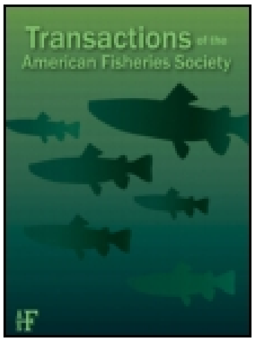

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ARTICLE

# Patterns of Fish Assemblage Structure and Habitat Use among Main- and Side-Channel Environments in the Lower Kootenai River, Idaho

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***Abstract***

**The lower Kootenai River, Idaho, was sampled during the summers of 2012 and 2013 to evaluate its fish assemblage structure at seven sites within main- and side-channel habitats where large-scale habitat rehabilitation was undertaken. Understanding the current patterns of fish assemblage structure and their relationships with habitat is important for evaluating the effects of past and future rehabilitation projects on the river. Species-specific habitat associations were modeled, and the variables that best explained the occurrence and relative abundance of fish were identified in order to guide future habitat rehabilitation so that it benefits native species. The results indicated that the side-channel habitats supported higher species richness than the main-channel habitats and that nonnative fishes were closely associated with newly rehabilitated habitats. This research provides valuable insight on the current fish assemblages in the Kootenai River and the assemblage-level responses that may occur as a result of future rehabilitation activities.**

The inherent nature of running waters has long made them a focus of human settlement and exploitation, resulting in various land- and water-use alterations (Behnke 1990; Bayley 1995). Large rivers throughout the world have been modified by development activities that serve human needs (e.g., transportation, irrigation, and power generation), which has caused the degradation and loss of fish habitat (Dynesius and Nilsson 1994; Nilsson et al. 2005). In particular, the presence of dams

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and their impoundments is considered one of the greatest threats to ecosystem health and biodiversity in aquatic environments. Furthermore, construction of levees and other shoreline development activities along rivers can have deleterious effects on the function of large rivers by restricting river access to floodplains. The restriction of flow into main channels, and the prevention of lateral water movement into floodplains during high-discharge events, decreases habitat complexity and heterogeneity in rivers (White et al. 2010; Schloesser et al. 2011).

Loss and homogenization of habitat have been implicated in the decline of various fluvial species in North America (Kinsolving and Bain 1993; Paragamian 2002; Pegg and McClelland 2004) as well as worldwide (Rahel 2000). In response to altered flow regimes and habitat change, fish assemblages have become less diverse and increasingly dominated by generalist species (Pflieger and Grace 1987; Paragamian 2002; Barko et al. 2004). Species that require seasonal variability in river discharge and the off-channel habitats (e.g., side channels) created by flooding typically display poor growth and recruitment when those factors are altered (Pringle et al. 2000; Galat and Zweimüller 2001; Giannico and Hinch 2003).

Rehabilitation is commonly implemented to mitigate for fish habitat losses in lotic systems. Engineered habitat structures have been widely used in large river systems throughout the Midwestern United States to restore habitat and to simulate floodplain environment for fish (Madejczyk et al. 1998; White et al. 2010; Schloesser et al. 2011). Engineered structures provide important physical habitats that meet the ecological needs of many fluvial species by creating isolated areas along the river continuum where the hydrologic dynamics mimic either pre-impoundment or prechannelization conditions. The decreased velocity and dispersed flow associated with engineered structures facilitate sedimentation and nutrient exchange, and they can moderate water temperature (Cushman 1985; Junk et al. 1989). Natural resource agencies have become more interested in using habitat rehabilitation to increase the abundance of focal fish species in fluvial systems because studies have shown that it benefits such species (Gore and Shields 1995; Lake et al. 2007; Romanov et al. 2012).

Both abiotic and biotic environmental characteristics influence fish assemblage and population structure at various spatial scales. In cases in which habitat rehabilitation has been used to support native fish populations, recolonization by and the improvement of habitat for nonnative fishes have often been ignored. Habitat use patterns frequently overlap between native and nonnative fishes, possibly confounding habitat rehabilitation for either one. For this reason, natural resource managers must carefully consider the potential overlap between native and nonnative fishes to prioritize and optimize rehabilitation projects that target native fish populations.

The Kootenai River is a large-floodplain river that has undergone extensive alteration. The river originates in British Columbia and flows into the panhandle of northern Idaho. The portion of the river in Idaho is characterized by a prominent floodplain that historically served as flooded terrestrial habitat during high-runoff events; however, many flood-related habitats (e.g., side channels, sloughs, and oxbows) have been eliminated as a result of instream and shoreline development. The primary flow modifications in the Kootenai River include the construction of levees along the floodplain of the lower portion and the construction of Libby Dam, which is a large hydropower facility (Knudson 1993). Libby Dam has been implicated in both the changes to natural flow regimes (e.g., temperature, nutrients, and discharge) and shifts in fish assemblage structure in the Kootenai River. Water development activities have reduced the original floodplain to ~25% of its historical extent (KTOI 2009). Moreover, the current discharge at Libby Dam is roughly 60% of the discharge that historically occurred during spring runoff (Duke et al. 1999).

The decline of important native fish species in the lower Kootenai River warranted recent efforts to improve aquatic habitat (Partridge 1983; Apperson 1990; Duke et al. 1999; Paragamian and Hansen 2009; Paragamian 2012). Rehabilitation projects were used to enhance the existing habitat so that it could support the various life history stages of the native fishes in the river. Habitat rehabilitation has been ongoing since 2011, and it is largely focused on improving the habitat in the existing side-channel environments of the lower portion of the Kootenai River. The lack of both off-channel habitat and heterogeneity in the river are believed to limit native fish colonization. Studies of habitat use by native fishes in other systems provided preliminary guidance for rehabilitation activities in the Kootenai River; however, baseline information (e.g., fish assemblage structure and general descriptions of fish responses to habitat rehabilitation) are needed to increase rehabilitative success in the Kootenai River.

Little is known about the structure of fish assemblages, and their relationships with environmental factors and side-channel habitats, in large western river systems. Rehabilitation projects on small streams are common: there is a large body of literature describing various rehabilitation techniques and their expected impacts on the biotic community (Regier et al. 1989; Kern 1992; Binns 2004). While rehabilitation projects are not as common on large rivers as on smaller streams, there is rising interest in using similar restoration tools on the two systems. Unlike small-stream projects, large-river projects are generally focused on improving the quantity and quality of the existing habitat rather than creating new habitat (Gore and Milner 1990; Gore and Shields 1995). Area improvements target native colonists, and their recovery is typically defined in terms of changes in ecological structure and/or function and their associated values (Gore and Shields 1995). Guided rehabilitation plans are central to achieving desired management outcomes in altered large rivers.

The objectives of this study were twofold. First, we sought to describe the fish assemblage structure throughout a portion of the Kootenai River where intensive habitat rehabilitation has already occurred and new projects are planned. Second, we sought to evaluate the habitat characteristics in the Kootenai River that are related to the occurrence and relative abundance of fishes in its braided section.

## METHODS

*Study area.*—The Kootenai River is the second largest tributary to the Columbia River, and it has an international watershed that encompasses portions of both Canada and the United States. The Kootenai River watershed is approximately 50,000 km$^2$ in area, mountainous, mostly forested, and greatly influenced by spring runoff from snowmelt (Knudson 1993). This river originates in Kootenay National Park in British Columbia and flows south into the United States, where it is impounded by Libby Dam near Jennings, Montana, forming Lake Koocanusa. Upon release from Libby Dam, the Kootenai River flows west into Idaho before returning to British Columbia, where it forms the southern arm of Kootenay Lake.

The Idaho portion of the Kootenai River is delineated into three distinct sections based on channel morphology: canyon, braided, and meander (Fossness and Williams 2009). The braided section (river kilometers 246–257) extends from the confluence of the Moyie River downstream to Bonners Ferry, Idaho, and it encompasses all of our study area (Figure 1). The braided section is characterized by a shallow (<2 m) and wide channel that has a heterogeneous substrate composition and high flow variability (KTOI 2009, 2012; Smith 2013). This section is unique because it still contains side-channel habitats that are characteristic of historical, pre-impoundment conditions and has greater complexity than the other sections of the river. Overall, the braided section has been highly degraded, yet many believe it will elicit the best response to habitat improvements.

