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# FISH ASSEMBLAGE STRUCTURE AND HABITAT ASSOCIATIONS IN A LARGE WESTERN RIVER SYSTEM[†]

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## ABSTRACT

Longitudinal gradients of fish assemblage and habitat structure were investigated in the Kootenai River of northern Idaho. A total of 43 500-m river reaches was sampled repeatedly with several techniques (boat-mounted electrofishing, hoop nets and benthic trawls) in the summers of 2012 and 2013. Differences in habitat and fish assemblage structure were apparent along the longitudinal gradient of the Kootenai River. Habitat characteristics (e.g. depth, substrate composition and water velocity) were related to fish assemblage structure in three different geomorphic river sections. Upper river sections were characterized by native salmonids (e.g. mountain whitefish *Prosopium williamsoni*), whereas native cyprinids (peamouth *Mylocheilus caurinus*, northern pikeminnow *Ptychocheilus oregonensis*) and non-native fishes (pumpkinseed *Lepomis gibbosus*, yellow perch *Perca flavescens*) were common in the downstream section. Overall, a general pattern of species addition from upstream to downstream sections was discovered and is likely related to increased habitat complexity and additions of non-native species in downstream sections. Assemblage structure of the upper sections were similar, but were both dissimilar to the lower section of the Kootenai River. Species-specific hurdle regressions indicated the relationships among habitat characteristics and the predicted probability of occurrence and relative abundance varied by species. Understanding fish assemblage structure in relation to habitat could improve conservation efforts of rare fishes and improve management of coldwater river systems. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: fish assemblage; rivers; habitat; populations; longitudinal gradient; species addition

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## INTRODUCTION

Lotic systems and their corresponding fish assemblages are highly imperilled due to widespread anthropogenic disturbances (Allan and Flecker, 1993; Søndergaard and Jeppesen, 2007; Hoagstrom *et al*., 2011). Consequently, factors that influence fish assemblage structure (species richness and evenness) have been widely investigated (Rahel and Hubert, 1991; Oberdorff *et al*., 1993; Magalhães *et al*., 2002). Gradients of lotic fish assemblage structure may be influenced by a number of biotic (e.g. non-native species introductions) and abiotic factors (e.g. temperature and depth) across longitudinal gradients (Rahel and Hubert, 1991; Rahel, 2000; Quist *et al*., 2005a). For example, Quist *et al*. (2005a) reported that both large-scale (e.g. elevation) and local factors (e.g. abundance of non-native piscivores, aquatic habitat) were related to the distribution of fishes in lotic systems of Wyoming. In addition, anthropogenic alterations (e.g. dam construction) can also influence fish assemblages and may disrupt gradients of fish assemblage structure (Ward and Stanford, 1983; Ward and Stanford, 1995; Quinn and Kwak, 2003; Quist *et al*., 2005b).

Lotic systems are dynamic and diverse, consequently, understanding transitions in fish assemblage structure within large rivers can be challenging. Numerous historical (e.g. river continuum and serial discontinuity) and recent (e.g. process domains and riverine ecosystem synthesis) concepts have been proposed in an attempt to understand shifts in the longitudinal structure in lotic systems (Vannote *et al*., 1980; Ward and Stanford, 1983; Montgomery, 1999; Thorp *et al*., 2006). Implicit in many of these concepts is that longitudinal gradients in fish assemblage structure emerge from two processes, zonation and addition (Rahel and Hubert, 1991; Hoagstrom *et al*., 2007). Zonation is characterized by the presence of distinct assemblages that emerge in response to large-scale gradients in geomorphology or thermal characteristics (Rahel and Hubert, 1991). Transition of fish assemblages from

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coldwater (salmonid) to warmwater (cyprinid and catostomid) dominated assemblages has been characterized as an example of zonation (Rahel and Hubert, 1991). Longitudinal addition is simply an increase in species richness from upstream to downstream; such patterns are common in riverine systems (Gehrke and Harris, 2000; Bistoni and Hued, 2002; Hoagstrom and Berry, 2008). Patterns of downstream species addition are generally attributed to increasing habitat complexity and niche space (Sheldon, 1968; Rahel and Hubert, 1991; Hoagstrom *et al*., 2007). Regardless of the specific mechanism, understanding the factors influencing gradients of fish assemblage structure is critical for the conservation of imperilled fishes and preservation of aquatic biodiversity; however, understanding the factors regulating processes at the population level is also important.

Fish populations are regulated by internal (e.g. growth) and external factors (e.g. aquatic habitat and piscivore abundances) and are sensitive to changes in environmental conditions (Murdock, 1994; Power, 2007; Pope *et al*., 2010). Population-level investigations often provide greater insight into drivers of a system than inferences from fish assemblages because species respond differently to environmental conditions thereby confounding assemblage-level patterns (Kwak and Peterson, 2007; Fischer *et al*., 2010). For instance, differences in fish assemblage structure were not apparent in stream reaches in Iowa with and without managed riparian buffers, but differences in population dynamics (i.e. growth rates) were clear for several species (e.g. central stoneroller *Campostoma anomalum* and creek chub *Semotilus atromaculatus*; Fischer *et al*., 2010). Additionally, populations provide a more immediate response to abiotic and biotic disturbances, as shifts in fish assemblage structure typically occur over long temporal scales (e.g. Quist *et al*., 2005b; Gido *et al*., 2010).

Although habitat largely regulates assemblages and population characteristics, biotic factors also have an important influence on species (Czech *et al*., 2000; Miller-Reed and Czech, 2005; Hoagstrom *et al*., 2011). In particular, the introduction of non-native species can disrupt systems and result in altered assemblage structure or species declines (e.g. Koel *et al*., 2005; Hansen *et al*., 2008). Specifically, non-native fishes have been reported to alter aquatic systems through direct (e.g. predation and competition) and indirect (e.g. habitat alteration) mechanisms. For instance, non-native lake trout *Salvelinus namaycush* were illegally introduced into Yellowstone Lake, Wyoming, and have had direct effects (i.e. predation) on Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* and indirect effects on other components of the Yellowstone system (e.g. grizzly bears *Ursus arctos*; Koel *et al*., 2005). Due to the potential deleterious effects of non-native species, control of their distribution and density is important (Kolar *et al*., 2010). While removal is common (Koel *et al*., 2005; Hansen *et al*., 2008; Coggins *et al*., 2011), it can often prove ineffective for some species (e.g. brook trout *Salvelinus fontinalis*; Meyer *et al*., 2006). Habitat modification has also been used to manage non-native fishes in lotic systems (e.g. Valdez *et al*., 2001; Brown and Ford, 2002; Scoppettone *et al*., 2005). Brown and Ford (2002) reported that the manipulation of hydrologic regimes in the Tuolumne River, California, could be a useful management strategy for restoring native fishes and controlling non-native species. Similarly, Valdez *et al*. (2001) suggested that experimentally raised flow conditions in the Colorado River, Arizona, could be used to displace non-native species (e.g. rainbow trout *Oncorhynchus mykiss*); however, events of greater discharge may be necessary for long-term suppression of non-native species. Understanding habitat relationships with native and non-native fishes in large rivers could be an important management tool in native species restoration efforts.

Due to the advantages of fish assemblage and population-level approaches, both were used to investigate relationships among assemblages and populations with habitat in the Kootenai River. We hypothesized that (1) longitudinal patterns of fish assemblage structure would be present and (2) the relationship between habitat and the occurrence and relative abundance of native and non-native fishes would vary by species.

## METHODS

### *Study area*

The Kootenai River is one of the largest tributaries of the Columbia River with an international watershed of approximately 50 000 km$^2$ (Knudson, 1994). The Kootenai River originates in the Kootenay National Park, British Columbia, Canada, and flows south into Montana and then Idaho before returning to British Columbia. Despite minimal anthropogenic disturbance in the upper watershed (i.e. Canada), many alterations have occurred in lower portions of the watershed, including land use changes (e.g. logging, agriculture and mining; Richards, 1997) and the construction of the Libby Dam near Libby, Montana (Knudson, 1994). Construction of the Libby Dam was completed in 1972 by the U.S. Army Corps of Engineers for flood control and power generation (Knudson, 1994). Completion of the Libby Dam altered natural regimes (i.e. hydrologic, nutrient and thermal; Whitfield and Woods, 1984; Knudson, 1994), and subsequent shifts in fish assemblage structure downstream of the Libby Dam have been reported (Paragamian, 2002). Additionally, the operation of the Libby Dam has been directly implicated in the decline of native imperilled species (i.e. burbot *Lota lota* and white sturgeon *Acipenser transmontanus*; Paragamian *et al*., 2000; Paragamian *et al*., 2001).

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The Idaho portion of the Kootenai River has three geomorphic sections (canyon, braided and meander; Fosness and Williams, 2009; Figure 1). The canyon section (257–312 river kilometre [rkm]) has high current velocities (>1 m/s), large substrate (cobble and boulder) and limited channel movement. The braided section (246–257 rkm) is a transitional zone characterized by high rates of sediment deposition, low average depth (<2 m) and a braided channel type. The most downstream section of the Kootenai River in Idaho is the meander section. The meander section (120–246 rkm) connects to Kootenay Lake, British Columbia, Canada, and is characterized by low water velocities (<0.5 m/s), fine substrate (silt and sand) and high maximum depths (>25 m; Fosness and Williams, 2009).

### *Sampling design and field sampling*

Field sampling occurred at 43 500-m long reaches during the summers (June–August) of 2012–2013. Each 500-m reach was subdivided into two 250-m subsections (hereafter referred to as a sampling site). Three sampling techniques (hoop nets, benthic trawl and boat-mounted electrofishing) surveyed all reaches repeatedly (two to three times) to increase the probability that all species were detected.

