MICROHABITAT USE BY NATIVE FISHES IN REHABILITATED REACHES OF THE KOOTENAI RIVER, IDAHO

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by

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AUTHORIZATION TO SUBMIT THESIS

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ABSTRACT

Fish and microhabitat data were collected at 542 locations in the Kootenai River, Idaho, during 2014 and 2015 to evaluate the effects of habitat rehabilitation on the fish assemblage. Samples were collected from locally-treated and locally-untreated areas of the river to investigate habitat conditions related to the occurrence and relative abundance of fishes. Fishes sampled from backwaters composed 71% of the overall catch and 84% of the catch from locally-untreated areas of the river. Assemblage-level ordinations and population-level regression models suggested that water depth and current velocity were the most important microhabitat variables influencing fish assemblage structure. Specifically, shallow habitats with low current velocities were important for native fishes and likely serve as rearing areas. These microhabitat conditions typically characterize backwater and channel-margin habitats that are vulnerable to anthropogenic perturbation. Conserving these habitats in large, regulated rivers would enable natural channel forming processes for the benefit of native fishes.

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DEDICATION

This thesis is dedicated to my grandmother, Beverly.

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INTRODUCTION

Physical habitat has long been recognized as one of the primary factors influencing the structure and composition of fish assemblages (Gorman and Karr 1978; Schlosser 1982). Understanding associations between fishes and their habitat has become an important focus of fish science (Rosenfeld 2003) and many natural resource agencies support programs that evaluate, monitor, and protect aquatic and riparian habitats for the benefit of fish populations (Fisher and Burroughs 2003). Individual fish species at all life stages have evolved with and are adapted to specific physical components of an aquatic system. Understanding the habitat needs for each life stage serves to provide scientists with an understanding of population- and assemblage-level habitat associations for conservation and management purposes (Schlosser 1991; Fisher et al. 2012).

Changes in habitat quality and quantity have been identified as primary factors for declining freshwater fish populations across North America (Ricciardi and Rasmussen 1999). In the Unites States and throughout the world, large river systems have been developed to serve societal needs (e.g., water storage, navigational routes, power generation, flood control) which has resulted in widespread degradation and loss of fish habitat (Dynesius and Nilsson 1994; Nilsson et al. 2005). Most notably, dams and their impoundments are considered among the greatest threats to ecosystem function; they have been implicated in restricting nutrient and sediment delivery, homogenizing channels, and altering thermal and discharge regimes (Baxter 1977). Levees constructed alongside rivers serve to confine flow and disconnect rivers from their floodplains. Dams and levees limit connections between aquatic and terrestrial environments, create movement barriers for fishes, and decrease aquatic habitat complexity (Ward and Stanford 1995). Consequently, these water development activities have been shown to cause declines in fluvial fish populations (Paragamian 2002; Quist et al. 2005).

With an increasing focus on species conservation, lotic systems have become a target for habitat restoration and rehabilitation projects in an attempt to mitigate the effects of anthropogenic disturbance (Gore and Shields 1995; Bernhardt et al. 2005; Lake et al. 2007). Placement of large woody habitat features and other engineered structures (e.g., riprapped shoreline) in rivers and streams has become one of the most common techniques used to improve fish habitat (Madejczyk et al. 1998; Schloesser et al. 2012; Roni et al. 2015). These structures are designed to meet the ecological needs for many riverine fishes by providing diverse physical habitat that may otherwise be absent in human-modified rivers. Engineered restoration structures serve to create dynamic habitats that function similarly to those of pre-modified conditions. In particular, engineered structures increase habitat complexity by decreasing current velocity and dispersing flow, thereby allowing sediment deposition, nutrient exchange, and localized fluctuations in water temperature (Cushman 1985; Junk et al. 1989).

The Kootenai River is a large western river that has experienced habitat alterations and improvements. The river originates in British Columbia, Canada, and flows into the United States passing through the states of Montana and Idaho. In Idaho, the river is characterized by a large floodplain that historically served as inundated terrestrial habitat during spring freshet and other high-water events. However, shoreline and instream developments have restricted the river's access to the floodplain. Beginning in the late 1800s, levees were constructed for flood control purposes on top of natural sand levees. Levee construction has eliminated approximately 20,230 hectares of floodplain habitat

(KTOI 2009). The construction of Libby Dam, a large hydroelectric power facility located near Libby, Montana, was completed in 1972 and has altered historic flow, temperature, and nutrient regimes (Woods 1982; Knudson 1994). Consequently, shifts in fish assemblage structure downstream of Libby Dam have been reported, including population declines of at least two species of conservation concern: Burbot *Lota lota* and White Sturgeon *Acipenser transmontanus* (Paragamian et al. 2000; Paragamian et al. 2001).

Declines in native fish populations of the lower Kootenai River (i.e., downstream of Libby Dam) have motivated efforts to improve aquatic habitat (Duke et al. 1999; KTOI 2009; Paragamian and Hansen 2009; Paragamian 2012). The Kootenai Tribe of Idaho and their collaborators initiated a large-scale and long-term habitat rehabilitation program to enhance existing habitat for the benefit of native fish at all life history stages (KTOI 2009). The objectives of the habitat rehabilitation program are numerous, but some of the primary projects include treatments designed to disperse flow, create floodplain habitats, increase substrate heterogeneity, and create complex in-water habitats by adding woody structures. This habitat rehabilitation program has an adaptive management component that relies on monitoring to assess the effectiveness of each project and the cumulative effects of multiple projects on habitat characteristics and fish populations. Information from this monitoring is used to modify the locations and designs of future habitat rehabilitation efforts.

Since 2011, several habitat rehabilitation projects have been implemented, primarily in a 12 km braided segment of river (KTOI 2009). Although rehabilitated habitats were found to support native fishes, nonnative fishes have also been documented in some rehabilitated areas of the Kootenai River (Watkins et al. 2015). Habitat alteration has been associated with range expansion of nonnative fishes (Moyle and Light 1996; Quist et al.

2005). Watkins et al. (2015) surveyed habitat rehabilitation projects in the Kootenai River to evaluate fish-habitat relationships and assess habitat rehabilitation efforts. An important finding of the research was that nonnative fishes were often found in association with areas of the river that had been rehabilitated. Their study focused on segment- and reach-levels (terminology following Frissell et al. 1998). As such, the exact role of habitat treatments on the occurrence of fishes could not be evaluated because fish are likely selecting habitat features at a much smaller spatial scale. Understanding the most appropriate scale (segment, reach, or microhabitat) for assessing and monitoring habitat rehabilitation activities is critically important for resource managers.

We investigated the microhabitat use by fishes in rehabilitated reaches of the Kootenai River to determine fine-scale habitat associations of fishes. We sought to describe microhabitat use by fishes at the assemblage and population levels to evaluate the response of fishes to habitat improvements. Results from this study will provide insight into the design of future habitat structures to maximize the benefit of the habitat rehabilitation program. The specific objectives of this study were to (1) describe microhabitat use by fishes and (2) develop predictive models of resource use.

STUDY AREA

The Kootenai River is the second largest tributary to the Columbia River, and has an international and interstate watershed that drains an area of approximately 50,000 km^2 (Knudson 1994). The river originates in Kootenay National Park, British Columbia, Canada, at an elevation of 3,618 m. From British Columbia, the river flows 775 km to its terminus, coursing through northwestern Montana where it is impounded by Libby Dam and forms Lake Koocanusa. From Libby Dam, the river flows south and west through Montana before entering the panhandle of Idaho. It then flows north and returns to British Columbia where it enters Kootenay Lake and joins the Columbia River at an elevation of 418 m (Bonde and Bush 1975).

In Idaho, the Kootenai River is categorized into three distinct segments based on geomorphology: canyon, braided, and meander (Smith et al. 2016). The canyon segment is characterized by high current velocities, large substrate, and a restricted floodplain. The braided segment is a transitional zone that is characterized by high rates of sediment deposition, low gradient, wide valley with prominent floodplain, and an anastomose channel where several habitat rehabilitation treatments have been constructed to date. The meander segment has low current velocities, low gradient, and a single, sinuous channel. The braided segment of the Kootenai River is particularly unique because it exhibits a high level of habitat complexity and dynamism when compared to the canyon and meander segments (Smith et al. 2016). Consequently, the braided segment has the highest fish species richness relative to the canyon and meander segments.

METHODS

Field sampling

Microhabitat associations of fishes were assessed using a prepositioned areal electrofishing device (PAED; Bain et al. 1985, Dauwalter et al. 2014). A PAED consisted of a cathode and anode that were powered by a Smith-Root LR-24 backpack electrofishing unit (Smith-Root, Inc.; Vancouver, Washington) positioned on shore. The electrodes were constructed with a 9.1 m length of insulated tinned-copper wire that terminated in a plug

(Midwest Lakes Electrofishing Systems; Polo, Missouri). The insulated wire was joined to a length of 4.8 mm diameter stainless steel aircraft (SSA) cable that remained exposed to complete the electrical circuit. The cathode was constructed with 6.1 m of SSA cable and the anode used 3.4 m. A wire rope clip secured a loop for the anode, producing a circle (surface area = 0.80 m^2).