*Sampling design and data collection.*—Sampling occurred at seven sites within the braided section of the Kootenai River during the summers of 2012 (July–September) and 2013 (May–September) (Figure 1). The sites were located in either the side-channel or main-channel environments. Because a focus of this study was to provide baseline data from sites that would undergo habitat rehabilitation in the future, we selected sites based on planned rehabilitation. However, some of the selected sites in the main channel were not slated to undergo rehabilitation but were chosen to supplement our sample and to provide opportunity for future comparisons of fish assemblage structure between rehabilitated and nonrehabilitated main channel areas. All of the side channel sites have planned or completed rehabilitation activities. Three side-channel complexes and four main-channel meanders were designated as sampling sites (hereafter referred to as sites). Each side-channel site was divided into many individual 100-m-long reaches (hereafter referred to as reaches) along the thalweg. Each main-channel site was divided into many individual 100-m-long reaches along both the inside and outside bends. At each reach, a global positioning system (Garmin International, Inc., Olathe, Kansas) was used to georeference the upper and lower termini (which were marked with fluorescent flags).

All reaches were sampled biweekly from May to September to account for temporal variability in fish assemblage structure. Previous studies have shown that electrofishing is an effective sampling technique for riverine fishes (Reynolds and Kolz 2012; Smith 2013); therefore, we sampled fish during the day with a pulsed-DC Infinity electrofishing unit (Midwest Lake Electrofishing Systems, Inc., Polo, Missouri) that was mounted on a boat and powered by a 5,000-W generator (American Honda Motor Co., Torrance, California). Electrofishing power output was standardized to 3,000 W based on the ambient water conductivity and temperature, as recommended by Miranda (2009). Two netters collected immobilized fish from the bow of the boat during sampling. Electrofishing effort began at the most upstream reach within each site, and a single pass was allocated to each bank (two for the side-channel and one for the main-channel reaches) before we proceeded to the following reach. Samples within each of the 100-m-long reaches were considered replicates that were nested within their respective sites. Effort was recorded as the number of seconds of “current on” electrofishing. Upon completion of the sampling within each reach, fish were identified to species, measured (total length; mm), and released. All fish were released in a location away from the subsequent sampling reaches to minimize the influence that immediate immigration back into the sampling areas could have on data accuracy.

Habitat data were collected to evaluate the influence of abiotic factors on fish assemblage structure, species occurrence, and relative abundance. Substrate composition, bank type, and woody debris were measured once in 2012 and once in 2013, and depth and velocity were estimated on each day of sampling.

The Kootenai River is highly regulated, and lateral water movements and high discharges are infrequent; therefore, the habitat characteristics for some of the variables were fairly static and only measured on an annual basis. Substrate was evaluated at 25-m intervals along each reach following Wilhelm et al. (2005). In the side channels, each transect extended across the entire channel; however, in the main-channel sites the transects were half the width of the channel (i.e., extending from the bank to the middle of the channel). All widths were measured using a laser rangefinder.

Substrate composition was estimated as the proportion belonging to one of five categories: silt–sand (<0.0004–0.2 mm), gravel (0.2–64.0 mm), cobble (64.0–256.0 mm), boulder (>256.0 mm), and bedrock (modified from Orth and Maughan 1982). Visual estimates of substrate composition were made at seven equidistant points along each transect (Neebling and Quist 2011). We also visually estimated the proportions of bank types belonging to the following four

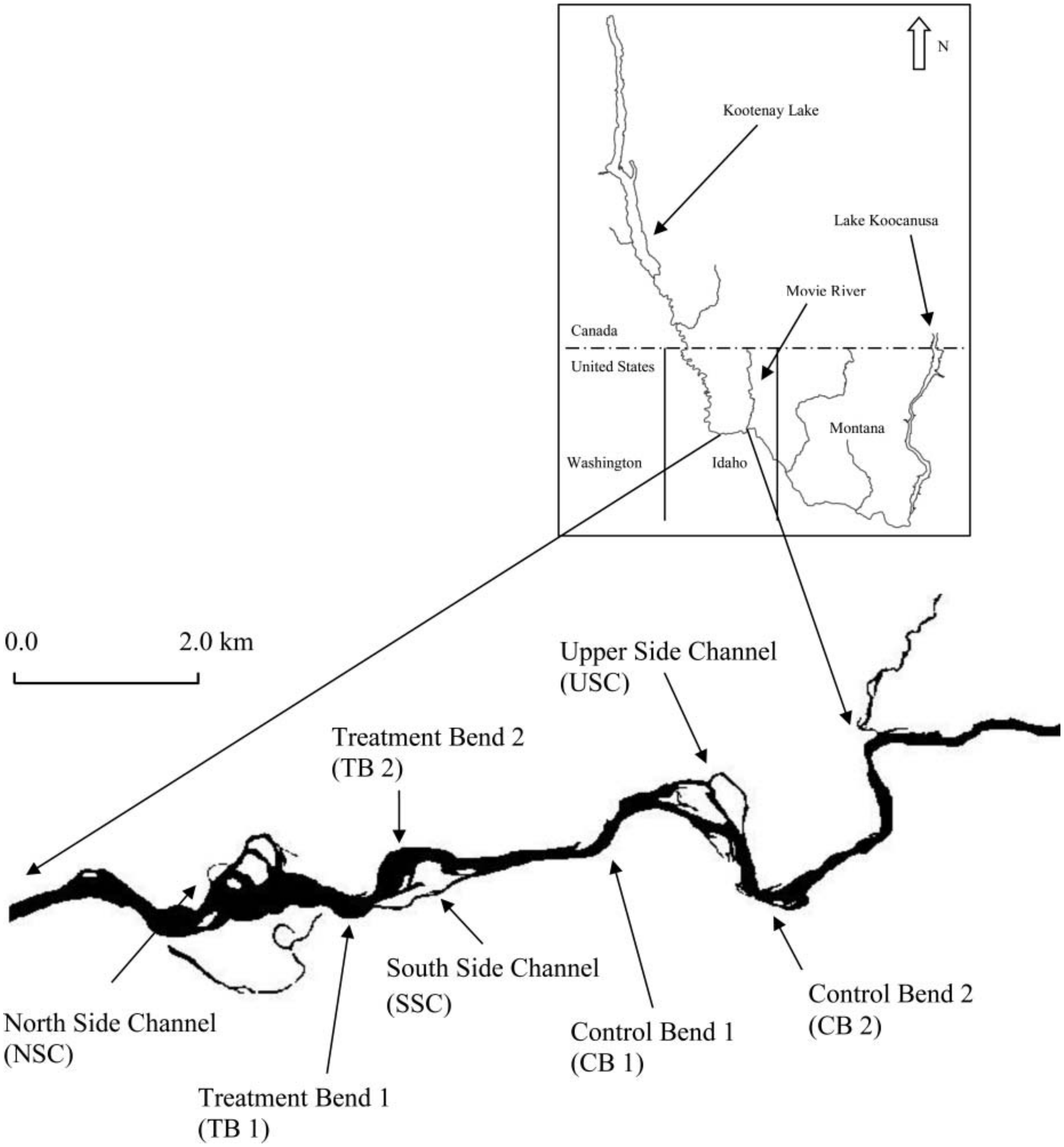

FIGURE 1. Map of the braided section of the Kootenai River showing the locations of the sampling sites. The braided section is located between the confluence of the Moyie River and the town of Bonners Ferry, Idaho.

categories: eroding, vegetated, silt–sand ($\leq$0.2 mm), and cobble–boulder (i.e., riprap structure; $\geq$64.0 mm). The amount of woody debris was calculated as the total surface area of woody instream cover that was greater than 0.2 m in diameter and greater than 0.5 m in length.

Estimates of mean water column velocity and mean water depth were obtained from the River Design Group (Whitefish, Montana). This group had previously compiled channel morphological and flow data throughout the braided section of the Kootenai River to establish baseline information on the river's habitat characteristics prior to its rehabilitation. Kootenai River hydraulics were simulated using a Flow and Sediment Transport with Morphological Evolution of Channels two-dimensional model (Nelson 1996). This model computed flow-field hydraulics on a curvilinear-fitted grid by solving depth-averaged, shallow-water equations that use an eddy viscosity turbulence closure and a dimensionless drag coefficient. The model's geometry was sampled at a nominal 3-m resolution from bathymetric data that was collected by the U.S. Geological Survey in 2009 and merged into a 2010 terrestrial Light Detection and Ranging radar–derived map. Hydraulic roughness in the model was set to vary spatially as a function of depth, and it used a nominal roughness height that varied from gravel to cobble. The hydraulic model was calibrated to the range of measured stage data that had been collected from a detailed gauge network in 2010 and 2011 (Czuba and Barton 2011). Models were postprocessed in ArcGIS version 10.1 (ESRI, Redlands, California) to develop a mean depth and velocity (and their associated variances) and the shear stress grids that were needed to simulate the flow conditions that occurred during fish sampling.