Hoop nets were used to target small-bodied and benthic fishes in habitats that were difficult to sample with other techniques. The hoop nets used in this study had six 60-cm-diameter circular steel hoop frames. Two throats (10-cm minimum diameter) were located between the second and fourth, and fourth and sixth hoop frames. The nets had an overall length of 3.7 m and were covered with 6.3-mm knotless delta style mesh. Four hoop nets were deployed following the completion of active sampling gears (i.e. electrofishing and trawls) and fished for approximately 12 h. Nets were baited with local non-game fishes (e.g. *Catostomus* spp.).

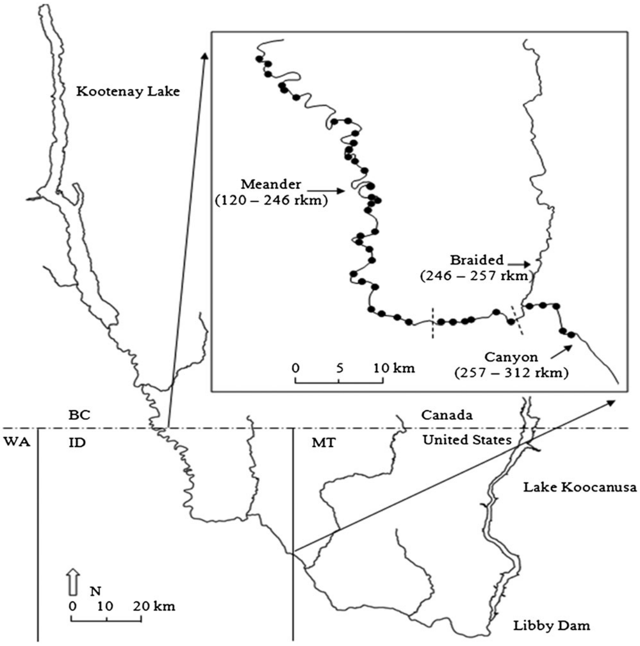

Figure 1. Forty-three sampling locations (black circles) and river sections (braided, canyon and meander) of the Kootenai River, United States and Canada. River kilometres (rkm) are included for each river section

In addition to hoop nets, a modified Missouri River benthic trawl (henceforth referred to as a trawl) was used to sample small-bodied and juvenile fishes in riverine habitats. The trawl was constructed with a large inner mesh in the body (0.10 cm diameter No. 7 multifilament nylon twine, 3.5-cm bar measure mesh) and a smaller outer mesh surrounding the body and composing the wings of the trawl (6.3-mm delta style, knotless mesh). A small mesh completely encompassing the larger inner mesh limited the loss of small-bodied fish through the trawl and minimized the chance of smaller fishes being damaged by large-bodied fish or debris collected by the trawl (Herzog *et al*., 2005). A chain (5-mm link diameter) was attached to the 3.7-m footrope to maintain contact with the bottom. Towlines on the trawl (2.2-cm twisted nylon rope) were 30.5 m in length and allowed the trawls to be fished along the bottom. Otter doors (61 cm × 30.5 cm) were attached to the trawl and prevented the trawl from collapsing while deployed. Trawls were deployed off the bow and pulled downstream at a velocity slightly faster than the current. Each trawl was fished for 50 m or until snagged. If a trawl sampled 30 m or less due to snagging, the trawl haul was removed from the analysis and was replicated until a haul sampled more than 30 m. A global positioning system receiver (Lowrance, Tulsa, OK, USA) was used to measure the distance sampled, and measurement started once the trawl was fully deployed. The distance (m) travelled with the trawl fully deployed was used to evaluate effort.

Previous research has shown that electrofishing has high detection probabilities for most fishes in the study system (Smith, 2013). Electrofishing gear consisted of an Infinity model electrofisher (Midwest Lake Electrofishing Systems, Inc., Polo, MO, USA) and a 5000 W Honda generator (American Honda Motor Co., Inc., Torrance, CA, USA). Electrofishing power output was standardized to 2750–3250 W (Miranda, 2009). Two netters were stationed near the bow of the boat to collect fish. Dip nets used to collect fish had a 6.3-mm knotless mesh. Pulsed-DC electrofishing was conducted during the day. The electrofishing effort was randomly allocated to one bank for the upstream sampling site and shifted to the alternate bank for the downstream sample site. Electrofishing was initiated in the uppermost portion of the reach and proceeded with a single pass in a downstream direction. Catch was enumerated at the completion of electrofishing effort for every sample site.

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Effort was recorded as the number of seconds with electricity being applied to the water.

Most fishes were identified in the field, measured (total length; mm), enumerated and released. However, due to difficulties in identifying some species and an inability to preserve a large number of fishes, catch of cottids (slimy sculpin *Cottus cognatus* and torrent sculpin *C. rhotheus*) were combined and hereafter referred to as Cottidae. All fish were released at a location away from subsequent sample sites.

Habitat characteristics were measured to evaluate relationships with fish assemblage composition and relative abundance (Table I). Proportion of bank type was classified into one of four categories: eroding, vegetation, silt-sand (≤0.2 mm) and cobble–boulder (≥64.0 mm). Wetted width, depth (m), flow velocities (m/s) and substrate type were measured using systematically assigned transects (six habitat transects for each sample reach). Wetted-width measurements were estimated to the nearest 0.5 m with a laser rangefinder at every transect (Wilhelm *et al*., 2005). Seven equidistant points across the wetted width of the transect were measured for depth, velocity and substrate composition (Neebling and Quist, 2011). Depth measurements were recorded using a Lowrance depth finder (Lowrance, Tulsa, OK, USA). In depths less than 1 m, mean water column velocities were measured at 60% of the depth using an electromagnetic flow meter (Kaufmann *et al*., 1999; Flotermersch *et al*., 2001; Marsh-McBirney, Loveland, CO, USA). If the depth was greater than 1 m, mean water column velocity measures were recorded at 20% and 80% of the depth. In addition to mean water column velocity, bottom velocity was thought to be a potentially important habitat characteristic for fishes, particularly benthic fishes. Bottom velocity measurements were collected 8 cm from the bottom. Substrate composition was estimated into one of five categories: organic matter-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). Substrate composition was classified using a combination of visual assignment, sounding rod and rope with a heavy anchor (Collins and Flotemersch, 2014).

### *Fish assemblage and habitat structure*

A principal component analysis was used to examine correlations among all collected habitat variables. Habitat variables were $\log_{10}$-transformed to meet normality assumptions. Variables were standardized by subtracting the variable-specific mean from individual values and dividing by the standard deviation to provide equal weight to all variables (Rahel and Jackson, 2007). Reach-averaged habitat variables and fish species richness were compared among river sections using a Kruskal–Wallis rank sum test (Higgins, 2004). A Bonferroni correction ($\alpha/K = 0.05/6$) was used to account for multiple comparisons of habitat characteristics among river sections (Higgins, 2004).

Fish assemblage relationships were investigated using non-metric multidimensional scaling (NMDS). Non-metric multidimensional scaling is a robust ordination technique that is widely used to assess fish assemblage relationships (e.g. Helms *et al*., 2005; Ruetz *et al*., 2007; Rowe *et al*., 2009). Fit of ordinations was evaluated with ordination stress. Final stress values less than 20.0 indicate a good fit of the ordination (McCune and Grace, 2002). Fish assemblage composition was investigated using an NMDS with presence–absence data pooled across all gears for every reach and for all species. In addition, assemblage structure was evaluated with two separate ordinations using reach-specific, average relative abundance of species by gear. Fish assemblage structure using relative abundance information was investigated by gear to minimize potential gear biases. Only the catch from gears with the greatest detectability (i.e. electrofishing and hoop nets; Smith, 2013) were used in the analyses of relative abundance data. Differences in assemblage structure among river sections

Table I. Mean and standard error (in parentheses) of habitat variables collected from 43 reaches on the Kootenai River during the summers (June−August) of 2012 and 2013

| Variable | Description | River section | | |
|---|---|---|---|---|
| | | Braided | Canyon | Meander |
| $\text{Bank}_{\text{Co−Bo}}$ | Percentage of bank consisting of large substrate (cobble and boulder; %) | 25.2 (8.5) | 46.6 (7.2) | 6.9 (1.7) |
| $\text{Bank}_{\text{Veg}}$ | Percentage of bank consisting of vegetation (%) | 30.0 (10.3) | 44.6 (12.9) | 41.7 (6.1) |
| $\text{CV}_{\text{Vel}}$ | Mean coefficient of variation in water column velocity | 0.54 (0.08) | 0.46 (0.10) | 0.32 (0.04) |
| Depth | Mean depth (m) | 2.5 (0.2) | 2.8 (1.3) | 7.7 (0.4) |
| Distance | Distance from Libby Dam, Libby, Montana (km) | 103.9 (1.5) | 91.9 (3.0) | 141.0 (1.6) |
| $\text{Substrate}_{\text{Co−Bo}}$ | Percentage of substrate consisting of cobble and boulder (%) | 30.2 (9.2) | 48.6 (7.6) | < 0.1 (0.1) |
| Width | Mean width (m) | 209.4 (26.7) | 124.1 (11.3) | 180.4 (4.1) |

Habitat variables are organized by river section (braided, canyon, meander). Variables were used to investigate relationships among fish assemblage and populations with habitat characteristics.

were investigated with a permutational multivariate analysis of variation (PERMANOVA). PERMANOVA was performed separately for species composition and electrofishing and hoop net relative abundance metrics of assemblage structure. If a significant difference ($p \leq 0.05$) among river sections was reported with the PERMANOVA, habitat vectors were fit to the NMDS ordination with rotational vector fitting (Faith and Norris, 1989). Habitat variables were fit onto the NMDS ordination if variables were significant ($p \leq 0.05$) with a permutation test (999 random iterations) using the Envfit function, Vegan package, Program R (Oksanen *et al*., 2011). Bray–Curtis dissimilarity measures were used for NMDS and PERMANOVA analyses with the MetaMDS and Adonis functions in the Vegan package, Program R (R Development Core Team, 2009; Oksanen *et al*., 2011; Oksanen, 2013).

