho Department of Environmental Quality). 2006. Assessment of water quality in Kootenai River and Moyie River subbasins (TMDL). Idaho Department of Environmental Quality, Coeur d'Alene Regional Office, Coeur d'Alene, Idaho.

Josephson, D. C. 1983. Environmental factors related to the abundance and distribution of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) and seasonal movements of brown trout in selected Virginia watersheds. Unpubl. master's thesis. Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

Kirchhofer, A. 1995. Morphological variability in the ecotone—an important factor for the conservation of fish species richness in Swiss rivers. Hydrobiologia 303:103–110.

Kozel, S. J., and W. A. Hubert. 1989. Factors influencing the abundance of Brook Trout (*Salvelinus fontinalis*) in forested mountain streams. Journal of Freshwater Ecology 5:113–122.

Kuehne, R. A. 1962. A classification of streams, illustrated by fish distribution in an eastern Kentucky creek. Ecology 43: 608–614.

Lotrich, V. A. 1973. Growth, production, and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. Ecological Monographs 43:377–397.

Lyons, J. 1992. The length of stream to sample with a towed electrofishing unit when fish species richness is estimated. North American Journal of Fisheries Management 12:198–203.

Lyons, J. 1996. Patterns in the species composition of fish assemblages among Wisconsin streams. Environmental Biology of Fishes 45:329–341.

Maret, T. R., C. T. Robinson, and G. W. Minshall. 1997. Fish assemblages and environmental correlates in least-disturbed streams in the upper Snake River basin. Transactions of the American Fisheries Society 126:200–216.

Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. Zero tolerance ecology: improving ecological inference by modeling the source of zero observations. Ecology Letters 8:1235–1246.

Matthews, W. J. 1986. Fish faunal "breaks" and streamorder in the eastern and central United States. Environmental Biology of Fishes 17:81–92.

Matthews, W. J. 1998. Patterns in Freshwater Ecology. Chapman and Hall, New York.

Maunder, M. N., and A. E. Punt. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research 70:141–159.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM Software Design, Gleneden Beach, Oregon.

McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior, p. 105–142. *In:* Frontiers of Economics. P. Zarembka (ed.). Academic Press, New York.

Meyer, K. A., and B. High. 2011. Accuracy of removal electrofishing estimates of trout abundance in Rocky Mountain streams. North American Journal of Fisheries Management 31:923–933.

Morin, R., and R. J. Naiman. 1990. The relation of stream order to fish community dynamics in a boreal forest watershed. Polske Archiwum Hydrobiologii 37:135–150.

Mujalli, R. O., and J. de Ona. 2013. Injury severity models for motor vehicle accidents: a review. Proceedings of the Institution of Civil Engineers: Transport 166:255–270.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2015. vegan: community ecology package. R package version 2.2-1. https://CRAN.R-project.org/package=vegan

Ott, R. L., and M. Longnecker. 2010. An Introduction to Statistical Methods and Data Analysis. Sixth edition. Brooks/Cole, Cengage learning, Belmont, California.

Paller, M. H. 1994. Relationships between fish assemblage structure and stream order in South Carolina coastal plain streams. Transactions of the American Fisheries Society 123:150–161.

Platts, W. S. 1983. Vegetation requirements for fisheries habitats, p. 184–188. *In:* Managing Intermountain Rangelands—Improvement of Range and Wildlife Habitats. S. B. Monsen and N. Shaw (compilers). U.S. Forest Service General Technical Report INT-157, Washington, D.C.

Price, A. L., and J. T. Peterson. 2010. Estimation and modeling of electrofishing capture efficiency for fishes in wadeable warmwater streams. North American Journal of Fisheries Management 30:481–498.

Quist, M. C., P. A. Fay, C. S. Guy, A. K. Knapp, and B. N. Rubenstein. 2003. Military training effects on terrestrial and aquatic communities on a grassland military installation. Ecological Applications 13:432–442.

Quist, M. C., W. A. Hubert, and D. J. Isaak. 2004. Fish assemblage structure and relations with environmental conditions in a Rocky Mountain watershed. Canadian Journal of Zoology 82:1554–1565.

Quist, M. C., F. J. Rahel, and W. A. Hubert. 2005. Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fishes. Ecology of Freshwater Fish 14:24–39.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rahel, F. J., and W. A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain–Great Plains stream: biotic zonation and additive patterns of community change. Transactions of the American Fisheries Society 120:319–332.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081–1093.

Rice, J. C. 2005. Understanding fish habitat ecology to achieve conservation. Journal of Fish Biology 67:1–22.

Riley, S. C., K. D. Fausch, and C. Gowan. 1992. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fish 1:112–122.

Ruetz, C. R., III, D. G. Uzarski, D. M. Krueger, and E. S. Rutherford. 2007. Sampling a littoral fish assemblage: comparison of small-mesh fyke netting and boat electrofishing. North American Journal of Fisheries Management 27:825–831.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada Bulletin 184.

Sheldon, A. L. 1968. Species diversity and longitudinal succession in stream fishes. Ecology 49:193–198.

Shepard, B. B. 2004. Factors that may be influencing nonnative brook trout invasion and their displacement of native westslope cutthroat trout in three adjacent southwestern Montana streams. North American Journal of Fisheries Management 24:1088–1100.

Simonson, T. D., and J. Lyons. 1995. Comparison of catch per effort and removal procedures for sampling stream fish assemblages. North American Journal of Fisheries Management 15:419–427.

Simonson, T. D., J. Lyons, and P. D. Kanehl. 1994. Quantifying fish habitat in streams: transect spacing, sample size, and a proposed framework. North American Journal of Fisheries Management 14:607–615.

Sindt, A. R., M. C. Quist, and C. L. Pierce. 2012. Habitat associations of fish species of greatest conservation need at multiple spatial scales in wadeable Iowa streams. North American Journal of Fisheries Management 32:1046–1061.

Smith, C. D., M. C. Quist, and R. S. Hardy. 2016. Fish assemblage structure and habitat associations in a large western river system. River Research and Applications 32: 622–638.

Waite, I. R., and K. D. Carpenter. 2000. Associations among fish assemblage structure and environmental variables in Willamette basin streams, Oregon. Transactions of the American Fisheries Society 129:754–770.

Wallace, R. L., and D. W. Zaroban. 2013. Native Fishes of Idaho. American Fisheries Society, Bethesda, Maryland.

Walrath, J. D., D. C. Dauwalter, and D. Reinke. 2016. Influence of stream condition on habitat diversity and fish assemblages in an impaired upper Snake River basin watershed. Transactions of the American Fisheries Society 145:821–834.

Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems, p. 29–42. *In:* Dynamics of Lotic Ecosystems. T. D. Fontaine and S. M. Bartell (eds.). Ann Arbor Science, Ann Arbor, Michigan.

Watkins, C. J., B. S. Stevens, M. C. Quist, B. B. Shepard, and S. C. Ireland. 2015. Patterns of fish assemblage structure and habitat use among main- and side-channel environments in the lower Kootenai River, Idaho. Transactions of the American Fisheries Society 144:1340–1355.

Winemiller, K. O., and M. A. Leslie. 1992. Fish assemblages across a complex tropical freshwater/marine ecotone. Environmental Biology of Fishes 34:29–50.

Zarkami, R., P. Goethals, and N. De Pauw. 2010. Use of classification tree methods to study the habitat requirements of Tench (*Tinca tinca*) (L. 1758). Caspian Journal of Environmental Sciences 8:55–63.

Zeileis, A., and C. Kleiber. 2015. Countreg: count data regression. R package version 0.1-5. https://r-forge.r-project.org/projects/countreg