*Fish assemblage structure.*—Nonmetric multidimensional scaling (NMDS) was used to describe (1) the patterns of similarity in fish assemblage structure among our sampling sites and (2) the coarse-scale associations between fish assemblages and their habitat characteristics. Nonmetric multidimensional scaling is a robust ordination technique that is commonly used to investigate the patterns in fish assemblage structure (e.g., Ruetz et al. 2007; Rowe et al. 2009). Our assemblage structure was evaluated with two measures: (1) the occurrence of fish (presence or absence) and (2) relative abundance (CPUE = number/h), which were pooled across several sampling events. The differences in the assemblage structures among sites were evaluated via a permutational multivariate analysis of variance (Loisl et al. 2014). If a significant difference ($P \leq 0.05$) was detected among sites, then habitat vectors were fitted to an ordination using rotational vector fitting (Faith and Norris 1989). Significantly correlated ($P \leq 0.05$) habitat variables were fitted to an ordination with a permutation test that used the Envfit function in the Vegan package of R version 3.0.1 (R Development Core Team 2012; Oksanen et al. 2011; Oksanen 2013). For all NMDS ordinations, we applied a Bray–Curtis distance measure that used the MetaMDS and Adonis functions in the Vegan package described above. To assess habitat variation among sites, environmental variables were compared using a multiple analysis of variance (MANOVA); if a significant difference was detected, individual one-way analysis of variance was used to identify which sites differed for each variable (Johnson 1998).

A cluster analysis was used to evaluate whether there was spatial similarity in fish assemblage structure in all 100-m-long sampling reaches. For both years, Jaccard's index of similarity (Jongman et al. 1995) was calculated for all possible pairs of species occurrence. The matrix of similarity values for species was then clustered with the unweighted pair-group method with arithmetic averages (Cairns and Kaesler 1971; Jongman et al. 1995; Matthews 1998; Quist et al. 2005). The resulting dendrogram displayed clusters of species that had similar occurrence in the sampling reaches. The cluster analysis was performed with PC-ORD software (McCune and Medford 2006), which can describe similarities in fish assemblages and identify groups of sympatric species.

*Species-specific habitat use.*—Patterns of habitat use for individual species were evaluated to provide further insight on the associations between habitats and fish populations in the Kootenai River. Generalized linear mixed models (Bolker et al. 2008) were used to identify the environmental characteristics that were most associated with the occurrence and relative abundance of selected fish species. Mixed-effects models were used to account for the lack of true independence and spatial-temporal structuring in our data (Hurlbert 1984; Irwin et al. 2013). The environmental covariates were treated as fixed effects that included random intercepts for both the reach and the sampling date so that we could induce a spatial-temporal correlation structure (Irwin et al. 2013). These random effects adjusted the model intercepts based on grouping factors (i.e., sampling date, site, and reach). Random intercepts for the reaches were nested within sites because reaches were expected to be more alike within sites than across sites. Thus, the temporal random effect induced correlation on all of the observations within similar time periods, whereas the spatial random effect allowed observations at a given reach (and across all reaches within a site) to be more alike. This allowed us to assess the relative magnitudes of the reach-level and site-level random effect variances not explained by model covariates.

Models were fit by maximum likelihood methods using the random effects module of AD Model Builder (ADMB; Fournier et al. 2012). Specifically, R applied ADMB to fit the models using the glmmADMB package (Bolker et al. 2008; Skaug et al. 2011). Only species detected in at least 10% of the reaches across all of the sampling events were retained for the species-specific analyses.

A binomial error distribution and logit link function were used in the logistic regression models of species occurrence. The distributions for the relative abundance models were first selected by creating global models (i.e., models containing the most parameters), and then Akaike's information criterion (AIC) was used to rank the models with different distributional assumptions. To account for possible data overdispersion (i.e., variance > mean), four global models were fitted for each species: Poisson and negative binomial distributions and zero-inflated versions of both. The negative binomial distribution had the lowest AIC value for all species; therefore, this distribution was used for the subsequent modeling of relative abundance.

The performance of the logistic regression models was evaluated by calculating the area under the receiver operating characteristic curve (AUC), which enabled us to evaluate the discrimination ability of the top model. The AUC is a common diagnostic statistic used to evaluate how well data fit logistic regression models by providing the probability of model concordance (Coelho et al. 2010). Evaluation of the mixed-effects

TABLE 1. Descriptions of habitat variables collected at seven sampling sites in the Kootenai River, Idaho, summer 2012 and 2013.

| Variable | Description |
|---|---|
| Woody cover | Mean surface area ($m^2$) of instream woody debris ($>0.2 \times 0.5$ m) |
| $Substrate_{Fine}$ | Proportion of substrate (%) consisting of fine particles ($\leq 2$ mm in diameter) |
| $Substrate_{Coarse}$ | Proportion of substrate (%) consisting of coarse particles ($\geq 64$ mm in diameter) |
| $Bank_{Co\text{-}Bo}$ | Proportion of bank (%) consisting of cobble and boulder (riprap) |
| $Bank_{Veg}$ | Proportion of bank (%) consisting of vegetation |
| Velocity | Mean water column velocity (m/s) |
| $CV_{Vel}$ | Coefficient of variation of water column velocity (%) |
| Depth | Mean water column depth (m) |
| $CV_{Depth}$ | Coefficient of variation of water column depth (%) |

negative binomial models followed the methods of Irwin et al. (2013), which identify any structural flaws in a model that can lead to major violations of assumptions. Specifically, model fit was evaluated from (1) diagnostic plots of the model predictions versus the observed data; (2) plots of Anscombe residuals (Anscombe 1949, 1953; Hilbe 2011; Irwin et al. 2013); and (3) root mean square errors from the top models. The root mean square error is a useful model evaluation metric because it provides an average prediction error for the observed data in the same units as the response variables (i.e., the counts of each species).

Prior to model creation, multicollinearity among the habitat covariates was assessed with Pearson's correlation coefficients, which were used to identify the correlations among all possible pairs of habitat covariates. Mean depth and mean velocity were significantly correlated (Pearson's $r = 0.83$; $P = 0.003$); because heterogeneity in velocity is known to be an important factor, we retained both the mean depth and the coefficient of variation (CV = [SD/mean] × 100) of velocity in the models. All of the environmental covariates that were used to explain the variations in the occurrence and relative abundance of fishes are provided in Table 1.

The candidate occurrence and relative abundance models consisted of 7–15 a priori models that were developed for each species. An information-theoretic approach was used to select the most parsimonious models among the candidate models for each species (Burnham and Anderson 2002). The candidate models contained the environmental variables that we hypothesized to be most important to each species (based on previous studies and general knowledge of fish ecology in large rivers). For lesser-studied species, the candidate models were generated from the literature on species with similar ecology. Candidate multiple-regression models were ranked using AIC values (Burnham and Anderson 2002). Those with a $\Delta$AIC value $\leq 2$ were considered to be equivalently parsimonious, and they were retained for interpretation (Burnham and Anderson 2002). Finally, the coefficient estimates and 95% confidence intervals of the top models were calculated to assess the precision of their covariates and to determine which covariates best explained the variations in the occurrence and relative abundance of each species.

## RESULTS

Seven sites that contained a total of 113 individual 100-m-long reaches were sampled during 18 events. A total of 8,293 individual fish belonging to eight families were collected over the course of the summers of 2012 and 2013. One federally threatened species, Bull Trout *Salvelinus confluentus*, and one imperiled species, Burbot *Lota lota*, were sampled at both the main- and side-channel sites (Table 2). The dominant species did not vary greatly: Largescale Sucker and Mountain Whitefish were the most common species at most sites (Table 2). A higher total number of species were sampled from the side-channel sites than from the main-channel sites. The side-channel sites also tended to have a greater relative abundance of rare species. Trout species, a recreationally important group of fishes in the Kootenai River, comprised little of the catch at all sites and were particularly low percentages of the total composition at both the north side channel and control bend 2 (Table 2). The north side channel displayed a particularly high percent composition (and relative abundance) of nonnative centrarchids and percids.