### *Species-specific habitat relationships*

In addition to investigations of habitat and fish assemblage structure, species-specific habitat relationships with presence–absence and relative abundance data were explored with hurdle regressions (Martin *et al*., 2005). Hurdle regressions consisted of two submodels: one submodel used logistic regression (binomial error distribution) to predict the probability of species presence for all reaches, and the remaining submodel investigated relationships among species-specific relative abundance and habitat characteristics (gamma error distribution) for reaches with at least one individual of the focal species (Maunder and Punt, 2004; Martin *et al*., 2005). Similar modelling approaches have been used to evaluate catch rate data in marine (e.g. Lo *et al*., 1992; Andrade, 2009; Arocha and Ortiz, 2012) and freshwater systems (e.g. Li *et al*., 2011).

Hurdle submodels were constructed using the GLM function of Program R (R Development Core Team, 2009). Species-specific models were created if a species was found in at least 10% of river reaches to ensure that an adequate sample size was available for modelling. Previous research has focused on using species-specific occupancy models to estimate detection probabilities by gear (i.e. hoop net, trawl and electrofishing) for all surveyed species in the Kootenai River system (Smith, 2013). Results of that research allowed us to select the most effective technique for each species.

Table II. Mean percentage of species composition of catch

| | River section | | |
|---|---|---|---|
| Taxa | Braided ($n = 870$) | Canyon ($n = 551$) | Meander ($n = 6405$) |
| **Acipenseridae** | | | |
| White sturgeon | 0.1 (1.4) | 0.0 (0.0) | < 0.1 (0.3) |
| **Cyprinidae** | | | |
| Longnose dace | 0.3 (2.4) | 0.0 (0.0) | < 0.1 (1.8) |
| Northern pikeminnow | 3.7 (7.7) | 5.4 (10.2) | 21.6 (7.7) |
| Peamouth | 1.7 (5.3) | 1.1 (4.6) | 41.8 (9.2) |
| Redside shiner | 33.5 (19.1) | 32.1 (20.9) | 7.7 (4.9) |
| **Catostomidae** | | | |
| Largescale sucker | 19.9 (16.3) | 24.3 (19.2) | 13.3 (6.3) |
| Longnose sucker | 0.9 (3.9) | 0.7 (3.8) | 1.0 (1.8) |
| **Ictaluridae** | | | |
| Brown bullhead | 0.8 (3.7) | 0.0 (0.0) | < 0.1 (0.4) |
| **Salmonidae** | | | |
| Brown trout | 0.0 (0.0) | 0.2 (1.9) | < 0.1 (0.2) |
| Bull trout | 0.0 (0.0) | 0.0 (0.0) | < 0.1 (0.2) |
| Cutthroat trout | 0.0 (0.0) | 0.2 (1.9) | 0.1 (0.5) |
| Kokanee | 10.7 (12.6) | 0.0 (0.0) | 2.1 (2.7) |
| Mountain whitefish | 21.7 (16.8) | 30.7 (20.6) | 4.8 (4.0) |
| Rainbow trout | 0.8 (3.7) | 0.9 (4.2) | 0.7 (1.5) |
| **Gadidae** | | | |
| Burbot | 0.2 (1.9) | 0.4 (2.7) | 0.2 (0.77) |
| **Cottidae** | 4.6 (8.6) | 3.3 (8.0) | 5.1 (4.1) |
| **Centrarchidae** | | | |
| Black crappie | 0.0 (0.0) | 0.0 (0.0) | < 0.1 (0.2) |
| Pumpkinseed | 1.0 (4.1) | 0.7 (3.8) | 1.4 (2.2) |
| Largemouth bass | 0.0 (0.0) | 0.0 (0.0) | < 0.1 (0.2) |
| **Percidae** | | | |
| Yellow perch | 0.9 (3.9) | 0.0 (0.0) | 0.3 (1.0) |

River sections include braided (number of reaches sampled; 6), canyon (5) and meander (32). All fish were sampled in the Kootenai River in the summers (June–August) of 2012 and 2013.

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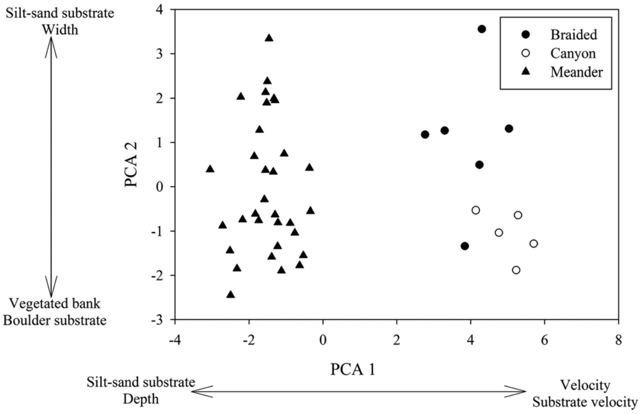

Figure 2. Principal component ordination of reach-specific ($n = 43$) habitat characteristics measured in the Kootenai River in 2012 and 2013 by river section (braided, canyon, meander). The first principal component axis (PCA 1) explained 48.1% of the variance ($\lambda = 7.22$), and 15.0% of the variance was explained with the second principal component axis (PCA 2; $\lambda = 2.25$). Habitat variables with the greatest PCA loadings for each axis were included

Species-specific data for hurdle regressions only used data from the most effective sampling technique for each species. Hurdle models require a species presence at a reach to investigate relationships among non-zero catch rates and habitat variables. Consequently, to avoid rare instances where a species was present (collected with other gears), but not sampled with the most effective gear for a species, presence–absence and relative abundance information were gathered only from the gear with the greatest species-specific detection probability (Smith, 2013). For example, detectability of brown bullhead *Ameiurus nebulosus* with hoop nets was greater than electrofishing and trawls in the summer in the study system. As a result, hoop net catch of brown bullhead was used to investigate relationships with habitat characteristics. In general, model fit was assessed using global models (i.e. model containing the most parameters; Burnham and Anderson, 2002). However, due to a reduced sample size in the second model stage for some species (i.e. few sites with one or more individuals collected), simple candidate models were often constructed with a single variable. In such instances, model fit was evaluated with the best-fitting model (Burnham and Anderson, 2002). Diagnostic plots and calculation of a dispersion parameter ($\hat{c}$ = Pearson's residual deviance/residual degrees of freedom) were used to evaluate model fit (McCullagh and Nelder, 1989). If $\hat{c}$ was greater than one, data were likely either overdispersed or there was a lack of model fit; estimated model variance was adjusted using $\hat{c}$ (Burnham and Anderson, 2002). McFadden's pseudo $R^2$ was used as an additional metric to investigate model fit (McFadden, 1974; Hosmer and Lemeshow, 1989). McFadden's pseudo $R^2$ was calculated as one minus the difference in the log likelihood of a model with an intercept and explanatory variables, and the log likelihood of an intercept-only model (McFadden, 1974). McFadden's pseudo $R^2$ values vary from 0.0 to 1.0 with values greater than 0.20, indicating good fit (Hox, 2010; Mujalli and de Oña, 2013); however, models with pseudo $R^2$ values as low as 0.10 have also been shown to have good model fit (Hosmer and Lemeshow, 1989).

Relationships among habitat characteristics were investigated with Spearman's correlation coefficient to reduce the risk of multicollinearity. The most ecologically important or interpretable variable of a highly correlated pair ($|\hat{\rho}| > 0.70$) was retained for consideration in *a priori* candidate models (Sindt *et al.*, 2012). However,

Table III. Habitat variable loadings from a principal component analysis (PCA) of habitat characteristics measured in the Kootenai River in 2012 and 2013

| Variable | Description | Axis 1 | Axis 2 |
|---|---|---|---|
| $\text{Bank}_{\text{Si-Sa}}$ | Percentage of bank consisting of fine substrate (silt and sand; %) | −0.01 | 0.54 |
| $\text{Bank}_{\text{Co-Bo}}$ | Percentage of bank consisting of cobble and boulder substrate (%) | 0.27 | −0.05 |
| $\text{Bank}_{\text{Erode}}$ | Percentage of eroding bank | −0.20 | 0.28 |
| $\text{Bank}_{\text{Veg}}$ | Percentage of bank consisting of vegetation (%) | −0.01 | −0.56 |
| $\text{CV}_{\text{Depth}}$ | Mean coefficient of variation in water depth | 0.24 | 0.23 |
| $\text{CV}_{\text{Vel}}$ | Mean coefficient of variation in water column velocity | 0.17 | 0.31 |
| Depth | Mean depth (m) | −0.34 | 0.01 |
| Distance | Distance from Libby Dam, Libby, MT (km) | −0.30 | −0.06 |
| $\text{Substrate}_{\text{Si-Sa}}$ | Percentage of substrate consisting of silt and sand (%) | −0.36 | −0.36 |
| $\text{Substrate}_{\text{Gr}}$ | Percentage of substrate consisting of gravel (%) | 0.35 | −0.01 |
| $\text{Substrate}_{\text{Co}}$ | Percentage of substrate consisting of cobble (%) | 0.32 | 0.03 |
| $\text{Substrate}_{\text{Bo}}$ | Percentage of substrate consisting of boulder (%) | 0.15 | −0.12 |
| $\text{Velocity}_{\text{Avg}}$ | Mean water column velocity | 0.35 | −0.04 |
| $\text{Velcity}_{\text{Sub}}$ | Mean water velocity near the substrate | 0.35 | −0.03 |
| Width | Mean width (m) | −0.04 | 0.38 |

All habitat characteristics collected during the study were included in the PCA analysis.