Fish and habitat surveys were conducted in 4 m^2 sites within the braided segment of the Kootenai River, Idaho, during summers and autumns of 2014 and 2015. Sites were established by randomly selecting a 500 m reach of shoreline and sampling fishes and habitat characteristics at eight locations (i.e., sites) that were spaced approximately 50 m apart. All sites were sampled from areas with an average depth of <1.0 m to allow capture of immobilized fish by a dip netter wearing chest waders. Reaches were identified to reduce travel time between sites and were not used as a unit of inference.

A sampling event began by deploying the anode. Next, the cathode was positioned approximately 1 m downstream of the anode to ensure consistent electrical fields among sites. The PAEDs were deployed in an upstream direction and each site remained undisturbed for a minimum of 30 minutes before electrifying the equipment. The time delay between deploying and electrifying the equipment (i.e., PAED “set time”) allows fishes to recolonize the area and assume normal behavior and habitat use (Dauwalter et al. 2014; Branigan et al. *in review*). Following the set time, PAEDs were electrified in the same order they were deployed by applying pulsed DC (500-800 W) for 20 s. A single netter collected all immobilized fishes with a dip net (6 mm mesh). Operators ensured that fishes were not frightened into the immobilization zone while approaching each site. Captured fishes were identified to species, measured (total length; mm), and released downstream to avoid recapture in subsequent sites. If a fish could not be identified, it was preserved in 10% formalin and transported to the University of Idaho. Overall, 542 sites were sampled during 2014 (n = 217) and 2015 (n = 325).

After fish were collected and processed, microhabitat characteristics were measured and recorded for each site. Because we used pulsed DC to electrify the PAEDs, fishes were immobilized beyond the confines of the 0.80 m^2 anode ring. Therefore, we collected habitat data within a 2 m square quadrat (surface area = 4 m^2) centered on the anode. This area fully encompassed the immobilization zone of the PAED and served as the unit of inference. A quadrat was constructed at each site to isolate the sampling unit and provide a consistent framework for microhabitat data collection. The quadrat was oriented perpendicular to the water current, such that three transects were created and positioned upstream, downstream, and bisecting the circular anode. Measurements of water depth, bottom current velocity, mean column current velocity, and substrate type were recorded at 0, 20, 40, 50, 60, 80, and 100% of the length of each transect. Current velocity was measured with a portable velocity meter (Flo-Mate Model 2000; Marsh-McBirney, Inc.; Loveland, Colorado) at 60% of the water depth when depth was less than 0.75 m. For depths greater than 0.75 m, velocity was recorded at 20% and 80% of the depth and averaged (Buchanan and Somers 1969). The dominant substrate type at each transect point was classified based on a modified Wentworth scale as: silt-clay (<0.064 mm diameter), sand (0.065-2 mm), gravel (3-15 mm), pebble (16-64 mm), cobble (64-256 mm), or boulder (>257 mm; Cummins 1962).

Instream cover features were also measured at each site. Instream cover was defined as any structure within the quadrat that had an area ≥0.04 m^2 along any two planes of dimension. Cover types consisted of submerged aquatic vegetation, emergent aquatic vegetation, branch complex, single log, log complex, bank roots, rootwad, stump, single boulder, boulder complex, and rip rap. For each cover feature in the quadrat, one length measurement was recorded along the longest axis and three evenly-spaced width measurements oriented perpendicular to the length measurement. Width measurements were averaged to generate an average width, which was then multiplied by the length measurement to estimate total area for each cover feature (Sindt et al. 2012).

In addition to microhabitat data, site characteristics were recorded to further describe each location. We categorized whether each site was located within a channel or a backwater habitat. Distances (m) from the center of the anode to the shore and to the thalweg were measured using a laser range finder. Each site was characterized as “treated” if it was located within 50 m of a localized treatment area, or “untreated”, if not. Even though two treatment classifications were used during this study, the entire braided segment of the Kootenai River may be considered “treated” in the context of habitat rehabilitation at the segment scale. Therefore, inferences drawn regarding treatment type were made with this caveat.

Habitat and fish assemblage structure

Associations among continuous habitat variables were assessed using principal components analysis (PCA). Supplemental classifications were created to partition sites into one of four categories: treated backwater, treated channel, untreated backwater, or untreated channel. One site was excluded from the PCA due to an anomalous measure of bottom velocity complexity. This particular site was composed entirely of large angular substrate (i.e., rip rap) and extreme variation in current velocity was observed. The PCA was fit using scaled data with FactorMineR package in Program R (Lê et al. 2008; R Core Team 2012).

Nonmetric multidimensional scaling (NMDS) was used to investigate fish assemblage structure and associated habitat characteristics. Nonmetric multidimensional scaling is an ordination technique commonly used to describe fish assemblage relationships (Rowe et al. 2009). Ordinations were fit for two groups of fish: age-0 and all fish. No stable ordinations were observed for fish greater than age 0, so catch for both age categories were combined. Empirical length-at-age data from the Kootenai River were used to estimate ages of Largescale Sucker *Catostomus macrocheilus* and Mountain Whitefish *Prosopium williamsoni* (M. C. Quist, unpublished data). Length criteria from Pearsons et al. (1992) were used to estimate age for Longnose Dace *Rhinichthys cataractae*, Redside Shiner *Richardsonius balteatus*, and Torrent Sculpin *Cottus rhotheus*. Ordinations were fit for both age classes of fish using presence-absence and count data. Due to large differences in counts of fish among sites and among habitat metrics, a Wisconsin double standardization and square root transformation were applied to count data to reduce ordination stress. The distance matrices used were comprised only of sites where at least one species was present (n_{all} = 249; n_{age0} = 178). Furthermore, catches of Longnose Sucker *Catostomus catostomus*, Northern Pikeminnow *Ptychocheilus oregonensis*, and Redband Trout *Oncorhynchus mykiss* were omitted from the NMDS ordinations and species-specific analyses (see below) because these species were observed in less than 3% of all samples. Habitat variables that were significant ($P \leq 0.05$) after a permutation test (999 iterations) were used in each ordination using the envfit function from the Vegan package in Program R (Oksanen et al. 2015). Due to marked differences in catch between backwaters and channels (see results), differences in fish assemblage structure among the habitat types were evaluated using permutational multivariate analysis of variation (PERMANOVA). A Bray-Curtis dissimilarity measure was used for NMDS and PERMANOVA analyses using MetaMDS and adonis functions from the Vegan package in Program R (Oksanen et al. 2015).

Species-specific habitat associations

Species-specific habitat relationships using occurrence (i.e., presence-absence) and count data (i.e., relative abundance) were assessed with hurdle models. Hurdle models are a two-stage regression, whereby the first stage predicts the probability of a species presence using logistic regression (binomial response variable) and the second stage predicts the relative abundance of a species using non-zero count data (e.g., negative-binomial error distribution; Martin et al. 2005). This modelling approach allows the factors that influence a species presence to be modelled separately from those influencing relative abundance (Wenger and Freeman 2008).

Hurdle models were constructed using GLM and ZEROTRUNC functions in Program R (R Core Team 2012; Zeileis and Kleiber 2015). Habitat-specific (i.e., backwater or channel) models were created to elucidate important habitat variables among lentic and lotic environments. Models were fit for species that were sampled from at least 14 backwater sites (10.0% of total) or 30 channel sites (7.5% of total) to ensure that adequate sample sizes were used to inform models. Model fit was assessed for each stage and habitat type using McFadden's pseudo R^2, which was calculated as one minus the difference in the log-likelihood values of the most parameterized model (i.e., global model) and an intercept-only model (McFadden 1974). McFadden's pseudo R^2 values vary from 0.0 to 1.0, and values as low as 0.10 have been reported as having good model fit (Hosmer and Lemeshow 1989).

Spearman's rank-order correlation was used to investigate relationships among habitat variables (Sindt et al. 2012). If high correlation existed between any pair of variables ($|\rho| > 0.70$), then the most ecologically important and interpretable variable was retained for modelling (Table 1). Mean depth and mean coefficient of variation (CV) of depth were highly correlated ($\rho = -0.83$), but were retained for the analysis because they could influence occurrence and relative abundances of fishes differently. However, these two variables were not included together in any model during the regression modelling procedure.

Thirteen to sixteen *a priori* candidate models were fit for each modelling stage for fishes that satisfied sample size requirements associated with each habitat type. Habitat treatment was coded as a binary categorical variable. Interactions with habitat treatment were evaluated by including interactive models in each candidate set using two habitat variables: woody cover and fine substrate. Given the high number of small-bodied fishes sampled, age categories (described above) were used to model age-0 fish separately from those estimated to be older than age 0. Candidate models were ranked using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). The model with the smallest AIC_c value from each candidate set was considered to be the top model, but models within two AIC_c units of the top model were also considered plausible (Burnham and Anderson 2002).