The NMDS ordinations provided several insights on the fish assemblage structure among the sampling sites. A two-dimensional solution was found for both the occurrence (stress = 4.7) and relative abundance (stress = 2.1) ordinations. The NMDS ordination that was fitted to the species occurrence data indicated that Largemouth Bass, Pumpkinseed, and Yellow Perch were most closely associated with the north side channel, whereas Burbot, Brown Trout, and Brook Trout were most closely associated with the south side channel (Figure 2). The NMDS ordination that was fit to the relative abundance data displayed a similar pattern: the north side channel had a higher relative abundance of Largemouth Bass, Pumpkinseed, and Yellow Perch than the other sites (Figure 3). Northern Pikeminnow and Peamouth were also more abundant in the north side channel than at the other six sites (Figure 3).

Instream habitat was relatively similar within the sites, but it varied among the sites (Table 3), suggesting that similar habitat variables independently structure fish assemblages within the sites. The habitat characteristics that were most similar among all of the sites included the proportion of cobble–boulder bank and the CV of velocity. In general, the habitats

TABLE 2. Species composition (%) at each sampling site, represented as the proportion of the total catch for all fishes sampled from the Kootenai River, summer 2012 and 2013. Sites include the north side channel (NSC; 22 reaches; $n = 1{,}908$), south side channel (SSC; 12 reaches; $n = 1{,}509$), upper side channel (USC; 22 reaches; $n = 2{,}290$), control bend 1 (CB 1; 15 reaches; $n = 665$), control bend 2 (CB 2; 15 reaches; $n = 938$), treatment bend 1 (TB 1; 15 reaches; $n = 621$), and treatment bend 2 (TB 2; 12 reaches; $n = 362$).

| | Site | | | | | | |
|---|---|---|---|---|---|---|---|
| Species | NSC | SSC | USC | CB 1 | CB 2 | TB 1 | TB 2 |
| Cyprinidae | | | | | | | |
| Longnose Dace *Rhinichthys cataractae* | 0.05 | 0.27 | 0.13 | 0.00 | 1.53 | 0.00 | 0.00 |
| Northern Pikeminnow *Ptychocheilus oregonensis* | 16.46 | 2.12 | 2.93 | 2.11 | 2.44 | 4.19 | 1.38 |
| Peamouth *Mylocheilus caurinus* | 16.51 | 2.52 | 2.31 | 1.20 | 0.71 | 5.64 | 0.83 |
| Redside Shiner *Richardsonius balteatus* | 17.77 | 4.64 | 14.41 | 1.20 | 23.80 | 1.93 | 2.21 |
| Catostomidae | | | | | | | |
| Largescale Sucker *Catostomus macrocheilus* | 28.41 | 36.05 | 37.42 | 62.92 | 31.64 | 37.68 | 47.52 |
| Longnose Sucker *Catostomus catostomus* | 2.46 | 0.46 | 2.10 | 0.45 | 0.71 | 4.35 | 1.38 |
| Ictaluridae | | | | | | | |
| Brown Bullhead[a] *Ameiurus nebulosus* | 0.05 | 0.00 | 0.09 | 0.00 | 0.10 | 0.00 | 0.00 |
| Salmonidae | | | | | | | |
| Brown Trout *Salmo trutta* | 0.05 | 0.20 | 0.00 | 0.30 | 0.00 | 0.16 | 0.00 |
| Brook Trout[a] *Salvelinus fontinalis* | 0.00 | 0.07 | 0.00 | 0.00 | 0.10 | 0.16 | 0.00 |
| Bull Trout *Salvelinus confluentus* | 0.00 | 0.13 | 0.04 | 0.15 | 0.00 | 0.16 | 0.00 |
| Westslope Cutthroat Trout *Oncorhynchus clarkii lewisii* | 0.52 | 0.20 | 0.13 | 0.15 | 0.20 | 0.32 | 0.00 |
| Kokanee *Oncorhynchus nerka* | 0.52 | 0.33 | 0.48 | 0.60 | 0.31 | 1.45 | 0.83 |
| Mountain Whitefish *Prosopium williamsoni* | 9.02 | 49.17 | 36.20 | 25.66 | 34.69 | 41.38 | 41.44 |
| Rainbow Trout *Oncorhynchus mykiss* | 1.52 | 2.58 | 2.75 | 3.16 | 1.53 | 2.09 | 2.76 |
| Gadidae | | | | | | | |
| Burbot *Lota lota* | 0.00 | 0.13 | 0.00 | 0.15 | 0.00 | 0.00 | 0.00 |
| Cottidae | | | | | | | |
| Torrent Sculpin *Cottus rhotheus* | 0.26 | 1.00 | 0.87 | 1.95 | 0.61 | 0.32 | 1.66 |
| Slimy Sculpin *Cottus cognatus* | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 |
| Centrarchidae | | | | | | | |
| Largemouth Bass[a] *Micropterus salmoides* | 0.42 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Pumpkinseed[a] *Lepomis gibbosus* | 5.36 | 0.07 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 |
| Percidae | | | | | | | |
| Yellow Perch[a] *Perca flavescens* | 0.63 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

[a] Nonnative species.

in the south and upper side channels were most similar to those of control bends 1 and 2, particularly in terms of the proportions of coarse substrate and vegetated bank. All of the sites were moderately diverse in depth and velocity, and there were no clear patterns between the side- and main-channel sites. The rehabilitated sites had significantly higher proportions of both cobble–boulder bank and woody debris (Table 3). Several environmental variables were significantly correlated with the NMDS scores, and they reflected patterns that were observed from previous comparisons with habitat variables. The CV of velocity was significantly correlated with the NMDS ordination for species occurrence ($r_s = 0.89$, $P = 0.004$; Figure 2), and the proportion of fine substrate, CV of velocity, and woody cover were all significantly correlated with the NMDS ordination for species relative abundance ($r_s = 0.32$, $P = 0.04$; $r_s = 0.45$, $P = 0.02$; and $r_s = 0.53$, $P = 0.02$, respectively; Figure 3).

The cluster analysis results complemented the NMDS ordination results. The dendrogram displayed a distinct cluster of native species: kokanee, Longnose Sucker, Largescale Sucker, Mountain Whitefish, Northern Pikeminnow, Peamouth, Rainbow Trout, and Redside Shiner (Figure 4). Nonnative species had no clear associations with native species and other nonnative species. Pumpkinseed and Largemouth Bass formed a distinct cluster, and they had exact reach similarity at all sites where they were detected. Both of these species had a high association with the north and south side channels with respect to occurrence, as shown in both the NMDS ordination (Figure 2) and the cluster analysis (Figure 4); however, their relative abundances were much higher in the north side channel (Figure 3).