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two highly correlated variables ($\hat{\rho} = -0.76$), depth and the proportion of cobble or boulder substrate, were both retained because they likely influenced occurrence and relative abundance of fishes differently.

Seven to fifteen *a priori* candidate models were generated for each submodel. Candidate models were ranked using Akaike's Information Criterion adjusted for a small sample size ($AIC_c$; Burnham and Anderson, 2002). If overdispersion ($\hat{c} > 1$) was present, quasi-$AIC_c$ ($QAIC_c$) values were used to rank candidate models (Burnham and Anderson, 2002). One additional parameter was added to $K$ if $\hat{c}$ was greater than one (Burnham and Anderson, 2002). Models were considered to have equal support if they were within two $AIC_c$ or $QAIC_c$ values (Burnham and Anderson, 2002).

## RESULTS

Sampling effort varied among reaches (Appendix) and resulted in the collection of 7920 fishes including 20 species and nine families. Three species of high conservation concern were sampled: bull trout *Salvelinus confluentus* (federally listed as threatened under the Endangered Species Act [ESA]), white sturgeon (federally listed as endangered under the ESA) and burbot (considered Critically Imperiled by the State of Idaho). Percentage of species occurrence varied by river section with the majority of catch in the canyon and braided sections composed of redside shiner *Richardsonius balteatus* and mountain whitefish *Prosopium williamsoni* (Table II). Species composing a high percentage of catch in the meander section included peamouth *Mylocheilus caurinus* and northern pikeminnow *Ptychocheilus oregonensis*. Species richness varied among river sections with the lowest richness in the canyon (mean richness ± SE; 7.6 ± 0.7) followed by the meander (9.0 ± 0.3) and the braided section (9.5 ± 0.8). Species richness was not significantly different among sections ($K = 3.26$, $p = 0.20$).

Habitat characteristics clustered by river section (Figure 2). The first principal component axis separated the braided and canyon river sections from the meander section (Table III). Reaches in the braided and canyon sections were separated along the second principal component axis and were shallow, had high current velocity and large substrate. Sites in the meander reach were deep, had low current velocity and were dominated by fine substrate. Habitat characteristics that varied significantly among river sections included the proportion of cobble–boulder bank type ($K = 17.1$; $p < 0.001$), proportion of cobble or boulder substrate ($K = 34.3$; $p < 0.001$), coefficient of variation in water velocity ($K = 11.7$; $p = 0.003$), average depth

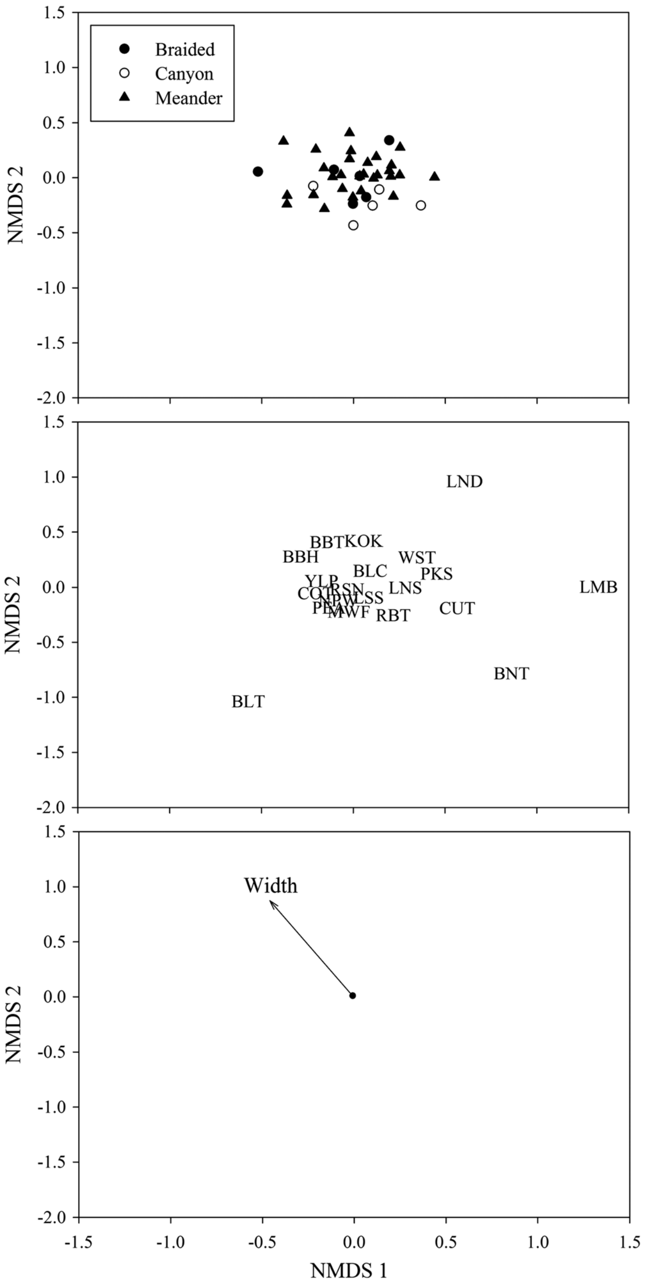

Figure 3. Non-metric multidimensional scaling ordination (stress = 21.6) of reach-specific ($n = 43$) fish assemblage presence–absence data from the Kootenai River organized river section (braided, canyon and meander). Species scores are displayed in the middle figure, and taxa include black crappie (BLC), brown bullhead (BBH), brown trout (BNT), burbot (BBT), bull trout (BLT), Cottidae (COT), cutthroat trout (CUT), kokanee (KOK), largemouth bass (LMB), largescale sucker (LSS), longnose dace (LND), longnose sucker (LNS), mountain whitefish (MWF), northern Pikeminnow (NPW), pumpkinseed (PKS), rainbow trout (RBT), redside shiner (RSN), white sturgeon (WST) and yellow perch (YLP). A cluster of species was present in the middle figure and includes COT, LSS, MWF, NPW, PEA, RSN and YLP. Significant ($p < 0.05$) habitat vectors were fit to the ordination and include width in the bottom figure

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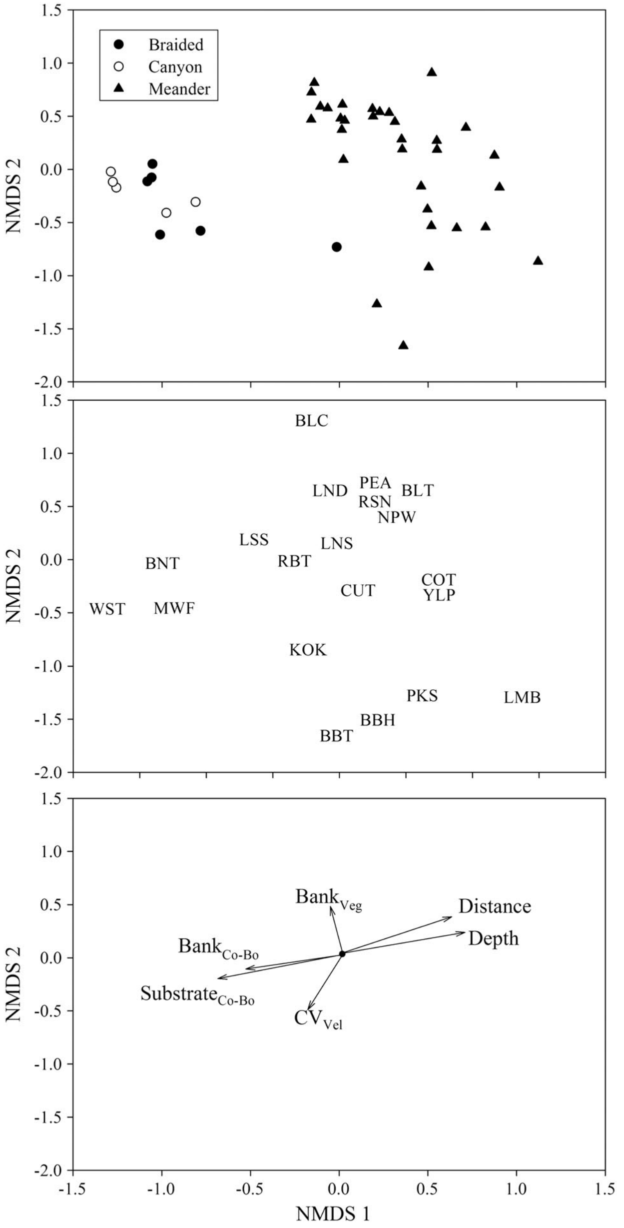