RESULTS

A total of 1,447 native fish representing four families and eight species was collected from 542 prepositioned electrofishing samples. Data collected in 2014 and 2015 were combined because preliminary regression analyses indicated similar patterns in habitat use between years. Differences were observed in the proportion of sites occupied and in the number of fish captured between backwater and channel habitats for age-0 fish and those older than age-0. Age-0 fish occurred in a much higher proportion of backwater sites than channel sites and many more age-0 fish were captured in backwater sites than in channel sites (Figure 1). Fishes sampled from backwater habitats accounted for 71% of the overall catch and 84% of the catch from untreated areas of the river. Of those fishes sampled from backwaters, 89% were estimated as age 0. Fish older than age 0 were slightly more abundant and occupied a higher proportion of sites in channels than backwater areas.

Largescale Sucker was the most abundant age-0 fish species sampled from both habitat types (Figure 2). Species occurrence and relative abundance of fishes greater than age 0 varied across habitat types. Redside Shiner was most abundant in backwaters, whereas Torrent Sculpin was most abundant in channel habitats.

The PCA displayed a large cluster of sites centered near the origin, indicating measured habitat variables did not clearly differentiate habitats. Nonetheless, patterns among the habitat types were evident (Figure 3). The first PCA axis explained 20.5% of the variation. Proportion of fine substrate and distance to thalweg were positively loaded on PCA axis 1 and proportion of large substrates and mean current velocity were negatively loaded on PCA axis 1. The second PCA axis explained 13.8% of the variation. Area of rocky cover features and CV of depth were positively loaded on PCA axis 2, whereas mean current velocity and mean depth were negatively loaded on PCA axis 2. Sites sampled in channel environments had higher mean current velocities and were in closer proximity to the thalweg compared to backwater sites. However, sites sampled from treated channels generally exhibited higher CV of depth and increased area of woody and rocky cover features. Sites sampled from untreated backwaters had a larger variation in substrate size when compared to sites sampled from treated backwaters.

Stable NMDS ordinations were generated for all fish using species occurrence (stress = 0.04; Figure 4) and count data (stress = 0.04; Figure 5). The PERMANOVA analyses using occurrence and count data indicated that the fish assemblage differed significantly between backwater and channel habitats ($P < 0.001$). Torrent Sculpin were associated only with channel habitats. Largescale Sucker, Longnose Dace, Mountain Whitefish, and Redside Shiner were associated with both channel and backwater habitats. The NMDS ordinations for both data types indicated that Largescale Sucker and Redside Shiner were most closely associated with high proportions of fine substrates, vegetated cover, and increased distance to the thalweg. Longnose Dace and Torrent Sculpin were associated with high proportions of large substrates, rocky and woody cover, and CV of depth. Mountain Whitefish were associated directly with mean depth and current velocity.

Stable NMDS ordinations were fit for age-0 fish using both species occurrence (stress = 0.03; Figure 6) and count data (stress = 0.04; Figure 7), and patterns were similar to those observed in ordinations using all fishes. Results from PERMANOVA analyses using occurrence and count data indicated that the age-0 fish assemblage differed between backwater and channel habitats ($P < 0.001$). Largescale Sucker and Redside Shiner were associated with higher proportions of fine substrate and increased distance to the thalweg.

Longnose Dace and Torrent Sculpin were associated with higher CV of depth. Mountain Whitefish was associated with deep water and fast current velocities.

Models predicting the occurrence of fishes were fit for three species sampled from backwaters and four species from channels. Patterns in habitat use emerged that indicated some species occupied benthic habitats (Table 2). Presence of age-0 Largescale Sucker and Longnose Dace were positively related to the proportion of large substrate and negatively related to mean depth. Torrent Sculpin older than age 0 displayed similar habitat associations and were positively related to the presence of woody cover. Presence of age-0 Mountain Whitefish was negatively related to woody cover except at treated sites where the relationship with woody cover was positive. Although Redside Shiner satisfied sample size requirements for modelling purposes, models generated using occurrence data consistently exhibited poor fit (Table 2).

Top models explaining the relative abundance of fishes sampled from backwaters and channels differed from those associated with occurrence (Table 3). In backwater habitats, the relative abundance of age-0 Largescale Sucker and Redside Shiner were negatively related to the proportion of large substrate and mean depth. Age-0 Longnose Dace were negatively related to mean current velocity. Fishes sampled from channel habitats had different relationships with microhabitat characteristics than fishes sampled from backwaters. Relative abundance of age-0 Largescale Sucker was positively related to the proportion of fine substrate. Relative abundance of age-0 Mountain Whitefish was also positively related to the proportion of fine substrate but only when sampled from treated sites. Age-0 Longnose Dace were abundant in shallow areas and low current velocities.

Relative abundance of Torrent Sculpin greater than age 0 was positively related to rocky cover features (e.g., riprapped shorelines, boulders).

DISCUSSION

Flow regulation and channel alteration have been identified as primary drivers of change in riverine fish assemblages across North America (Rinne et al. 2005). Anthropogenic alteration of large rivers modifies the timing, duration, and frequency of flood events that are responsible for maintaining important ecological processes (Poff and Ward 1989; Ward and Stanford 1995). Flooding enhances habitat complexity through the formation of lotic and lentic water bodies that vary in area, connectivity, and local microhabitat conditions (Welcomme 1979; Junk et al. 1989; Ward and Stanford 1995). In regulated systems like the Kootenai River, connections to off-channel units and inundated floodplains are limited and habitat complexity is often low. In particular, the formation of shallow, slow current velocity (SSCV) habitats are minimized due to channelization and flow regulation (Poff et al. 1997; Bowen et al. 2003). Substrate diversity and instream cover availability are also related to discharge and are especially reduced in regulated floodplain rivers (Gore and Shields 1995). The availability and diversity of depth, current velocity, substrate, and instream cover are thought to serve as the abiotic components that structure lotic fish assemblages at small scales (Gorman and Karr 1978; Bain et al. 1988). However, the characteristics of these habitat features are largely a function of discharge and often become homogenized in large rivers as a result of flow regulation (Ligon et al. 1995).

Fish assemblage structure differed between backwaters and channels of the Kootenai River, but similar patterns in habitat use emerged. Our analyses suggested that water depth and current velocity were the most important microhabitat variables influencing habitat use by fishes. We found that occurrence and abundance of age-0 fish for many species were positively related to SSCV habitats. Shallow water provides refuge from predation by larger-bodied fishes that typically avoid shallow habitats due to their vulnerability to terrestrial predators (Power 1984; Schlosser 1987). Habitats characterized by slow current velocities offer refuge from swift currents that may displace small fishes (Ottaway and Clarke 1981). Furthermore, areas of reduced flow might also provide conditions necessary for phytoplankton and zooplankton production, both of which serve as food resources for small-bodied or young fishes (Spaink et al. 1998; Nunn et al. 2007a, 2007b). In concert, shallow habitats with slow current velocities warm quickly and can extend the growth season for fishes (Ward and Stanford 1995). Moyle and Vondracek (1985), Watkins et al. (1997), and Reinhold et al. (2016) reported on the importance of SSCV habitats in large river systems. Unfortunately, the formation of SSCV habitats are often dramatically reduced in systems where channelization and flow regulation occur (Poff et al. 1997; Bowen et al. 2003), as has occurred in the Kootenai River system.

Relationships describing the occurrence and relative abundance of fishes were variable with regard to substrate type. In general, the occurrence of fishes was positively related to large substrate, whereas relative abundance was negatively related to large substrate. Disentangling the exact mechanism(s) responsible for the observed pattern between fish abundance and substrate type is difficult because flow regulates substrate composition, water residence time, and potential food resources (Allan 1995; Dodds and Whiles 2010). For example, backwaters that contained higher proportions of large substrates (e.g., gravel, cobble) were most often lotic channels during periods of high flow prior to being sampled as a backwater. Conversely, backwaters containing a high proportion of fine substrates (e.g., silt, sand) were generally lentic throughout the study. The negative relationship between fish abundance and large substrate may be attributed in part to the observed variation in flow and subsequent substrate characteristics. Alternatively, the relationship may be attributed to greater food availability associated with water residence time. Backwater habitats have been shown to contain twice the amount of organic matter and up to 100 times the amount of zooplankton when compared to channel habitats, largely due to the retention of water (Speaker et al. 1984; Spaink et al. 1998; Ward and Stanford 1995). Regardless of the mechanism, the disproportionately high catch of fish in backwaters suggests that these areas are important for native fish production and are likely serving as nursery habitat for young fish (Kwak 1988; Scheidegger and Bain 1995; Copp 1997a, 1997b; Freeman et al. 2001). In addition, our analyses indicated that backwaters had different fish assemblages than channels, providing further evidence that backwater habitats are important for structuring fish assemblages.