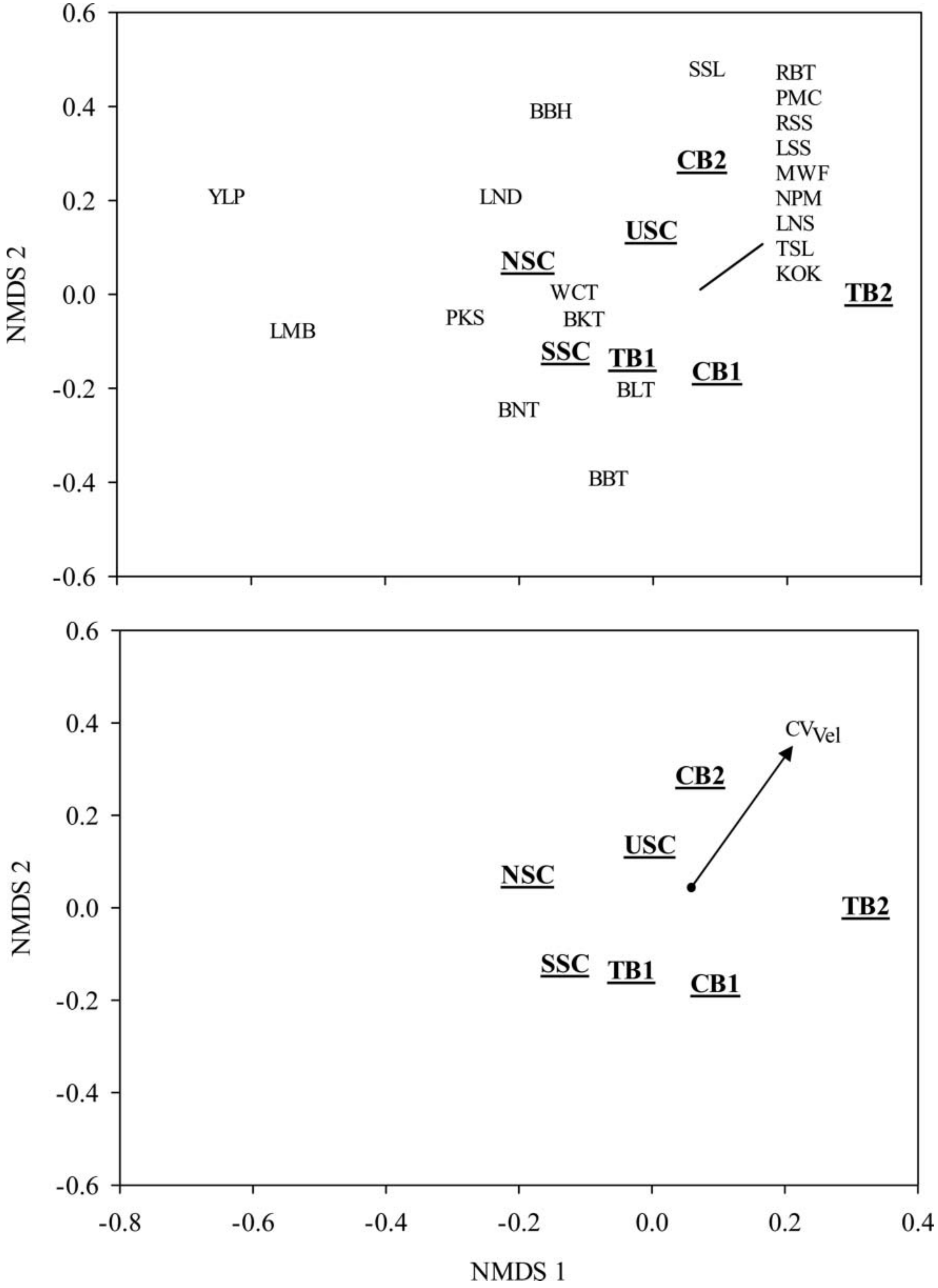

FIGURE 2. Nonmetric multidimensional scaling ordination (stress = 4.7) of fish assemblage structure using occurrence data from seven sites in the Kootenai River, summer 2012 and 2013. Site and species scores are provided in the top panel, and significant ($P \leq 0.05$) habitat vectors are shown in the lower panel. Sites are indicated by bold type and underlining; see Figure 1 for an explanation of the site codes. The taxa indicated in the top panel include Burbot (BBT), Brown Bullhead (BBH), Brook Trout (BKT), Bull Trout (BLT), Brown Trout (BNT), kokanee (KOK), Largemouth Bass (LMB), Longnose Dace (LND), Longnose Sucker (LNS), Largescale Sucker (LSS), Mountain Whitefish (MWF), Northern Pikeminnow (NPM), Pumpkinseed (PKS), Peamouth (PMC), Rainbow Trout (RBT), Redside Shiner (RSS), Slimy Sculpin (SSL), Torrent Sculpin (TSL), Westslope Cutthroat Trout (WCT), and Yellow Perch (YLP). Descriptions of the environmental variables that were fit to the NMDS ordinations are given in Table 1.

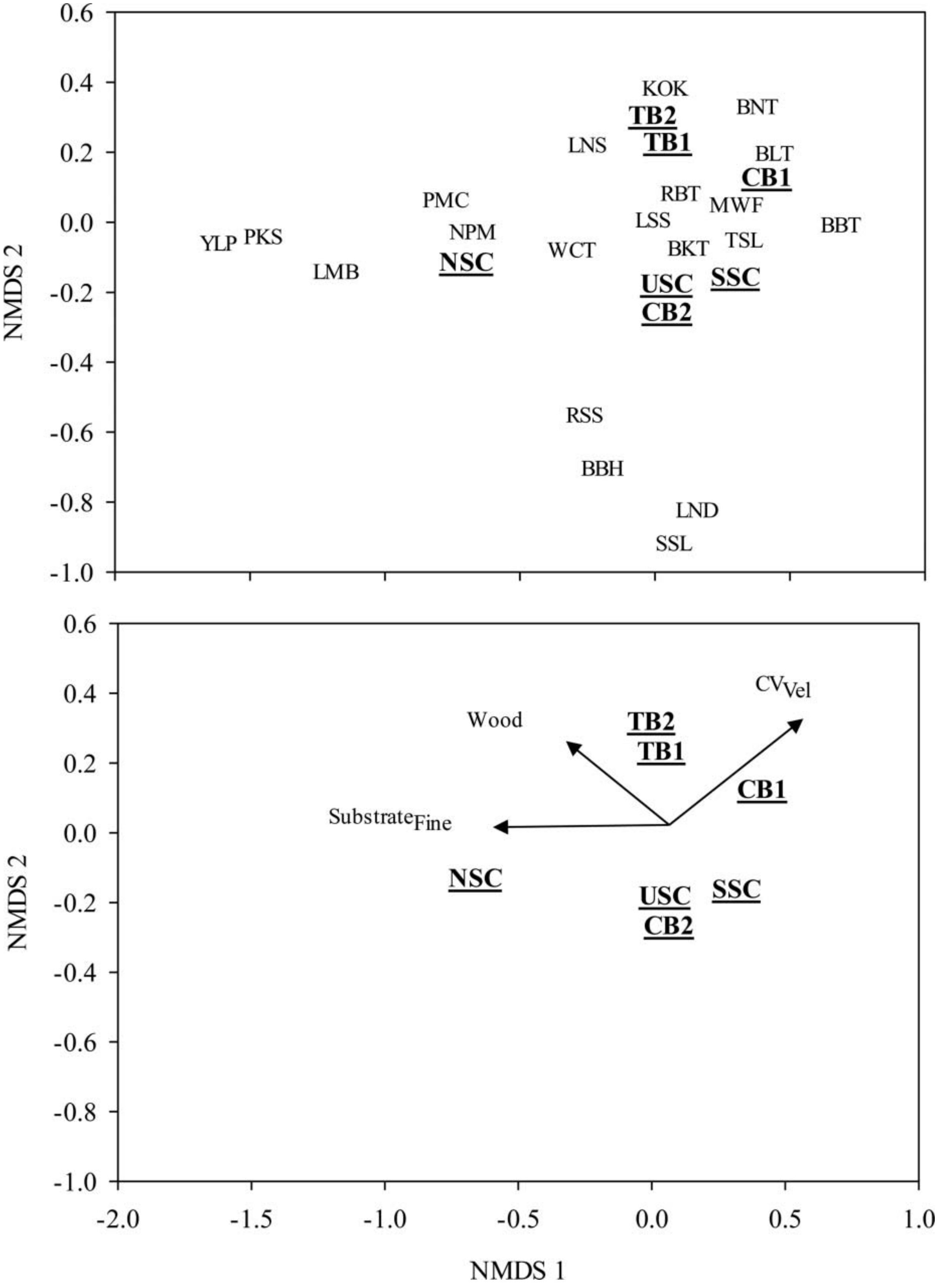

FIGURE 3. Nonmetric multidimensional scaling ordination (stress = 2.1) of the fish assembalge structure using relative abundance data from seven sites in the Kootenai River, summer 2012 and 2013. See Figure 2 for species codes.