Figure 4. Non-metric multidimensional scaling ordination (stress = 12.6) of reach-specific ($n = 43$) fish assemblage relative abundance data collected with electrofishing from the Kootenai River organized river section (braided, canyon and meander). Species scores are displayed in the middle figure, and taxa include black crappie (BLC), brown bullhead (BBH), brown trout (BNT), burbot (BBT), bull trout (BLT), Cottidae (COT), cutthroat trout (CUT), kokanee (KOK), largemouth bass (LMB), largescale sucker (LSS), longnose dace (LND), longnose sucker (LNS), mountain whitefish (MWF), pumpkinseed (PKS), redside shiner (RSN), white sturgeon (WST) and yellow perch (YLP). Significant ($p < 0.05$) habitat vectors were fit to the ordination and include proportion of bank consisting of vegetation ($\text{Bank}_{\text{Veg}}$), proportion of cobble–boulder bank ($\text{Bank}_{\text{Co-Bo}}$), mean coefficient of variation of water velocity ($\text{CV}_{\text{Vel}}$), mean depth (Depth), distance from the Libby Dam (Distance),and proportion of substrate consisting of cobble and boulder ($\text{Substrate}_{\text{Co-Bo}}$)

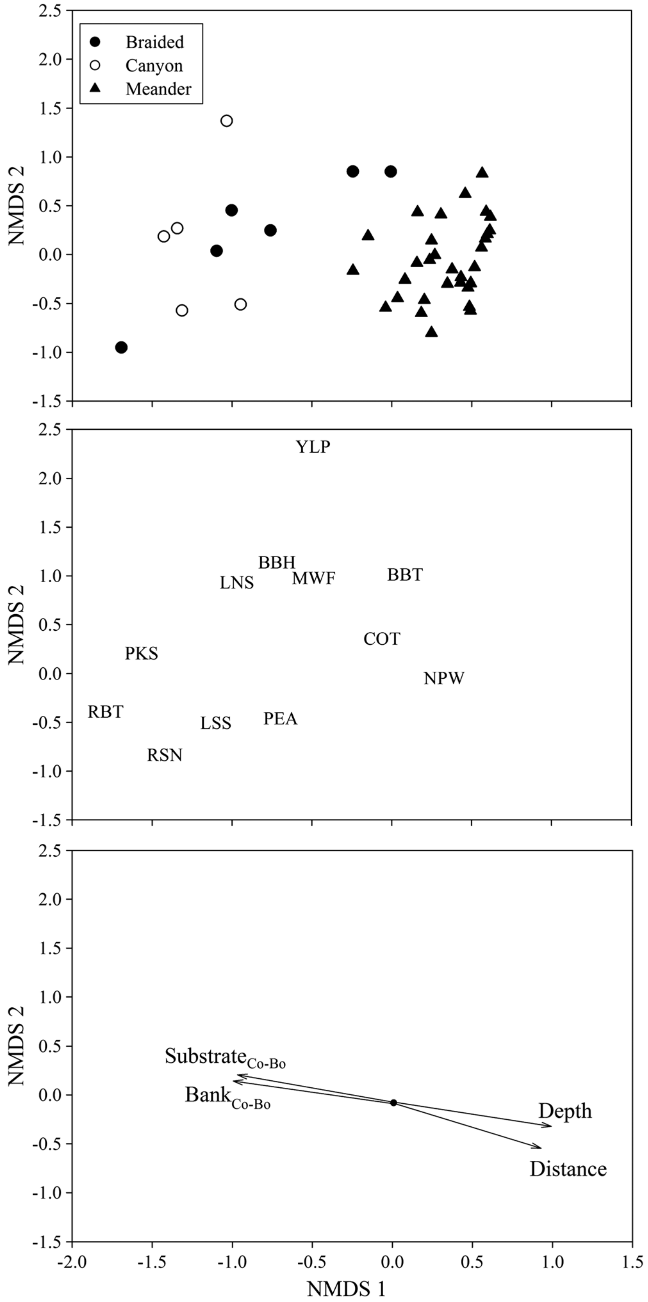

Figure 5. Non-metric multidimensional scaling ordination (stress = 11.1) of reach-specific ($n = 43$) fish assemblage relative abundance data collected with hoop nets from the Kootenai River organized river section (braided, canyon and meander). Species scores are displayed in the middle figure, and taxa include brown bullhead (BBH), burbot (BBT), Cottidae (COT), kokanee (KOK), largescale sucker (LSS), longnose sucker (LNS), mountain whitefish (MWF), pumpkinseed (PKS), redside shiner (RSN) and yellow perch (YLP). Significant ($p < 0.05$) habitat vectors were fit to the ordination and include proportion of cobble–boulder bank ($\text{Bank}_{\text{Co-Bo}}$), mean depth (Depth), distance from the Libby Dam (Distance) and proportion of substrate consisting of cobble and boulder ($\text{Substrate}_{\text{Co-Bo}}$)

Table IV. Candidate models investigating species occurrence using binomial logistic regression among all river reaches ($n = 43$)

| Taxa | Model name | AIC$_c$ or QAIC$_c$ | Δ AIC$_c$ or QAIC$_c$ | $K$ | $w_i$ | $-2Log(l)$ | $\hat{c}$ | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| **Cyprinidae** | | | | | | | | |
| Northern pikeminnow | $-\text{Substrate}_{\text{Co-Bo}}$ | 24.34 | 0.00 | 2 | 0.50 | −10.02 | 0.49 | 0.35 |
| | $+\text{CV}_{\text{Vel}}, -\text{Substrate}_{\text{Co-Bo}}$ | 25.96 | 1.62 | 3 | 0.22 | −9.67 | 0.48 | 0.37 |
| | $-Bank_{Veg}, +CV_{Vel}, -Substrate_{Co\text{-}Bo}$ | 28.35 | 4.01 | 4 | 0.07 | −9.65 | 0.49 | 0.38 |
| Peamouth | $-\text{Substrate}_{\text{Co-Bo}}$ | 21.31 | 0.00 | 2 | 0.94 | −8.50 | 0.41 | 0.51 |
| | $+Bank_{Veg}, +Depth, +Distance$ | 33.91 | 12.60 | 4 | 0.00 | −12.43 | 0.64 | 0.28 |
| Redside shiner | $-\text{Substrate}_{\text{Co-Bo}}, -\text{CV}_{\text{Vel}}$ | 30.65 | 0.00 | 3 | 0.33 | −12.02 | 0.60 | 0.42 |
| | $-\text{Substrate}_{\text{Co-Bo}},$ | 31.80 | 1.16 | 2 | 0.18 | −13.75 | 0.78 | 0.33 |
| | $-\text{CV}_{\text{Vel}}, +\text{Depth}$ | 31.81 | 1.16 | 3 | 0.18 | −12.60 | 0.63 | 0.39 |
| | +Distance | 32.35 | 1.70 | 2 | 0.14 | −14.02 | 0.68 | 0.32 |
| | $-Bank_{Veg}, +CV_{Vel}, -Depth$ | 34.22 | 3.57 | 4 | 0.05 | −12.58 | 0.65 | 0.39 |
| **Catostomidae** | | | | | | | | |
| Largescale sucker | $+\text{Bank}_{\text{Veg}}$ | 18.54 | 0.00 | 2 | 0.30 | −7.12 | 0.34 | 0.12 |
| | −Depth | 19.95 | 1.41 | 2 | 0.15 | −7.83 | 0.38 | 0.03 |
| | $+\text{CV}_{\text{Vel}}$ | 20.24 | 1.70 | 2 | 0.13 | −7.97 | 0.39 | 0.01 |
| | +Distance | 20.43 | 1.88 | 2 | 0.12 | −8.06 | 0.39 | 0.01 |
| | −Depth, +Distance | 20.46 | 1.92 | 3 | 0.11 | −6.92 | 0.35 | 0.14 |
| | $+Bank_{Veg}, -Depth, +CV_{Vel}$ | *22.71* | 4.17 | 4 | 0.04 | −6.83 | 0.35 | 0.16 |
| Longnose sucker | $-\text{Depth}, -\text{Substrate}_{\text{Co-Bo}}$ | 50.52 | 0.00 | 4 | 0.18 | −20.73 | 1.33 | 0.10 |
| | $-\text{Substrate}_{\text{Co-Bo}}$ | 50.56 | 0.04 | 3 | 0.17 | −21.97 | 1.37 | 0.05 |
| | $-Depth, -Bank_{Veg}, -Substrate_{Co\text{-}Bo}$ | 50.82 | 0.30 | 5 | 0.15 | −19.60 | 1.28 | 0.15 |
| | $-\text{Bank}_{\text{Veg}}$ | 51.11 | 0.59 | 3 | 0.13 | −22.25 | 1.39 | 0.04 |
| | $-\text{Bank}_{\text{Co-Bo}}$ | 52.13 | 0.16 | 3 | 0.08 | −22.76 | 1.42 | 0.01 |
| | $+\text{CV}_{\text{Vel}}, -\text{Substrate}_{\text{Co-Bo}}$ | 52.39 | 1.87 | 4 | 0.07 | −21.67 | 1.39 | 0.06 |
| **Ictaluridae** | | | | | | | | |
| Brown bullhead | $+\text{Bank}_{\text{Co-Bo}}$ | 19.41 | 0.00 | 2 | 0.16 | −7.56 | 0.37 | 0.07 |
| | $-\text{Depth}, -\text{Substrate}_{\text{Co-Bo}}$ | 19.70 | 0.29 | 3 | 0.14 | −6.54 | 0.33 | 0.19 |
| | $+\text{CV}_{\text{Vel}}$ | 19.96 | 0.54 | 2 | 0.12 | −7.83 | 0.39 | 0.03 |
| | −Distance | 20.02 | 0.61 | 2 | 0.12 | −7.86 | 0.38 | 0.03 |
| | $-\text{Substrate}_{\text{Co-Bo}}$ | 20.02 | 0.61 | 2 | 0.12 | −7.86 | 0.38 | 0.03 |
| | −Depth | 20.03 | 0.62 | 2 | 0.12 | −7.86 | 0.38 | 0.03 |
| | $+\text{Bank}_{\text{Veg}}$ | 20.44 | 1.03 | 2 | 0.09 | −8.07 | 0.39 | 0.01 |
| | $-Depth, -Distance, -Substrate_{Co\text{-}Bo}$ | 21.74 | 2.33 | 4 | 0.05 | −6.35 | 0.32 | 0.22 |
| **Salmonidae** | | | | | | | | |
| Cutthroat trout | $-\text{Bank}_{\text{Veg}}$ | 36.94 | 0.00 | 2 | 0.26 | −16.32 | 0.80 | 0.06 |
| | $+\text{Bank}_{\text{Co-Bo}}$ | 38.18 | 1.24 | 2 | 0.14 | −16.94 | 0.83 | 0.03 |
| | +Depth | 38.42 | 1.48 | 2 | 0.12 | −17.06 | 0.83 | 0.02 |
| | $-\text{Bank}_{\text{Veg}}, +\text{Depth}$ | 38.80 | 1.86 | 3 | 0.10 | −16.09 | 0.80 | 0.07 |
| | $-\text{Substrate}_{\text{Co-Bo}}$ | 38.84 | 1.91 | 2 | 0.10 | −17.27 | 0.80 | 0.01 |
| | +Distance | 38.91 | 1.98 | 2 | 0.10 | −17.31 | 0.85 | 0.01 |
| | $-CV_{Vel}, +Depth, +Substrate_{Co\text{-}Bo}$ | 43.11 | 6.17 | 4 | 0.01 | −17.03 | 0.87 | 0.02 |
| Kokanee | $-\text{Substrate}_{\text{Co-Bo}}$ | 47.94 | 0.00 | 3 | 0.43 | −20.66 | 1.12 | 0.20 |
| | $-\text{Depth}, -\text{Substrate}_{\text{Co-Bo}}$ | 48.96 | 1.02 | 4 | 0.26 | −19.96 | 1.12 | 0.23 |
| | $+\text{CV}_{\text{Vel}}, -\text{Substrate}_{\text{Co-Bo}}$ | 49.84 | 1.90 | 4 | 0.17 | −20.39 | 1.14 | 0.21 |
| | $+CV_{Vel}, -Depth, -Substrate_{Co\text{-}Bo}$ | 50.77 | 2.83 | 5 | 0.11 | −19.57 | 1.12 | 0.24 |
| Mountain whitefish | $-\text{Bank}_{\text{Veg}}$ | 9.09 | 0.00 | 2 | 0.45 | −2.39 | 0.12 | 0.50 |
| | −Depth | 11.00 | 1.91 | 2 | 0.17 | −3.35 | 0.16 | 0.29 |
| | $+CV_{Vel}, -Depth, -Distance$ | 15.48 | 6.40 | 4 | 0.02 | −3.22 | 0.16 | 0.32 |
| Rainbow trout | −Depth | 45.99 | 0.00 | 3 | 0.18 | −19.69 | 1.39 | 0.03 |
| | $+\text{Substrate}_{\text{Co-Bo}}$ | 46.44 | 0.45 | 3 | 0.14 | −19.91 | 1.40 | 0.02 |
| | $-\text{Bank}_{\text{Veg}}$ | 46.46 | 0.47 | 3 | 0.14 | −19.92 | 1.40 | 0.02 |
| | −Distance | 46.80 | 0.81 | 3 | 0.12 | −20.09 | 1.42 | 0.01 |
| | $-\text{CV}_{\text{Vel}}$ | 46.93 | 0.94 | 3 | 0.11 | −20.16 | 1.42 | 0.01 |
| | $-\text{Bank}_{\text{Co-Bo}}$ | 47.05 | 1.06 | 3 | 0.10 | −20.22 | 1.41 | 0.01 |
| | $-\text{Bank}_{\text{Co-Bo}}, -\text{Depth}$ | 47.65 | 1.66 | 4 | 0.08 | −19.30 | 1.39 | 0.05 |
| | $-Depth, +Distance, +Substrate_{Co\text{-}Bo}$ | 50.63 | 4.64 | 5 | 0.02 | −19.51 | 1.45 | 0.04 |