Despite the aforementioned relationships with streamflow and substrate, the occurrence and relative abundance of fishes were related to SSCV habitats that were characterized by a variety of substrates. Fine substrates are relatively scarce throughout the braided section of the Kootenai River but can be found in off-channel units (i.e., side channels; Watkins et al. 2015). In channel habitats, the relative abundance of age-0 Largescale Sucker was positively related to fine substrate. This association was also evident in the NMDS ordinations. Nearshore habitats characterized by shallow water, low current velocities, and fine substrate have been identified as important rearing areas for imperiled catostomid species of the Little Colorado River, Arizona (Childs et al. 1998). In the Kootenai River, these habitats are likely functioning in a similar manner. Large substrates can be found in both channel and backwater habitats in the Kootenai River and were related to the occurrence of age-0 Largescale Sucker and Longnose Dace, and Torrent Sculpin older than age 0. Longnose Dace was the only species for which relative abundance was positively related to large substrates and is likely reflective of the ecology of the species. The diet of Longnose Dace consists primarily of benthic macroinvertebrates (Wydoski and Whitney 2003), which are generally more abundant in large substrates (Thompson et al. 2001). Although Longnose Dace are typically associated with riffle habitats and high current velocities (Wydoski and Whitney 2003), juveniles are common in areas with low current velocities (Mullen and Burton 1995). In addition to supporting high macroinvertebrate density (Flecker and Allan 1984), rocky substrates may also benefit small-bodied fishes by providing refuge from biotic (e.g., predation) and abiotic (e.g., current velocity) pressures (Persson and Eklöv 1995). As such, habitats composed of shallow, slow-moving water and large substrates likely provide ideal rearing habitat for age-0 fish.

Habitats characterized by the presence of woody cover features were related to the occurrence of Torrent Sculpin and Mountain Whitefish. Placement of instream woody cover features is one of the primary techniques being used to enhance habitat in the Kootenai River. The occurrence of Torrent Sculpin greater than age 0 was positively related to woody cover, presumably as a response to predators. Laboratory experiments have shown that Torrent Sculpin congregate in areas with cover when only fine substrates are available, but distribute when cobble (i.e., cover) is available (Brusven and Rose 1981). We found similar results where the relative abundance of Torrent Sculpin was positively related to rocky cover features (e.g, rip rap, boulders). In addition to providing cover, wood decreases current velocity and retains fine sediments and organic material (Speaker et al. 1984). The occurrence and relative abundance of age-0 Mountain Whitefish was negatively related to woody cover and fine substrate. However, these relationships reversed when the species was sampled from treated sites, which may be related to foraging strategies during early life stages. Chironomid larvae are a major prey item of age-0 Mountain Whitefish (Stalnaker and Gresswell 1974) and unlike many macroinvertebrates, chironomid densities are usually highest in fine substrates (Allan 1995). Although the proposed mechanisms associated with use of wood by Torrent Sculpin and Mountain Whitefish are speculative, these results are of particular interest when applied to the context of the habitat rehabilitation program because it indicates that small-bodied native fishes are using the engineered habitat features.

The fish assemblage of Kootenai River has been evaluated at multiple spatial and temporal scales to assess the effect of habitat rehabilitation on the entire fish assemblage and population abundance of a few targeted fish species. Previous evaluations of the Kootenai River have established that fish assemblages differed among geomorphic sections (Smith et al. 2016) and among main- and side-channels (Watkins et al. 2015). Nonnative fishes were documented in newly-rehabilitated areas in 2013 (e.g., Pumpkinseed *Lepomis gibbosus*, Brown Bullhead *Ameiurus nebulosus*; Watkins et al. 2015; Smith et al. 2016). In our study, no nonnative fishes were sampled which may be due to their absence or the scale of sampling. Our inferences were focused on the microhabitat level (4 m^2 area) whereas Watkins et al. (2015) and Smith et al. (2016) sampled fishes at the river segment and reach scales (several kilometers of river). In addition to sampling nonnative species, the authors documented the occurrence of several native species that were not present in our samples (e.g., Peamouth *Mylocheilus caurinus*, kokanee *Oncorhynchus nerka*) along with increased fish counts. The spatial scale assessed in our study was useful for obtaining species-specific microhabitat data, but 52% of our samples contained no fish. Fish may be absent from samples for several reasons (e.g., abiotic pressures, biotic interactions, gear avoidance), but sampling such a small relative space may be an underlying cause. While it is surprising that no nonnative fishes were sampled in this study, over 1,400 native individuals representing eight species were documented. This highlights the applicability of the sampling scale in a large river system to some extent, but emphasizes the importance of evaluating and monitoring fish populations across multiple spatial scales (Fausch et al. 2002; Sindt et al. 2012).

The current study highlights the importance of SSCV habitats to juvenile and small-bodied fishes in a large river system like the Kootenai River. The availability of SSCV habitats are dependent on flow (Bowen et al. 2003; Reinhold et al. 2016) and a lack of these areas in other large river systems has prompted their artificial development. For example, a variety of approaches (e.g., notching dikes) have been used to create new SSCV habitats in the Missouri River to provide refuge for small-bodied and juvenile native fishes (Ridenour et al. 2009; Papanicolaou et al. 2011; Schloesser et al. 2012). Engineered SSCV habitats in the Mississippi River, USA, and Huntspill River, UK, have resulted in increased abundance and diversity of age-0 fishes when compared to main channel areas (Langler and Smith 2001; Barko et al. 2004). River restoration is a multi-billion dollar industry (Bernhardt et al. 2005), yet most programs fail to monitor or evaluate biological responses to the improvements (Kondalf and Micheli 1995; Roni et al. 2002). The results of this study and those conducted in other large channelized rivers emphasize the importance of SSCV habitats as an integral component of habitat rehabilitation. Incorporating SSCV habitats into the design of habitat enhancement efforts would benefit several fish species of the Kootenai River. In particular, backwaters appear to be important for native fish production and likely provide prey for piscivorous fishes, some of which are species of conservation concern (White Sturgeon, Burbot, Bull Trout *Salvelinus confluentus*). The observed differences in the relationships between occurrence and relative abundance of fishes with regard to substrate type warrants further investigation. Such inquiry may elucidate potential mechanisms that govern fish assemblage structure in SSCV habitats and further guide the design of rehabilitation activities. Low-velocity floodplain habitat is scarce in the Kootenai River system, but the abundance of fish sampled from backwaters suggests that they may serve as a vestige of the historical floodplain. Prioritizing the conservation and enhancement these areas in regulated rivers would enable natural channel forming processes for the benefit of native fishes.

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Table 1. Summary statistics for habitat variables measured at 542 prepositioned electrofishing sites on the Kootenai River, Idaho, during the summers (May-August) and autumns (October-November) of 2014 and 2015. Habitat variables were separated by habitat type (i.e., backwater or channel).

		Habitat type							
		Backwater				Channel			
Variable	Description	Mean	SE	Min	Max	Mean	SE	Min	Max
Depth	Mean depth (m)	0.37	0.02	0.07	0.99	0.46	0.01	0.05	1.03
CV_{Depth}	Mean CV of depth	20.48	0.93	2.96	67.20	26.36	0.93	2.42	114.32
Vel_{MC}	Mean column current velocity (m/s)	0.02	0.001	0.00	0.11	0.27	0.01	0.00	1.20
CV_{VelMC}	Mean CV of mean column current velocity	450.27	106.63	18.71	14832.40	111.76	19.93	8.02	5538.42
Sub_{Fine}	Proportion of substrate that is fine (silt, sand)	0.49	0.03	0.00	1.00	0.30	0.02	0.00	1.00
Sub_{Large}	Proportion of substrate that is large (cobble, boulder)	0.13	0.02	0.00	0.86	0.20	0.01	0.00	1.00
$Cover_{Veg}$	Proportion of sampling area with aquatic macrophytes as cover	0.35	0.08	0.00	4.00	0.10	0.03	0.00	4.00
$Cover_{Rock}$	Proportion of sampling area with boulder or riprap as cover	0.0002	0.0002	0.00	0.04	0.10	0.02	0.00	4.00
$Cover_{Wood}$	Proportion of sampling area with branch complex, log, log complex, rootwad, or stump as cover	0.15	0.04	0.00	3.00	0.39	0.03	0.00	4.00
$Dist_{Thal}$	Distance from center of sampling area to thalweg	199.19	13.72	8.00	585.00	43.94	3.08	0.00	350.00

Table 2. Top binomial logistic regression models used to evaluate the occurrence of fishes in backwaters and channels from the Kootenai River during 2014 and 2015. Akaike's Information Criterion (AIC_c) adjusted for small sample size was used to rank models; only models with a $\Delta AIC \leq 2$ from each candidate set are included. Models in italics indicate the global model used for respective candidate sets. Effect of model covariates are indicated as (positive [+], negative [-]).