TABLE 3. Mean estimates (SEs in parentheses) of the habitat variables measured at seven sampling sites in the Kootenai River, summer 2012 and 2013. See Table 2 for site codes. Within rows, means with the same letter are not significantly different ($P < 0.05$).

| | Site | | | | | | |
|---|---|---|---|---|---|---|---|
| Variable | NSC | SSC | USC | CB 1 | CB 2 | TB 1 | TB 2 |
| Woody cover | 48.47 (3.36) z | 12.08 (0.87) x | 34.21 (2.82) y | 3.43 (0.49) xw | 0.00 (0.00) w | 0.00 (0.00) w | 64.62 (6.14) z |
| Substrate$_{\text{Fine}}$ | 81.97 (1.63) z | 0.00 (0.00) x | 18.41 (1.79) y | 1.36 (0.07) x | 0.00 (0.00) x | 15.00 (1.82) y | 12.53 (1.74) y |
| Substrate$_{\text{Coarse}}$ | 18.03 (1.61) w | 100 (0.00) z | 81.59 (1.79) y | 98.64 (0.10) z | 100 (0.00) z | 30.00 (1.49) x | 37.48 (1.56) x |
| Bank$_{\text{Co-Bo}}$ | 0.00 (0.00) w | 10.42 (1.47) yx | 23.64 (1.72) z | 8.93 (1.09) x | 28.67 (2.62) z | 4.67 (1.25) x | 15.01 (1.04) y |
| Bank$_{\text{Veg}}$ | 57.92 (1.50) x | 87.51 (1.85) z | 45.00 (2.04) w | 81.07 (1.31) z | 71.33 (2.62) y | 21.33 (2.82) v | 47.50 (3.01) w |
| Velocity | 0.31 (0.01) u | 0.80 (0.02) w | 0.68 (0.01) v | 1.31 (0.02) z | 1.04 (0.03) x | 1.05 (0.02) x | 1.08 (0.02) y |
| CV$_{\text{Vel}}$ | 44.64 (1.18) y | 35.95 (0.70) wv | 38.76 (0.80) xw | 32.04 (0.47) v | 42.65 (1.33) yx | 37.72 (0.87) wv | 50.99 (1.37) z |
| Depth | 1.92 (0.06) w | 1.50 (0.04) v | 1.48 (0.04) v | 2.67 (0.07) x | 3.35 (0.18) z | 2.64 (0.08) x | 2.84 (0.12) y |
| CV$_{\text{Depth}}$ | 43.10 (0.98) y | 36.64 (0.93) x | 43.84 (1.12) y | 40.22 (0.98) yx | 53.91 (1.12) z | 40.72 (1.41) y | 53.33 (1.87) z |

Models explaining habitat use were developed for Largescale Sucker, Mountain Whitefish, Northern Pikeminnow, Peamouth, Rainbow Trout, Redside Shiner, and Torrent Sculpin. All remaining species were rare; therefore, habitat use models could not be developed for them due to convergence issues. The regression models revealed several habitat use patterns that varied among species and families (Table 4). The presence of Mountain Whitefish and Rainbow Trout was positively related to the proportion of coarse substrate, and the presence of Peamouth and Redside Shiner was positively related to the proportion of fine substrate. The presence of Redside Shiner was positively related to the proportion of vegetated bank but negatively related to the CV of current velocity. The presence of Northern Pikeminnow was positively related to mean depth, but this pattern was not observed for other native cyprinids.

The models that predicted the relative abundance of native species based on environmental characteristics (Table 5) differed only slightly from those that predicted the occurrence of those species (Table 4). The proportion of cobble–boulder bank was positively related to the relative abundance of Torrent Sculpin, and the proportion of coarse substrate was positively related

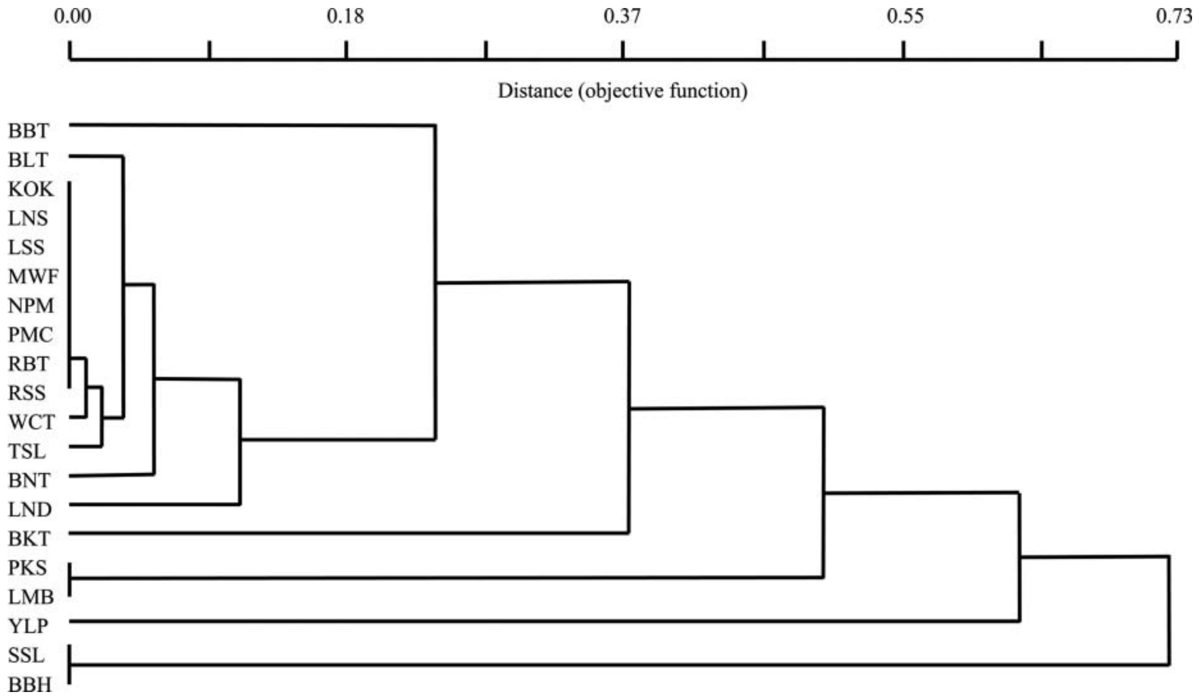

FIGURE 4. Dendrogram of the reach similarity among all of the fish species sampled from the Kootenai River, May–September 2012 and 2013, based on Jaccard's index of similarity. See Figure 2 for species codes.

TABLE 4. The top multiple-regression models for the occurrence of fishes in the Kootenai River, summer 2012–2013. Akaike's information criterion (AIC) was used to rank the models. The negative log-likelihood (–Log[*l*]) and the area under the receiver operating characteristic curve (AUC) are also included for each model. The relationships between the covariates (Table 1) and species occurrence are designated as negative or positive.

| Species | Model | AIC | ΔAIC | −Log(*l*) | AUC |
|---|---|---|---|---|---|
| Largescale Sucker | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$ | 1,277.39 | 0.00 | −632.70 | 0.88 |
| | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$, +CV$_{\mathrm{Vel}}$ | 1,278.08 | 0.69 | −633.04 | 0.86 |
| Mountain Whitefish | +Substrate$_{\mathrm{Coarse}}$ | 1,184.18 | 0.00 | −587.09 | 0.81 |
| | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$ | 1,184.88 | 0.70 | −586.44 | 0.81 |
| | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$, +CV$_{\mathrm{Vel}}$ | 1,185.20 | 1.02 | −586.60 | 0.78 |
| Northern Pikeminnow | +Depth, −CV$_{\mathrm{Vel}}$ | 672.03 | 0.00 | −330.01 | 0.77 |
| | +Depth | 672.83 | 0.80 | −331.41 | 0.77 |
| Peamouth | +Substrate$_{\mathrm{Fine}}$ | 540.74 | 0.00 | −265.37 | 0.71 |
| Rainbow Trout | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$, −Depth, +CV$_{\mathrm{Vel}}$, +Woody cover | 857.28 | 0.00 | −419.64 | 0.64 |
| Redside Shiner | +Substrate$_{\mathrm{Fine}}$, −CV$_{\mathrm{Vel}}$ | 430.30 | 0.00 | −209.15 | 0.76 |
| | +Substrate$_{\mathrm{Fine}}$, −CV$_{\mathrm{Vel}}$, +Bank$_{\mathrm{Veg}}$ | 432.17 | 1.87 | −209.06 | 0.75 |
| Torrent Sculpin | +Bank$_{\mathrm{Co\text{-}Bo}}$ | 344.30 | 0.00 | −167.15 | 0.62 |
| | +Bank$_{\mathrm{Co\text{-}Bo}}$, +CV$_{\mathrm{Vel}}$ | 346.29 | 1.99 | −167.14 | 0.61 |

to the relative abundance of Largescale Sucker, Mountain Whitefish, and Rainbow Trout. In contrast, the proportion of fine substrate was positively related to the relative abundance of native cyprinids (e.g., Peamouth and Redside Shiner). Heterogeneity of velocity was also important to cyprinids: the CV of velocity was negatively related to the relative abundance of both Peamouth and Redside Shiner (Table 5).