(*Continues*)

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Table IV (Continued)

| Taxa | Model name | $AIC_c$ or $QAIC_c$ | $\Delta$ $AIC_c$ or $QAIC_c$ | $K$ | $w_i$ | $-2Log(l)$ | $\hat{c}$ | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| **Gadidae** | | | | | | | | |
| Burbot | $-\text{Bank}_{\text{Co-Bo}}$ | 46.52 | 0.00 | 3 | 0.22 | −19.95 | 1.13 | 0.05 |
| | $+\text{Bank}_{\text{Veg}}$ | 46.71 | 0.20 | 3 | 0.20 | −20.05 | 1.13 | 0.05 |
| | +Distance | 46.81 | 0.29 | 3 | 0.19 | −20.10 | 1.14 | 0.04 |
| | +Depth | 48.36 | 1.85 | 3 | 0.09 | −20.87 | 1.18 | 0.01 |
| | $-\text{CV}_{\text{Vel}}$ | 48.50 | 1.99 | 3 | 0.08 | −20.94 | 1.19 | 0.01 |
| | $-Depth, +Distance, +Substrate_{Co\text{-}Bo}$ | 50.76 | 4.24 | 5 | 0.03 | −19.57 | 1.16 | 0.07 |
| **Centrarchidae** | | | | | | | | |
| Pumpkinseed | $-\text{Substrate}_{\text{Co-Bo}}$ | 46.59 | 0.00 | 3 | 0.40 | −19.99 | 1.11 | 0.14 |
| | $-\text{Bank}_{\text{Veg}}, -\text{Substrate}_{\text{Co-Bo}}$ | 48.08 | 1.48 | 4 | 0.19 | −19.51 | 1.11 | 0.16 |
| | $-Bank_{Veg}, -Depth, -Substrate_{Co\text{-}Bo}$ | 50.59 | 4.00 | 5 | 0.05 | −19.48 | 1.14 | 0.16 |
| **Percidae** | | | | | | | | |
| Yellow perch | +Distance | 40.19 | 0.00 | 2 | 0.36 | −17.94 | 0.88 | 0.13 |
| | $-\text{Substrate}_{\text{Co-Bo}}$ | 42.16 | 1.98 | 2 | 0.13 | −18.93 | 0.92 | 0.08 |
| | $+Bank_{Veg}, +Depth, +Distance$ | 44.50 | 4.31 | 4 | 0.04 | −17.72 | 0.91 | 0.14 |

Akaike's Information Criterion ($AIC_c$) or quasi-Akaike's information criterion ($QAIC_c$) adjusted for small sample size ranked the candidate models. The total number of parameters ($K$), model weight ($w_i$) and two times the nsegative log-likelihood ($-2Log(l)$) are included. Global models or model with the best fit (dispersion parameter and McFadden's pseudo $R^2$; $\hat{c}$, $R^2$) out of each candidate suit are italicized. Direction of effect for each habitat covariate is indicated (positive [+], negative [−]).

($K = 24.1$; $p < 0.001$) and average width ($K = 13.3$; $p = 0.001$).

Stable NMDS ordinations were present for species occurrence (stress = 21.6; Figure 3), electrofishing relative abundance (12.6; Figure 4) and hoop net relative abundance (11.1; Figure 5). The PERMANOVA analyses indicated that fish assemblage composition differed among river reaches with species occurrence ($F_{2,40} = 2.60$; $p = 0.01$), electrofishing relative abundance ($F_{2,40} = 10.66$; $p < 0.001$) and hoop net relative abundance data ($F_{2,40} = 12.99$; $p < 0.001$). The species occurrence ordination indicated that brown trout *Salmo trutta* were most common in the canyon section, whereas largemouth bass *Micropterus salmoides* and bull trout were most common in the meander section. Ordinations of electrofishing and hoop net relative abundance indicated that mountain whitefish, rainbow trout and redside shiner were most abundant in the canyon and braided sections. In contrast, burbot, brown bullhead and largemouth bass were most abundant in the meander section.

Habitat characteristics were significantly correlated to NMDS axes and indicated differences in assemblage structure and habitat characteristics among river sections. For instance, width was significantly correlated ($\hat{r_s} = 0.27$; $p = 0.003$) with NMDS axes for species occurrence and appeared to separate reaches in the meander from those in the braided and canyon sections. Additionally, several habitat variables were significantly correlated with axes from the relative abundance NMDS (electrofishing), including the proportion of cobble–boulder bank type ($\hat{r_s} = 0.35$; $p < 0.001$), proportion of vegetated bank ($\hat{r_s} = 0.16$; $p = 0.03$), coefficient of variation in water velocity ($\hat{r_s} = 0.22$; $p = 0.006$), average depth ($\hat{r_s} = 0.48$; $p < 0.001$), distance from the Libby Dam ($\hat{r_s} = 0.52$; $p < 0.001$) and proportion of cobble or boulder substrate ($\hat{r_s} = 0.53$; $p < 0.001$). Habitat variables were significantly correlated with NMDS axes of the hoop net catch ordination and included the proportion of cobble–boulder bank type ($\hat{r_s} = 0.40$; $p < 0.001$), average depth ($\hat{r_s} = 0.42$; $p < 0.001$), distance from the Libby Dam ($\hat{r_s} = 0.44$; $p < 0.001$) and the proportion of cobble or boulder substrate ($\hat{r_s} = 0.69$; $p < 0.001$).