Habitat type	Species	Estimated age	Model name	AIC_c	$\Delta\ AIC_c$	K	w_i	R^2
Backwater								
	Largescale Sucker	Age 0	+Sub_{Large}, -Depth, -Vel_{MC}	166.57	0.00	4	0.66	0.18
			+Sub_{Large}, -Depth, -Vel_{MC}, +$Dist_{Thal}$	167.90	1.33	5	0.34	0.19
	Longnose Dace	Age 0	+Sub_{Large}, -Depth	112.23	0.00	3	0.50	0.21
			-Depth	113.43	1.20	2	0.27	0.19
	Redside Shiner	Age 0	-Sub_{Large}	118.02	0.00	2	0.15	0.01
			-Depth	118.59	0.58	2	0.11	<0.01
			+$Cover_{Veg}$	118.62	0.61	2	0.11	<0.01
			+Sub_{Fine}	118.74	0.73	2	0.10	<0.01
			-$Dist_{Thal}$	119.14	1.13	2	0.09	<0.01
			-Vel_{MC}	119.16	1.14	2	0.09	<0.01
			+$Cover_{Wood}$	119.19	1.18	2	0.08	<0.01
			-Sub_{Large}, -Depth	119.32	1.31	3	0.08	<0.01
			-Sub_{Large}, -$Dist_{Thal}$	119.77	1.75	3	0.06	<0.01
Channel								
	Largescale Sucker	Age 0	+Sub_{Large}, -Depth, -Vel_{MC}	160.93	0.00	4	0.56	0.28
			-Depth, -Vel_{MC}	162.47	1.55	3	0.26	0.27
	Longnose Dace	Age 0	+Sub_{Large} , -Depth -Vel_{MC}	235.83	0.00	4	0.72	0.11
	Mountain Whitefish	Age 0	-$Cover_{Wood}$	209.66	0.00	2	0.42	0.06
			-$Cover_{Wood}$, +Sub_{Fine}	209.82	0.16	3	0.39	0.07
			-$Cover_{Wood}$, +TRT, +TRT×$Cover_{Wood}$	211.37	1.71	4	0.18	0.07
	Torrent Sculpin	>Age 0	*+Sub_{Large}, -Depth, -Vel_{MC}, +$Cover_{Wood}$*	314.46	0.00	5	0.99	0.11

Table 3. Top linear regression models used to evaluate the relative abundance of fishes in backwaters and channels from the Kootenai River during 2014 and 2015. Akaike's Information Criterion (AIC_c) adjusted for small sample size was used to rank models; only models with a $\Delta AIC \leq 2$ from each candidate set are included. Effect of model covariates are indicated as (positive [+], negative [-]).

Habitat type	Species	Estimated age	Model name	AIC_c	ΔAIC_c	K	w_i	R^2
Backwater								
	Largescale Sucker	Age 0	$-Sub_{Large}$ -Depth, $-Vel_{MC}$	308.04	0.00	4	0.65	0.09
	Longnose Dace	Age 0	$-Vel_{MC}$	119.22	0.00	2	0.56	0.05
	Redside Shiner	Age 0	$-Sub_{Large}$	102.57	0.00	2	0.55	0.17
			$-Sub_{Large}$, -Depth	103.65	1.08	3	0.32	0.19
Channel								
	Largescale Sucker	Age 0	$+Sub_{Fine,}$ $-Cover_{Wood}$	101.82	0.00	3	0.57	0.12
	Longnose Dace	Age 0	-Depth, $-Vel_{MC}$	94.52	0.00	3	0.35	0.11
			$+Sub_{Large}$, -Depth, $-Vel_{MC}$	95.02	0.50	4	0.29	0.14
	Mountain Whitefish	Age 0	$-Sub_{Fine}$, -TRT, $+TRT \times Sub_{Fine}$	90.70	0.00	4	0.71	0.15
	Torrent Sculpin	>Age 0	$+Cover_{Rock}$	101.50	0.00	2	0.99	0.22

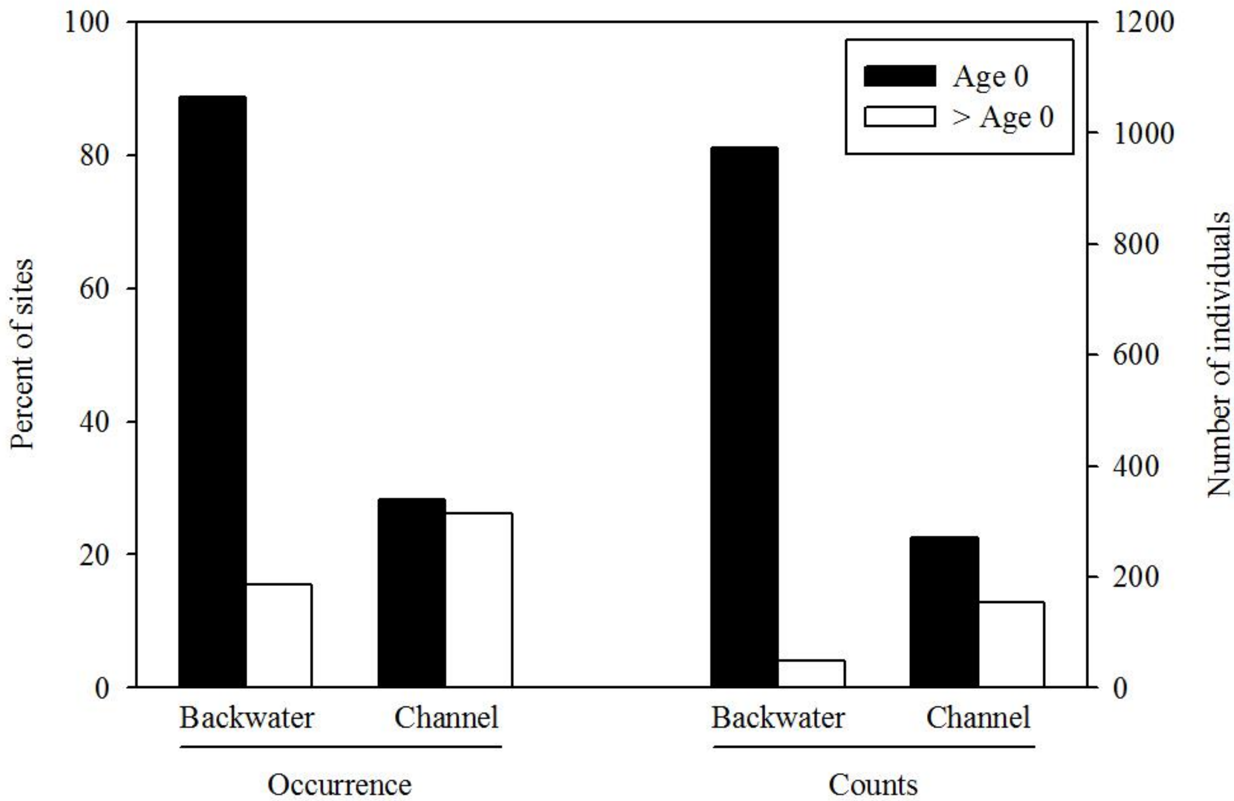

Figure 1. Summary of fish occurrence and abundance by estimated age and habitat type (i.e., backwater or channel) from 542 prepositioned electrofishing sites on the Kootenai River, Idaho during 2014 and 2015. One-hundred-forty-one sites were sampled in backwater habitats; 401 sites were sampled from channel habitats.