The parameter estimates of the top models for each species were compared to evaluate both the precision and the significance of the environmental covariates. Model uncertainty was evident for all those species for which multiple models were retained in the confidence set; however, the top group of models often contained redundancy of important covariates. For example, all of the top models that predicted the relative abundance of Northern Pikeminnow contained mean depth; similarly, the top models for Largescale Sucker contained both substrate and depth. Further, the 95% confidence intervals around the parameter estimates for any additional covariates (e.g., the CV of velocity for Northern Pikeminnow) often encompassed zero. Therefore, the model estimates were imprecise and we overestimated the importance of depth in explaining the variation in the relative abundance of Northern Pikeminnow. This same pattern occurred for almost all other species in which a single environmental covariate was both

TABLE 5. The top multiple-regression models for the relative abundance of fishes sampled from the Kootenai River, summer 2012–2013. Akaike's information criterion (AIC) was used to rank the models. The negative log-likelihood (–Log[*l*]), α (a dispersion parameter), and the root mean square error (RMSE) are also included. The relationships between the covariates (Table 1) and relative abundance are designated as negative or positive.

| Species | Model | AIC | ΔAIC | −*Log*(*l*) | α | RMSE |
|---|---|---|---|---|---|---|
| Largescale Sucker | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$, +CV$_{\mathrm{Vel}}$, −Depth | 4,036.88 | 0.00 | −2,009.44 | 1.70 | 2.39 |
| | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$, +CV$_{\mathrm{Vel}}$, −Depth, +Woody cover | 4,037.28 | 0.40 | −2,008.64 | 1.71 | 2.40 |
| Mountain Whitefish | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$, +CV$_{\mathrm{Vel}}$, −Depth | 4,385.58 | 0.00 | −2,184.67 | 2.23 | 2.51 |
| | +Substrate$_{\mathrm{Coarse}}$, +Bank$_{\mathrm{Veg}}$, +CV$_{\mathrm{Vel}}$, −Depth, +Woody cover | 4,385.72 | 0.14 | −2,182.86 | 2.26 | 2.52 |
| Northern Pikeminnow | +Depth | 1,036.67 | 0.00 | −512.92 | 0.35 | 1.50 |
| | +Depth, +CV$_{\mathrm{Vel}}$, | 1,037.84 | 1.17 | −511.34 | 0.36 | 1.50 |
| Peamouth | +Substrate$_{\mathrm{Fine}}$, | 1,013.63 | 0.00 | −500.81 | 0.70 | 1.87 |
| | +Substrate$_{\mathrm{Fine}}$, −CV$_{\mathrm{Vel}}$ | 1,015.45 | 1.82 | −500.73 | 0.69 | 1.88 |
| | +Substrate$_{\mathrm{Fine}}$, +Bank$_{\mathrm{Veg}}$ | 1,015.50 | 1.87 | −500.75 | 0.69 | 1.90 |
| Rainbow Trout | +Substrate$_{\mathrm{Coarse}}$, +CV$_{\mathrm{Vel}}$ | 1,064.60 | 0.00 | −525.29 | 3.38 | 0.44 |
| Redside Shiner | +Substrate$_{\mathrm{Fine}}$, −CV$_{\mathrm{Vel}}$, +Bank$_{\mathrm{Veg}}$ | 848.86 | 0.00 | −416.43 | 0.20 | 6.41 |
| | +Substrate$_{\mathrm{Fine}}$, −CV$_{\mathrm{Vel}}$ | 849.62 | 0.76 | −418.10 | 0.22 | 6.57 |
| Torrent Sculpin | +Bank$_{\mathrm{Co\text{-}Bo}}$ | 456.74 | 0.00 | −222.37 | 0.47 | 0.33 |
| | +Bank$_{\mathrm{Co\text{-}Bo}}$, +Substrate$_{\mathrm{Coarse}}$ | 457.41 | 0.67 | −221.70 | 0.48 | 0.33 |

TABLE 6. Parameter estimate, standard error (SE), and lower and upper 95% confidence limits for each parameter from the most parsimonious models predicting the occurrence of species in the Kootenai River, summer 2012–2013.

| | | | | 95% confidence limits | |
|---|---|---|---|---|---|
| Species | Model parameter | Estimate | SE | Lower | Upper |
| Largescale Sucker | $\text{Substrate}_{\text{Coarse}}$ | 0.004 | 0.005 | −0.005 | 0.014 |
| | $\text{Bank}_{\text{Veg}}$ | 0.011 | 0.004 | 0.004 | 0.019 |
| Mountain Whitefish | $\text{Substrate}_{\text{Coarse}}$ | 0.022 | 0.005 | 0.012 | 0.032 |
| Northern Pikeminnow | $\text{CV}_{\text{Vel}}$ | 0.004 | 0.008 | −0.013 | 0.020 |
| | Depth | 0.181 | 0.089 | 0.007 | 0.356 |
| Peamouth | $\text{Substrate}_{\text{Fine}}$ | 0.026 | 0.006 | 0.015 | 0.037 |
| Rainbow Trout | $\text{Substrate}_{\text{Coarse}}$ | 0.014 | 0.004 | 0.007 | 0.021 |
| | $\text{Bank}_{\text{Veg}}$ | −0.008 | 0.004 | −0.016 | −0.001 |
| | $\text{CV}_{\text{Vel}}$ | −0.001 | 0.007 | −0.015 | 0.013 |
| | Depth | −0.134 | 0.089 | −0.312 | 0.035 |
| | Woody cover | 0.007 | 0.003 | 0.002 | 0.012 |
| Redside Shiner | $\text{Substrate}_{\text{Fine}}$ | 0.009 | 0.008 | 0.007 | 0.023 |
| | $\text{CV}_{\text{Vel}}$ | 0.037 | 0.014 | 0.010 | 0.064 |
| Torrent Sculpin | $\text{Bank}_{\text{Co-Bo}}$ | 0.014 | 0.006 | 0.002 | 0.027 |

precise and important in explaining the occurrence and relative abundance of each species (Tables 6, 7). The only cases in which this pattern was not observed were the models that predicted the occurrence of Rainbow Trout and Redside Shiner. In the top model for Rainbow Trout occurrence, the surface area of woody cover and the proportion of coarse substrate were equally important covariates (Table 6). For Redside Shiner, the important covariates were the proportion of fine substrate and the CV of velocity (Table 6).

## DISCUSSION

Fish assemblages are structured by their relationships with both abiotic and biotic factors (Schlosser 1982; Fischer and

TABLE 7. Parameter estimate, standard error (SE), and lower and upper 95% confidence limits for each parameter from the most parsimonious models predicting the relative abundance of species in the Kootenai River, summer 2012–2013.

| | | | | 95% confidence limits | |
|---|---|---|---|---|---|
| Species | Model parameter | Estimate | SE | Lower | Upper |
| Largescale Sucker | $\text{Substrate}_{\text{Coarse}}$ | 0.005 | 0.003 | 0.003 | 0.010 |
| | $\text{Bank}_{\text{Veg}}$ | 0.004 | 0.003 | −0.001 | 0.010 |
| | $\text{CV}_{\text{Vel}}$ | −0.004 | 0.004 | −0.011 | 0.003 |
| | Depth | −0.137 | 0.058 | −0.235 | −0.006 |
| Mountain Whitefish | $\text{Substrate}_{\text{Coarse}}$ | 0.016 | 0.003 | 0.010 | 0.023 |
| | $\text{Bank}_{\text{Veg}}$ | 0.002 | 0.002 | −0.003 | 0.006 |
| | $\text{CV}_{\text{Vel}}$ | −0.001 | 0.003 | −0.007 | 0.005 |
| | Depth | −0.154 | 0.049 | −0.251 | −0.058 |
| Northern Pikeminnow | Depth | 0.248 | 0.137 | 0.040 | 0.452 |
| Peamouth | $\text{Substrate}_{\text{Fine}}$ | 0.021 | 0.004 | 0.014 | 0.028 |
| Rainbow Trout | $\text{Substrate}_{\text{Coarse}}$ | 0.010 | 0.003 | 0.004 | 0.016 |
| | $\text{CV}_{\text{Vel}}$ | −0.144 | 0.080 | −0.301 | 0.012 |
| Redside Shiner | $\text{Substrate}_{\text{Fine}}$ | 0.009 | 0.012 | 0.001 | 0.031 |
| | $\text{Bank}_{\text{Veg}}$ | −0.034 | 0.014 | −0.061 | −0.007 |
| | $\text{CV}_{\text{Vel}}$ | 0.031 | 0.018 | −0.005 | 0.067 |
| Torrent Sculpin | $\text{Bank}_{\text{Co-Bo}}$ | 0.013 | 0.007 | 0.001 | 0.026 |

Paukert 2008), which can vary at relatively small spatial scales. In large rivers, the abiotic characteristics that are associated with the off-channel habitats are among the most limiting for native fishes. Side channels in the Kootenai River are scarce, but they provide exceptional diversity with regard to fish habitat. In this study, habitat and fish assemblage structure varied between side- and main-channel environments, and the differences in habitat characteristics explained much of the variation in assemblage structure. In most cases, the substrate type, depth, and heterogeneity of velocity best explained the variability in both the occurrence and relative abundance of native species. Important habitat variables also tended to be consistent among families and to be directly related to the ecological needs of individual species.