Initial stages of hurdle regression models indicated that the probability of species presence varied by species and habitat characteristic (Table IV). In general, the presence of native species (kokanee *Oncorhynchus nerka*, northern pikeminnow, peamouth and redside shiner) was negatively related to the proportion of cobble or boulder substrate. The proportion of vegetated bank was positively related to the probability of occurrence of largescale sucker *Catostomus macrocheilus*, but negatively related to mountain whitefish. Depth was negatively related to the probability of largescale sucker presence. Reaches with a high coefficient of variation in water velocity had a greater probability of northern pikeminnow presence, but were negatively related to the probability of redside shiner occurrence. In general, the occurrence of non-native species was related to similar habitat characteristics as for native fishes. For instance, the proportion of cobble or boulder substrate was negatively related to the probability of occurrence of many non-native fishes (e.g. brown bullhead, pumpkinseed *Lepomis gibbosus*; Table IV). Brown bullhead occurrence was also positively related to the proportion of cobble–boulder bank type and

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Table V. Candidate models investigating relative abundance of species in relation to habitat characteristics. Sample size varied by species ($n = 6$ to 43)

| Taxa | Model name | $\mathrm{AIC_c}$ or $\mathrm{QAIC_c}$ | $\Delta$ $\mathrm{AIC_c}$ or $\mathrm{QAIC_c}$ | $K$ | $w_i$ | $-2Log(l)$ | $\hat{c}$ | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| **Cyprinidae** | | | | | | | | |
| Northern pikeminnow | $-\mathrm{CV_{Vel}}$, +Distance | 128.60 | 0.00 | 4 | 0.58 | −59.69 | 0.70 | 0.18 |
| | $+\mathrm{Bank_{Veg}}$, $-\mathrm{Substrate_{Co\text{-}Bo}}$ | 130.24 | 3.74 | 4 | 0.26 | −60.52 | 0.73 | 0.17 |
| | *+Depth, +Distance,* $-\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | 132.33 | 8.29 | 5 | 0.01 | −62.51 | 0.83 | 0.14 |
| Peamouth | $-\mathrm{Substrate_{Co\text{-}Bo}}$ | 362.01 | 0.00 | 4 | 0.70 | −176.38 | 0.95 | 0.03 |
| | $+\mathit{Bank}_{\mathit{Veg}}$, *+Depth, +Distance* | 371.29 | 9.28 | 6 | 0.01 | −178.24 | 1.11 | 0.02 |
| Redside shiner | $-\mathrm{Bank_{Veg}}$ | 190.12 | 0.00 | 4 | 0.44 | −90.39 | 1.35 | 0.02 |
| | $-\mathit{Bank}_{\mathit{Co\text{-}Bo}}$, $+\mathit{CV}_{\mathit{Vel}}$, *−Depth* | 197.10 | 6.99 | 6 | 0.01 | −91.05 | 1.50 | 0.01 |
| **Catostomidae** | | | | | | | | |
| Largescale sucker | −Depth, $+\mathrm{Bank_{Veg}}$ | 376.09 | 0.00 | 4 | 0.46 | −183.49 | 0.86 | 0.04 |
| | −Depth, +Distance | 376.86 | 0.77 | 4 | 0.31 | −183.88 | 0.89 | 0.04 |
| | $-\mathit{CV}_{\mathit{Vel}}$, *−Depth, +Distance* | 379.16 | 3.07 | 5 | 0.10 | −183.72 | 0.89 | 0.04 |
| Longnose sucker | $-\mathrm{Bank_{Co\text{-}Bo}}$ | 120.13 | 0.00 | 3 | 0.21 | −56.17 | 0.85 | 0.01 |
| | $-\mathrm{Substrate_{Co\text{-}Bo}}$ | 120.75 | 0.61 | 3 | 0.15 | −56.77 | 0.87 | 0.01 |
| | −Distance | 120.77 | 0.63 | 3 | 0.15 | −56.78 | 0.87 | 0.01 |
| | $-\mathrm{Bank_{Veg}}$ | 121.14 | 1.00 | 3 | 0.13 | −56.97 | 0.89 | 0.01 |
| | $+\mathrm{CV_{Vel}}$ | 121.29 | 1.16 | 3 | 0.12 | −57.05 | 0.89 | 0.01 |
| | +Depth | 121.31 | 1.18 | 3 | 0.12 | −57.05 | 0.89 | 0.01 |
| | *+Depth,* $-\mathit{Bank}_{\mathit{Veg}}$, $-\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | 125.11 | 4.98 | 5 | 0.02 | −55.89 | 0.90 | 0.02 |
| **Ictaluridae** | | | | | | | | |
| Brown bullhead | $+\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | 9.80 | 0.00 | 3 | 0.40 | 10.10 | 0.12 | −0.40 |
| | $-\mathrm{Bank_{Veg}}$ | 10.95 | 1.15 | 3 | 0.23 | 9.52 | 0.15 | −0.32 |
| | −Depth | 11.12 | 1.31 | 3 | 0.21 | 9.44 | 0.15 | −0.31 |
| **Salmonidae** | | | | | | | | |
| Cutthroat trout | $+\mathit{CV}_{\mathit{Vel}}$ | 20.41 | 0.00 | 3 | 0.85 | −1.21 | 0.05 | 0.78 |
| Kokanee | −Distance | 173.51 | 0.00 | 3 | 0.68 | −83.21 | 0.88 | 0.11 |
| | $+\mathit{CV}_{\mathit{Vel}}$, *−Depth,* $-\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | 180.44 | 6.93 | 5 | 0.02 | −83.72 | 0.99 | 0.11 |
| Mountain whitefish | −Depth, −Distance | 285.23 | 0.00 | 4 | 0.85 | −138.07 | 0.47 | 0.19 |
| | $+\mathit{CV}_{\mathit{Vel}}$, *− Depth,* $+\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | 290.63 | 5.40 | 5 | 0.06 | −139.48 | 0.51 | 0.18 |
| Rainbow trout | $-\mathrm{Bank_{Veg}}$ | 108.13 | 0.00 | 3 | 0.19 | −50.49 | 0.49 | 0.01 |
| | $+\mathrm{Bank_{Co\text{-}Bo}}$ | 108.38 | 0.25 | 3 | 0.17 | −50.62 | 0.49 | 0.01 |
| | +Distance | 108.92 | 0.79 | 3 | 0.13 | −50.89 | 0.50 | 0.01 |
| | $+\mathrm{CV_{Vel}}$ | 109.15 | 1.03 | 3 | 0.12 | −51.01 | 0.51 | 0.01 |
| | −Depth | 109.28 | 1.15 | 3 | 0.11 | −51.10 | 0.51 | 0.01 |
| | $+\mathrm{Substrate_{Co\text{-}Bo}}$ | 109.35 | 1.22 | 3 | 0.11 | −49.90 | 0.51 | 0.01 |
| | −Depth, +Distance | 109.81 | 1.68 | 4 | 0.08 | −50.60 | 0.49 | 0.02 |
| | *−Depth, +Distance,* $+\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | 112.70 | 4.57 | 5 | 0.02 | −49.77 | 0.51 | 0.03 |
| **Gadidae** | | | | | | | | |
| Burbot | −Distance | −37.00 | 0.00 | 3 | 0.28 | 23.21 | 0.10 | −0.06 |
| | −Depth | −36.53 | 0.47 | 3 | 0.22 | 22.98 | 0.11 | −0.04 |
| | $+\mathrm{CV_{Vel}}$ | −35.48 | 1.52 | 3 | 0.13 | 22.46 | 0.12 | −0.02 |
| | $+\mathrm{Substrate_{Co\text{-}Bo}}$ | −35.20 | 1.80 | 3 | 0.11 | 22.31 | 0.12 | −0.01 |
| | *−Depth, −Distance,* $-\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | −24.50 | 12.50 | 5 | 0.00 | 23.25 | 0.13 | −0.06 |
| **Centrarchidae** | | | | | | | | |
| Pumpkinseed | −Distance | 72.60 | 0.00 | 4 | 0.53 | −29.80 | 1.36 | 0.06 |
| | $-\mathrm{Bank_{Veg}}$ | 74.04 | 1.44 | 4 | 0.26 | −30.52 | 1.53 | 0.10 |
| | $-\mathit{Bank}_{\mathit{Veg}}$, *−Depth,* $-\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | 82.38 | 9.78 | 6 | 0.00 | −28.19 | 1.27 | 0.17 |
| **Percidae** | | | | | | | | |
| Yellow perch | $+\mathit{Substrate}_{\mathit{Co\text{-}Bo}}$ | 46.94 | 0.00 | 3 | 0.26 | −17.47 | 0.53 | 0.06 |
| | $+\mathrm{Bank_{Co\text{-}Bo}}$ | 47.27 | 0.34 | 3 | 0.22 | −17.64 | 0.53 | 0.05 |
| | −Depth | 48.05 | 1.11 | 3 | 0.15 | −18.03 | 0.60 | 0.03 |
| | $+\mathrm{CV_{Vel}}$ | 48.06 | 1.12 | 3 | 0.15 | −18.03 | 0.61 | 0.02 |
| | $-\mathrm{Bank_{Veg}}$ | 48.33 | 1.39 | 3 | 0.13 | −18.16 | 0.62 | 0.02 |
| | −Distance | 48.64 | 1.71 | 3 | 0.11 | −18.32 | 0.65 | 0.01 |

Akaike's Information Criterion ($\mathrm{AIC_c}$) or quasi-Akaike's information criterion ($\mathrm{QAIC_c}$) adjusted for small sample size ranked the candidate models. The total number of parameters ($K$), model weight ($w_i$) and two times the negative log-likelihood ($-2Log(l)$) are included. Global models or model with the best fit (dispersion parameter and McFadden's pseudo $R^2$; $\hat{c}$, $R^2$) out of each candidate suit are italicized. Direction of effect for each habitat covariate is indicated (positive [+], negative [−]).

negatively related to depth. Pumpkinseed presence was positively related to the proportion of vegetated bank. Initial model stages appeared to have good fit and predicted species occurrence well for most species with the exception of several rare species (e.g. rainbow trout, longnose suckers *Catostomus catostomus*).