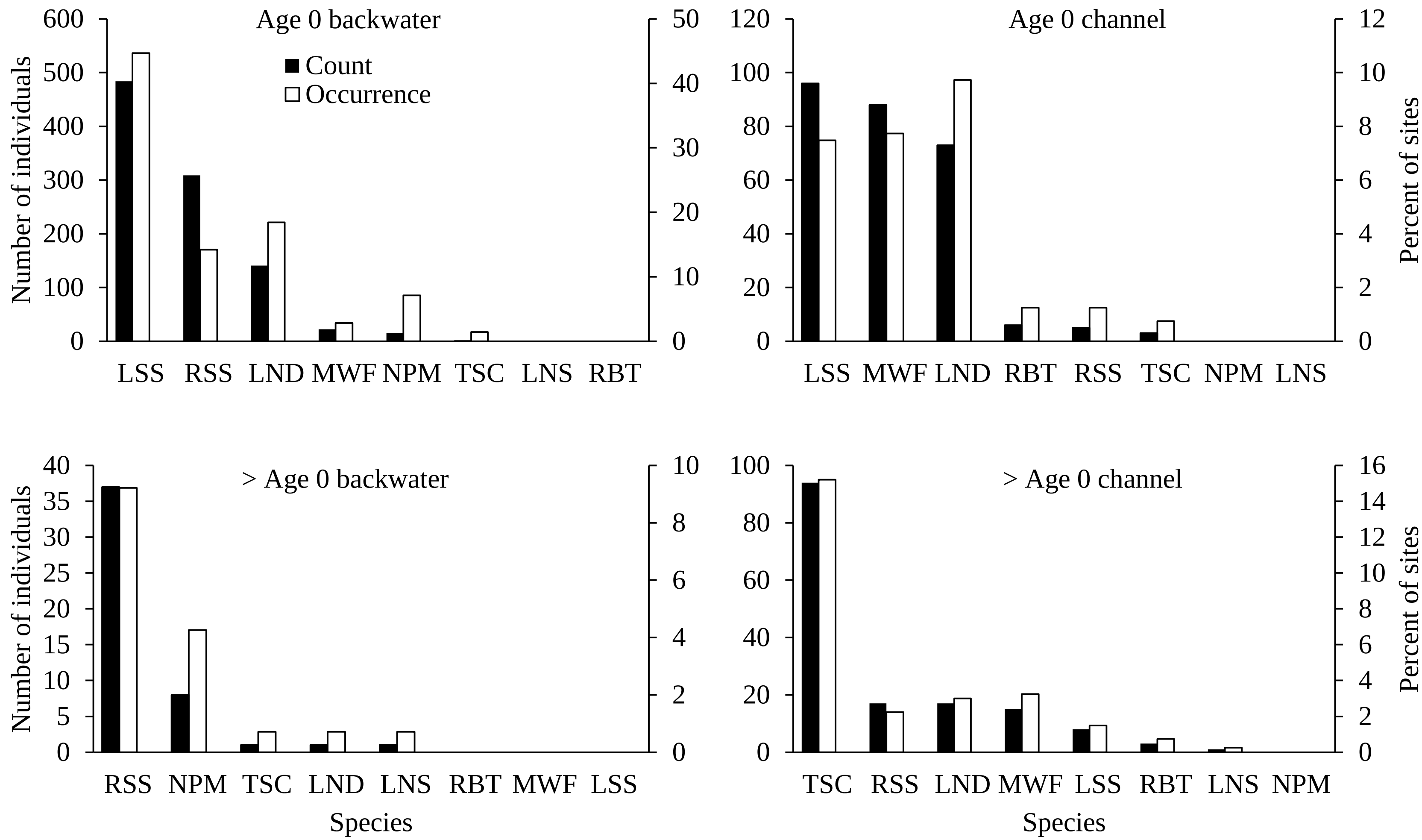

Figure 2. Summary of species occurrence and abundance for age-0 and >age-0 fish sampled from 542 sites on the Kootenai River, Idaho, during 2014 and 2015 (LSS = Largescale Sucker; LND = Longnose Dace; LNS = Longnose Sucker; MWF = Mountain Whitefish; NPM = Northern Pikeminnow; RBT = Redband Trout; RSS = Redside Shiner; TSC = Torrent Sculpin). A total of 141 sites was sampled from backwater habitats and 401 from channel habitats.

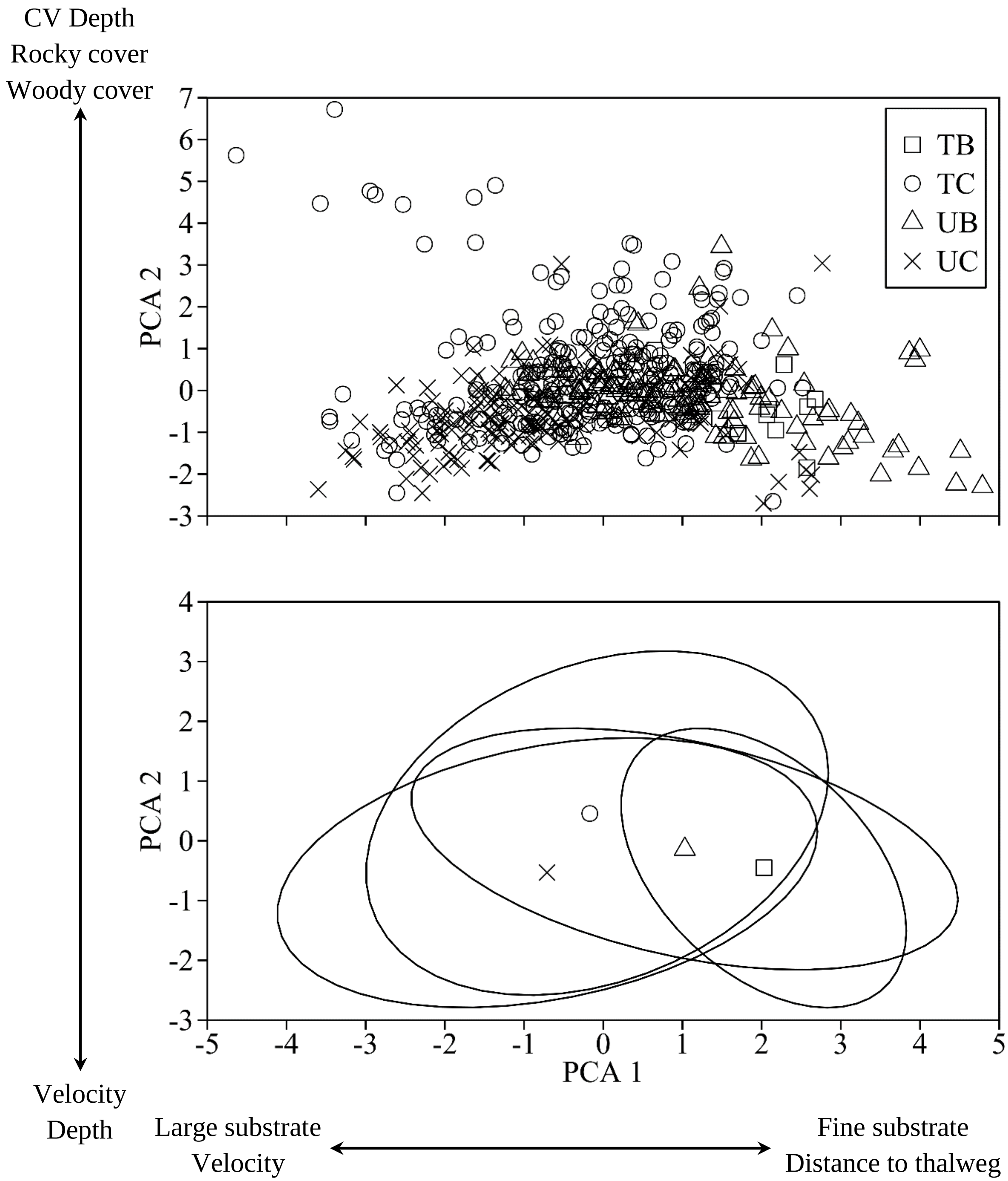

Figure 3. Principal component ordination of habitat characteristics measured at 541 prepositioned electrofishing sites in the Kootenai River in summers (May-August) and autumns (October-November) of 2014 and 2015. The first principal component axis (PCA 1) explained 20.51% of the variation and the second principal component axis (PCA 2) explained 13.76% of the variation. Ellipses represent 95% confidence bounds for each treatment and habitat type (TB = treated backwater; TC = treated channel; UB = untreated backwater; UC = untreated channel).