Habitats were different among sites; however, they were most variable between the side- and main-channel sites and between the rehabilitated and non-rehabilitated sites. Of all the variables measured in this study, heterogeneity of depth and velocity were the most similar. Estimates of mean depth and velocity displayed high variability among the side-channel habitats and between the side- and main-channel habitats. The side channels were shallower on average, and they had slower current velocities than the main-channel habitats. Heterogeneity of velocity appeared to be somewhat related to substrate diversity: sites that had high proportions of coarse substrate also had lower CVs of velocity. For example, the south side channel had higher mean current velocity than the other three side channels, and it also had a bottom that was uniformly composed of coarse substrate. Substrate composition diversity is typically correlated with a high variation in current velocity because water movement will sort out substrate particles by size (Tett et al. 1978; Willis et al. 2005). On average, the side-channel environments in the Kootenai River displayed a greater variability in current velocity than the main-channel environments, resulting in high substrate diversity. Sites located at the downstream portion of the braided section generally had higher proportions of fine sediment, likely due to reduced current velocities near the meander section. Woody instream cover was not abundant in the braided section, and rehabilitated sites predictably had more woody debris.

Species richness was generally higher, and rare species were more common, in the side-channel habitats than in the main-channel habitats of the Kootenai River. This is consistent with the results of previous studies that have documented a higher occurrence and relative abundance of rare species in off-channel habitats (Fisher and Willis 2000; Eder 2009; Whiteman et al. 2011). Similar findings have been reported in other large-floodplain rivers where extensive habitat loss has occurred. Whiteman et al. (2011) reported higher relative abundances of Shoal Chub *Macrhybopsis hyostoma*, Sturgeon Chub *M. gelida*, Silver Chub *M. storeriana*, and River Shiner *Notropis blennius* in the side-channel habitats of the lower Missouri River than in the main-channel habitats, and they found the side channels to be characterized by high depth diversity, abundant fine substrate, and low current velocities. We similarly found the relative abundance of cyprinids (e.g., Peamouth and Northern Pikeminnow) to be associated with the low current velocities and fine substrates that are characteristic of side-channel environments (Torgersen et al. 2006). Three other rare species (Pumpkinseed, Largemouth Bass, and Yellow Perch) were also closely associated with the side-channel environments, particularly the north side channel. These three nonnative species showed high reach similarity, and their relative abundance was correlated with fine substrate in the north side channel. Furthermore, their overall patterns were closely associated with the low current velocity, and abundant woody instream cover found in the north side channel.

Our study suggests that specific habitat characteristics are important for predicting the occurrence and relative abundance of many native fishes in the Kootenai River and provides further evidence that habitat complexity is important in structuring fish assemblages. Substrate type, bank type, and heterogeneity of velocity were identified as the most important variables in predicting the occurrence of most species. The proportions of coarse substrate and vegetated bank explained the occurrence and relative abundance of both salmonids and catostomids, similar to findings in other North American systems (Scott and Crossman 1973; Lanka et al. 1987; Rahel and Hubert 1991), including previous work on the Kootenai River (Smith 2013). Coarse substrates are important habitats for many of the macroinvertebrates that serve as primary food resources for insectivorous fishes in lotic systems (Flecker and Allan 1984). In addition, the availability of terrestrial food resources can be influenced by the amount of vegetated riparian habitat (Baxter et al. 2005). Food resources have been shown to influence the dynamic rate functions of fluvial species, especially when proximity to suitable riparian habitat is a limiting factor (Rosenfeld et al. 2008). Our findings further support the belief that coarse substrate is an important habitat need of many lotic fishes, despite the limits such habitat can impose on species (e.g., cyprinids) that prefer fine substrate. Our results are consistent with the habitat use patterns identified by Smith (2013), who found that salmonids and catostomids were most abundant in the canyon and braided sections of the Kootenai River and least abundant in the meander section, where coarse substrate is rare.

The expansion of nonnative fishes is a growing concern and an active area of research in fisheries biology (Rahel 2000; Quist and Hubert 2004; Benjamin and Baxter 2010). We found that native species had few reaches in common with nonnative species. The lack of reach similarity between native and nonnative fishes may result from negative biotic interactions (Richter et al. 1997). Native fishes are often displaced by nonnative fishes through either indirect (e.g., competition for food and space; Thompson and Rahel 1996; Gido and Brown 1999) or direct (e.g., predation; Ruzycki et al. 2003) mechanisms. Maiolie and Elam (1993) reported declines in kokanee

*Oncorhynchus nerka* abundance in Lake Pend Oreille, Idaho, following the introduction of the nonnative Lake Trout *Salvelinus namaycush*. In Iowa lakes, Jackson et al. (2010) found that Common Carp *Cyprinus carpio* degraded the water quality and created turbid conditions that negatively influenced the native, sight-feeding fishes (e.g., Bluegill *Lepomis macrochirus* and black basses *Micropterus* spp.). The growth, recruitment, and abundance of native fishes are often negatively influenced by resource competition and predation from nonnative fishes. A negative association between native and nonnative fishes may also result from a habitat disturbance, which is often created by land and water uses and sometimes from the unintended consequences of rehabilitation activities around newly constructed treatments.

The increased occurrence of nonnative fishes has been previously associated with habitat alterations in riverine systems throughout the western United States, systems that are similar to the Kootenai River (Hughes and Gammon 1987; Richards 1997). Our results indicate that nonnative fishes (e.g., Pumpkinseed, Largemouth Bass, and Yellow Perch) were more common and abundant in the north side channel complex, which is the most extensively rehabilitated site in the braided section of the Kootenai River. Habitat alteration has been shown to facilitate the range expansion and increased abundance of nonnative fishes because nonnatives are often readily adaptable to disturbed habitat conditions (MacDougall and Turkington 2005; Light and Marchetti 2007). We observed higher relative abundances of nonnative fishes in newly disturbed areas around rehabilitation treatments than in non-rehabilitated areas. Our results support other findings that show strong relationships between disturbances and the range expansion of nonnative fishes (Taylor et al. 2001; Quist et al. 2005), but our findings also raise concerns about possible expansion and colonization by nonnative fishes in the Kootenai River. Although we observed higher occurrences and relative abundances at the rehabilitated areas than at the non-rehabilitated areas, these observations were only made at the most downstream site, which was the site closest to the meander section. The meander section is deep, and it has low current velocity and less habitat heterogeneity than the braided section. The fish assemblage in the meander section is largely dominated by cyprinids and nonnative fishes (Smith 2013), suggesting that nonnative fishes could colonize newly disturbed habitats upstream. Smith (2013) reported habitat use patterns by nonnative fishes that are similar to those we found in the restored side-channel habitats of the Kootenai River (e.g., the north side channel); therefore, the north side channel is likely to be conducive to the persistence of nonnative fishes that have already established viable populations in the meander section.

This study showed that habitat associations among taxa are variable but related to the ecology of each species; that fish assemblages vary between main- and side-channel habitats; and that the north side channel of the Kootenai River has a higher relative abundance of nonnative fishes than the other sites. Two mechanisms may be related to the expansion of nonnative fishes upstream into the braided reach. The first of these is the proximity of source populations in the meander section. The second is the ability of nonnative fishes to easily colonize rehabilitated habitats because they are more tolerant of disturbance than native fish. We hypothesize that the colonization of treatment areas by nonnative species is a combination of both mechanisms. We also suggest that management plans that seek to improve native species habitat need to account for the potential expansion of and colonization by nonnatives as well as their interaction with native species. These considerations will likely help managers identify areas where habitat rehabilitation will be most successful.

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