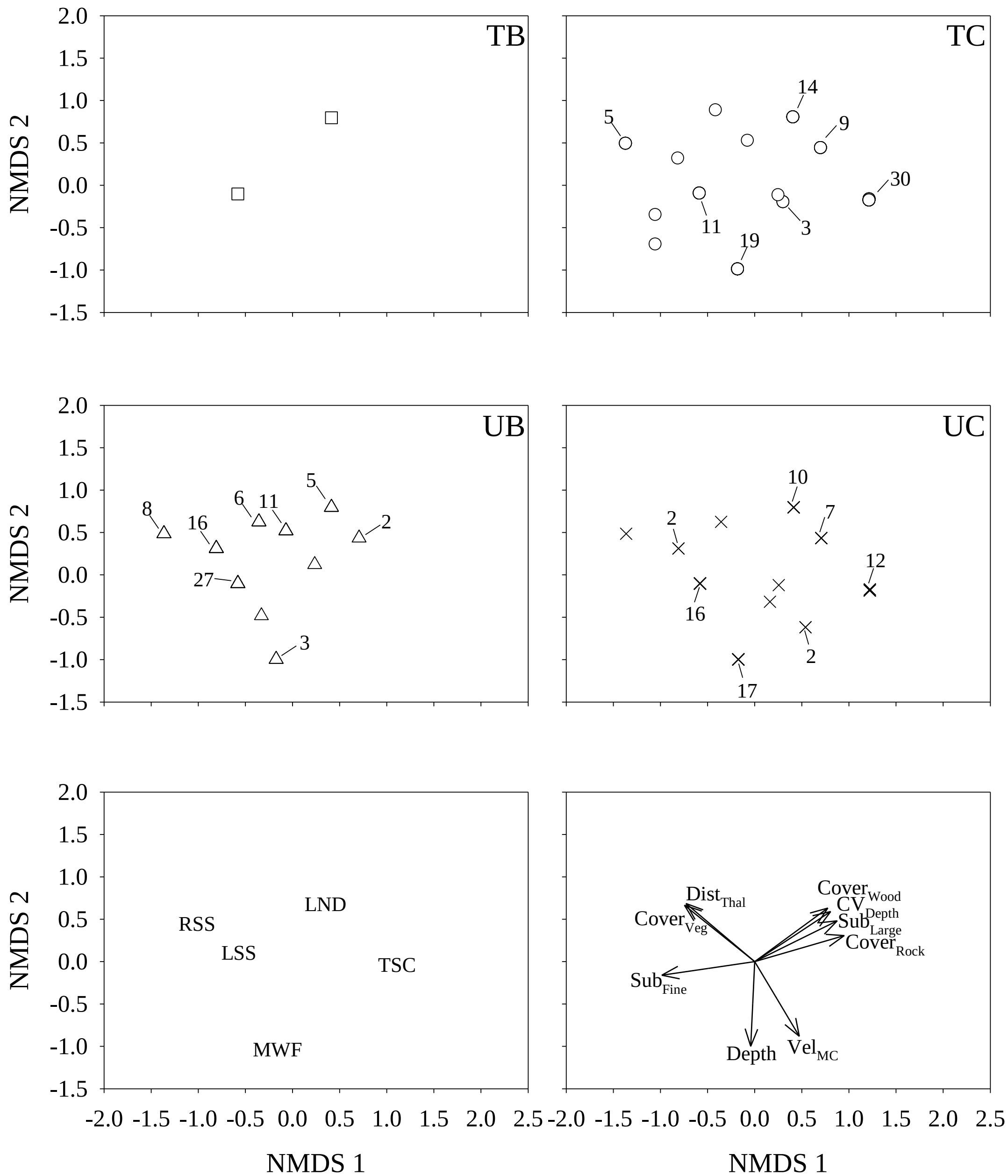

Figure 4. Nonmetric multidimensional scaling ordination (stress = 0.04) of site-specific fish assemblage occurrence data organized by treatment and habitat type for all fish (TB = treated backwater, *n* = 2; TC = treated channel, *n* = 97; UB = untreated backwater, *n* = 80; UC = untreated channel, *n* = 70). The numbers associated with each symbol in the top four panels indicate the number of sites ordinated to that position. Species scores are displayed in the lower left panel and include Largescale Sucker (LSS), Longnose Dace (LND), Mountain Whitefish (MWF), Redside Shiner (RSS), and Torrent Sculpin (TSC). Significant habitat vectors ($P < 0.05$) were fit to the ordination and include rocky cover ($Cover_{Rock}$), vegetated cover ($Cover_{Veg}$), woody cover ($Cover_{Wood}$), mean coefficient of variation of depth (CV_{Depth}), mean depth (Depth), distance to thalweg ($Dist_{Thal}$), proportion of fine substrate (Sub_{Fine}), proportion of large substrate (Sub_{Large}), and mean current velocity (Vel_{MC}).

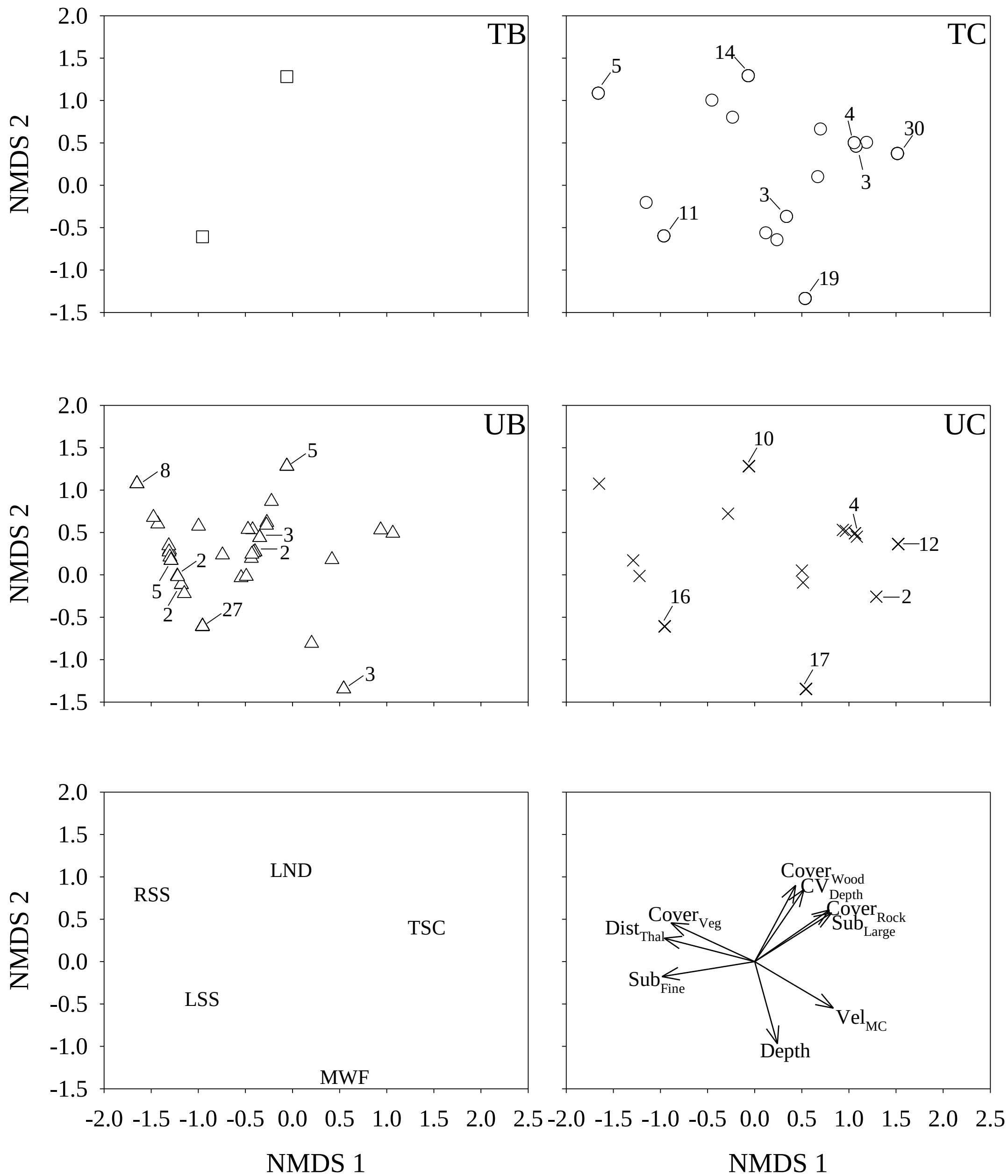

Figure 5. Nonmetric multidimensional scaling ordination (stress = 0.04) of site-specific fish assemblage relative abundance data organized by treatment and habitat type for all fish (TB = treated backwater, n = 2; TC = treated channel, n = 97; UB = untreated backwater, n = 80; UC = untreated channel, n = 70). The numbers associated with each symbol in the top four panels indicate the number of sites ordinated to that position. Species scores are displayed in the lower left panel and include Largescale Sucker (LSS), Longnose Dace (LND), Mountain Whitefish (MWF), Redside Shiner (RSS), and Torrent Sculpin (TSC). Significant habitat vectors ($P < 0.05$) were fit to the ordination and include rocky cover ($Cover_{Rock}$), vegetated cover ($Cover_{Veg}$), woody cover ($Cover_{Wood}$), mean coefficient of variation of depth (CV_{Depth}), mean depth (Depth), distance to thalweg ($Dist_{Thal}$), proportion of fine substrate (Sub_{Fine}), proportion of large substrate (Sub_{Large}), and mean current velocity (Vel_{MC}).

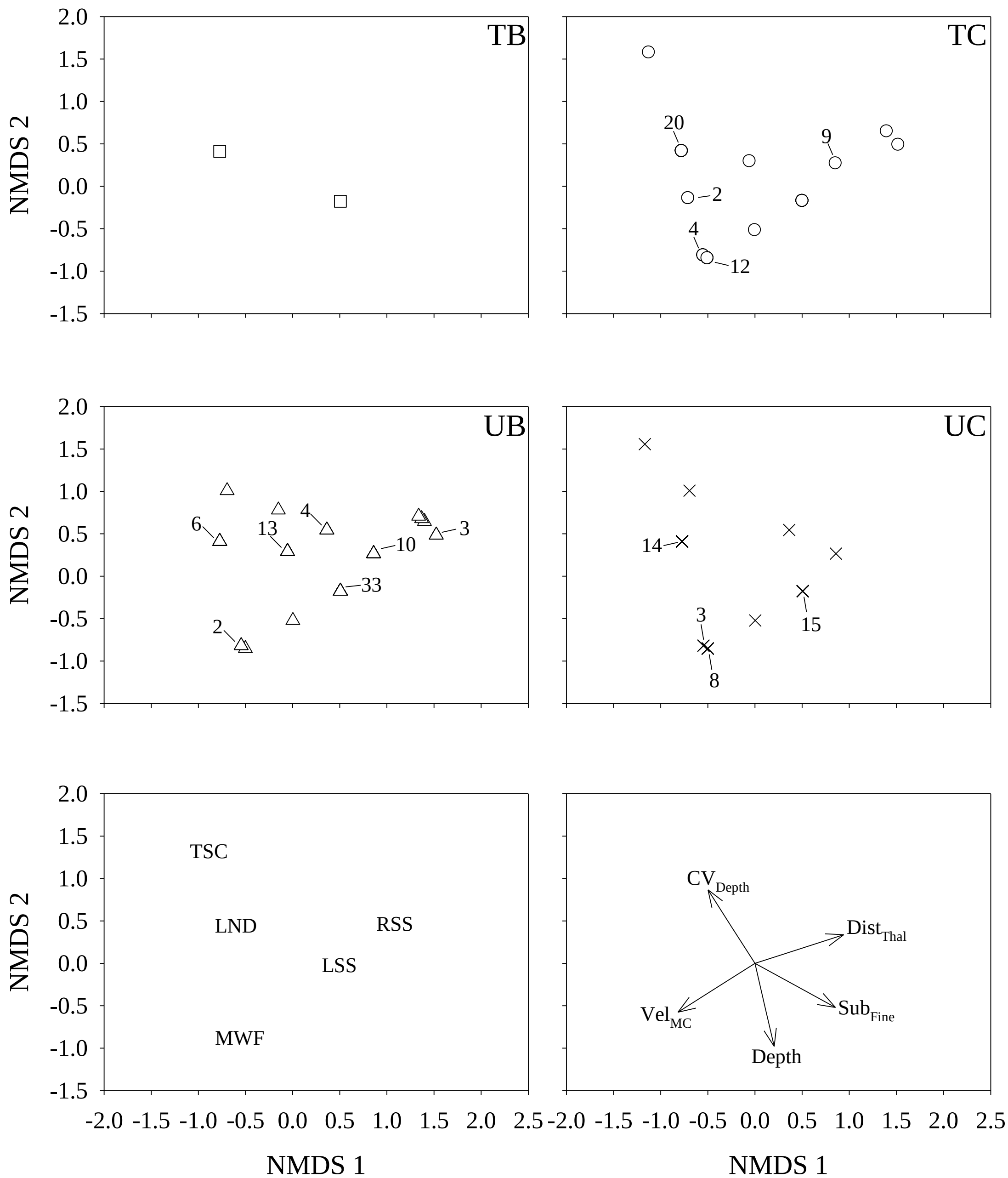

Figure 6. Nonmetric multidimensional scaling ordination (stress = 0.03) of site-specific fish assemblage occurrence data organized by treatment and habitat type for age-0 fish (TB = treated backwater, *n* = 2; TC = treated channel, *n* = 53; UB = untreated backwater, *n* = 78; UC = untreated channel, *n* = 45). The numbers associated with each symbol in the top four panels indicate the number of sites ordinated to that position. Species scores are displayed in the lower left panel and include Largescale Sucker (LSS), Longnose Dace (LND), Mountain Whitefish (MWF), Redside Shiner (RSS), and Torrent Sculpin (TSC). Significant habitat vectors ($P < 0.05$) were fit to the ordination and include mean coefficient of variation of depth (CV_{Depth}), mean depth (Depth), distance to thalweg ($Dist_{Thal}$), proportion of fine substrate (Sub_{Fine}), and mean current velocity (Vel_{MC}).

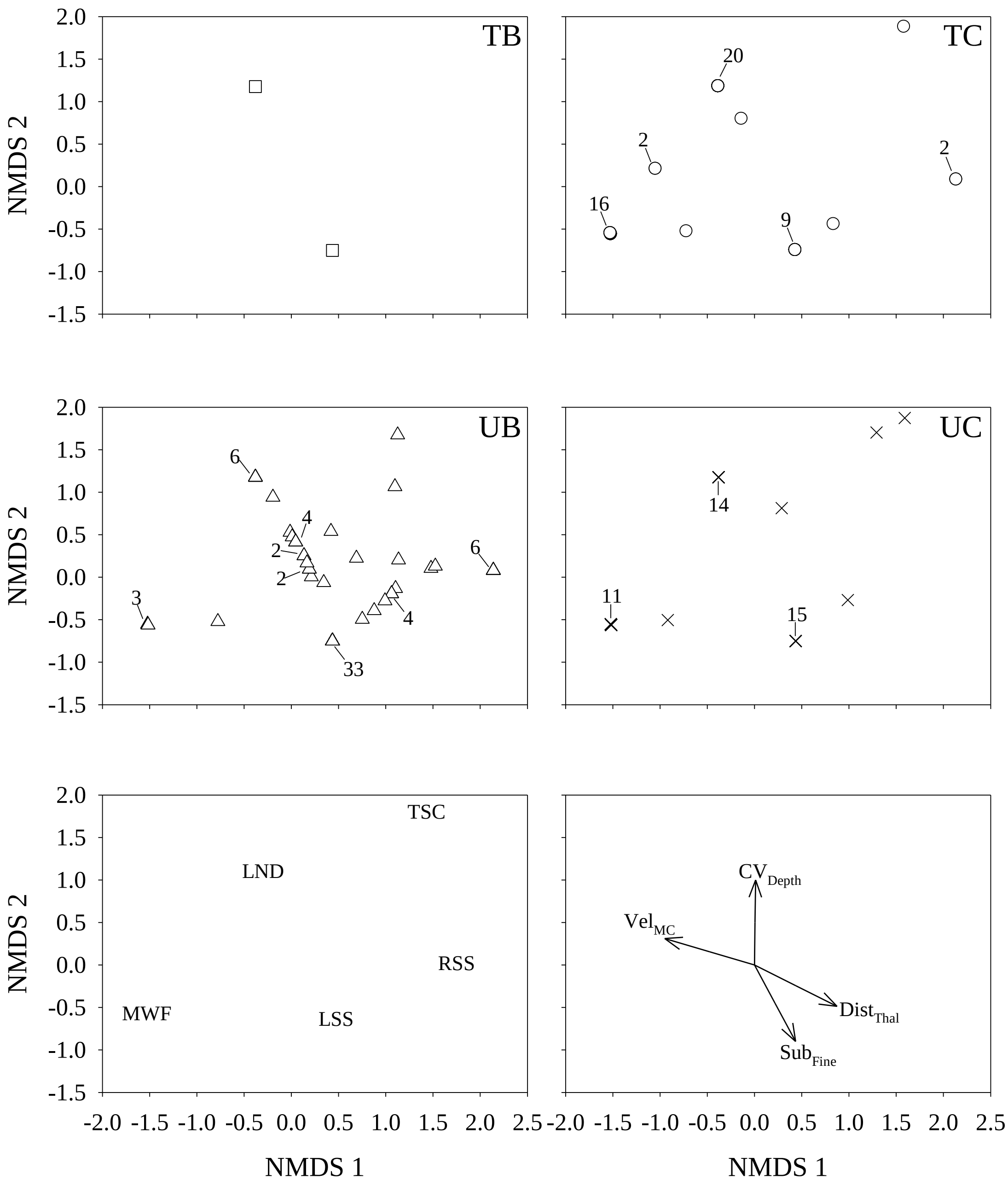

Figure 7. Nonmetric multidimensional scaling ordination (stress = 0.03) of site-specific fish assemblage relative abundance data organized by treatment and habitat type for age-0 fish (TB = treated backwater, n = 2; TC = treated channel, n = 53; UB = untreated backwater, n = 78; UC = untreated channel, n = 45). The numbers associated with each symbol in the top four panels indicate the number of sites ordinated to that position. Species scores are displayed in the lower left panel and include Largescale Sucker (LSS), Longnose Dace (LND), Mountain Whitefish (MWF), Redside Shiner (RSS), and Torrent Sculpin (TSC). Significant habitat vectors ($P < 0.05$) were fit to the ordination and include mean coefficient of variation of depth (CV_{Depth}), distance to thalweg ($Dist_{Thal}$), proportion of fine substrate (Sub_{Fine}), and mean current velocity (Vel_{MC}).