The second stage of the hurdle regressions indicated that similar relationships with habitat characteristics were apparent for species occurrence and relative abundance (Table V). For example, catch of northern pikeminnow was negatively related to the proportion of cobble or boulder substrate in both model stages. Relationships of other habitat characteristics varied among model stages for most species. For instance, the coefficient of variation in flow was positively related to the occurrence of northern pikeminnow, but negatively related to their relative abundance. The distance from the Libby Dam was positively related to the relative abundance of northern pikeminnow and inversely related with catch rates of mountain whitefish. Vegetated bank was negatively related to the catch rates of redside shiner, whereas a positive relationship was apparent with catch of northern pikeminnow (Table V). Similar relationships were found between habitat and the abundance of non-native species. For example, the relative abundance of brown bullhead was positively related to the proportion of cobble or boulder substrate. The proportion of cobble–boulder bank was positively related to yellow perch *Perca flavescens* catch rates. The distance to the Libby Dam and the proportion of vegetated bank were negatively related to the relative abundance of pumpkinseed.

## DISCUSSION

Biotic (e.g. aquatic vegetation) and abiotic (e.g. elevation and temperature) characteristics commonly influence fish assemblage structure and produce discernible patterns (Rahel and Hubert, 1991; Quist *et al*., 2005b; Eitzmann and Paukert, 2010; Schultz *et al*., 2012). Patterns of fish assemblage structure were apparent in the Kootenai River. Specifically, a transition in relative abundance was apparent with salmonids common in the upper river sections and a cyprinid-dominated fish assemblage in the lower river sections. Despite a transition in assemblage structure, distinct zonation patterns were not apparent. Rather, a transition with species replacement and addition from lotic (e.g. mountain whitefish) to more lentic species (e.g. northern pikeminnow, peamouth and pumpkinseed) was observed. A lack of zonation is likely attributed to minimal elevation and thermal gradients in the Idaho portion of the Kootenai River and operation of the Libby Dam (e.g. regulated temperatures). Previous studies reporting zonation patterns of fish assemblage structure documented greater elevation and thermal gradients (Rahel and Hubert, 1991; Brunger-Lipsey *et al*., 2005). For instance, Rahel and Hubert (1991) reported zonation patterns in a western stream system with a much larger elevation gradient (~900 m). Within-zone additions (i.e. addition of species within a zone due to increasing downstream habitat complexity) have been reported to structure other western lotic systems (Rahel and Hubert, 1991; Quist *et al*., 2004). Quist *et al*. (2004) found downstream addition of native (e.g. Paiute sculpin *Cottus beldingii*) and non-native (e.g. brown trout) fishes within the coldwater zone of the Salt River basin of Idaho and Wyoming. In addition, construction and operation of the Libby Dam may have disrupted natural zonation patterns in the Kootenai River as predicted by the serial discontinuity concept (Ward and Stanford, 1983). Altered zonation patterns have been reported in a California stream in response to impoundment and altered hydraulic regimes (Marchetti and Moyle, 2001). Additional forms of anthropogenic alteration (e.g. altered land use in watersheds and pollution) have also been shown to disrupt zonation patterns (Vila-Gispert *et al*., 2002).

A pattern of species additions was discovered along the longitudinal gradient of the Kootenai River with braided and meander sections having the greatest species richness. Contrary to the species addition concept of increased species richness with downstream progression (Sheldon, 1968), species richness was greatest in the middle (braided) section of the Kootenai River. The braided section is a transitional zone characterized by high habitat complexity (low depths, variable water velocities, braided channel type; Fosness and Williams, 2009). In addition to high habitat complexity, the braided section likely also has high levels of habitat dynamism when compared with those in meander and canyon sections. High dynamism in the braided reach is likely related to the braided channel type and the presence of a variety of habitats created at different discharge levels. In contrast, channel movement and habitat availability varies little in relation to discharge in the meander and canyon sections. Habitat complexity and diversity have been positively related to increased species richness in a variety of lotic systems (Gorman and Karr, 1978; Angermeier and Karr, 1983; Gratwicke and Speight, 2005). Gorman and Karr (1978) reported significant correlations between fish species and habitat diversity in temperate (Indian Creek, Indiana) and tropical (Rio Frijoles, Panama) streams. Positive relationships with fish species richness and habitat complexity have also been observed in shallow marine systems of the British Virgin Islands (Gratwicke and Speight, 2005). Increased species richness in the braided and meander sections are likely also related to the addition of non-native fishes to the assemblage (brown bullhead, pumpkinseed and yellow perch). Lionberger and Hubert (2007) attributed

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downstream species addition patterns to the presence of non-native fishes (common carp *Cyprinus carpio*, walleye *Sander vitreus* and yellow perch) in Wyoming rivers. Increased occurrence of non-native fishes has also been reported from upstream to downstream sections of the Willamette River, Oregon (Hughes and Gammon, 1987), and the Tiber River, Italy (Lorenzoni *et al*., 2006).

In addition to longitudinal patterns of species addition, fish assemblages in the Kootenai River appeared to cluster into sections with similar habitat characteristics. Upper river sections (braided and canyon) were characterized by large substrate and fast water velocities, and the fish assemblage was composed of native salmonids (rainbow trout and mountain whitefish), catostomids (largescale sucker) and cyprinids (redside shiner). The meander section was characterized by native cyprinids (northern pikeminnow and peamouth) and non-native species (brown bullhead, largemouth bass *Micropterus salmoides*, pumpkinseed and yellow perch). Lower river sections had fine substrates, low flow velocities and high depths. Our results are similar to those of Hughes and Gammon (1987) who found distinct fish assemblages that correspond to major habitat transitions in the Willamette River. Specifically, native salmonids (i.e. rainbow trout and cutthroat trout) were common in upper river sections; non-native species (e.g. goldfish *Carassius auratus*, yellow bullhead *Ameiurus natalis* and largemouth bass) were only found in downstream areas of the river. Increased occurrence of non-native species in the lower portion of the Willamette River was attributed to high levels of anthropogenic alteration (Hughes and Gammon, 1987). Similar to the Willamette River, high levels of anthropogenic alteration are present in the meander section of the Kootenai River (levee construction and land use changes; Richards, 1997) and may explain increased non-native species occurrence. Previous research indicates that widespread alteration of lotic systems often promotes the colonization of non-native fishes (Moyle and Light, 1996; MacDougall and Turkington, 2005; Light and Marchetti, 2007). Light and Marchetti (2007) concluded that habitat alteration tended to support the invasion of non-native fishes in California's streams and rivers. Additionally, the likelihood of colonization of non-indigenous fishes was up to 200 times greater in highly altered systems (i.e. impoundments) compared with undisturbed natural lakes in the Laurentian Great Lakes region (Johnson *et al*., 2008).

Observed species-specific relationships with habitat characteristics are related to their ecology. For instance, the proportion of cobble or boulder substrate was negatively related with the occurrence and (or) relative abundance of many native (e.g. peamouth, northern pikeminnow and kokanee) and non-native fishes (i.e. brown bullhead and pumpkinseed). Such species commonly occupy lakes or rivers with low current velocities (Scott and Crossman, 1973). In contrast, the relative abundance of mountain whitefish was positively related to the proportion of cobble or boulder substrate. Previous research has shown similar habitat use of mountain whitefish in western rivers (Scott and Crossman, 1973; Hughes and Gammon, 1987; Rahel and Hubert, 1991). The presence of large substrates (i.e. cobble or boulder) may provide greater macroinvertebrate abundances and refugia from biotic (predation) and abiotic (flow velocities) factors (Flecker and Allan, 1984; Persson and Eklöv, 1995). Conversely, fine substrates support the growth of aquatic vegetation, and both native (i.e. peamouth and northern pikeminnow) and non-native (i.e. brown bullhead) fishes commonly use aquatic vegetation (Scott and Crossman, 1973; Killgore *et al*., 1989; Gadomski *et al*., 2001). Similarly, the occurrence or relative abundance of native (largescale sucker and northern pikeminnow) and non-native fishes (brown bullhead) was positively related to the proportion of vegetated bank type. Submerged terrestrial and aquatic vegetation may increase feeding efficiency and survival, particularly for juvenile fishes (Rozas and Odum, 1988; Dibble *et al*., 1997). Other habitat characteristics that were important in predicting species occurrence and relative abundance (i.e. depth and the distance from the Libby Dam) appear to be related to river sections. For instance, a positive relationship between northern pikeminnow catch and distance from the Libby Dam indicated a higher relative abundance in the most downstream section (meander), where areas of low water velocity and abundant cover (i.e. aquatic vegetation and submerged terrestrial vegetation) are most common. Similar habitat use of northern pikeminnow has been reported in large rivers (Scott and Crossman, 1973). Furthermore, occurrence of mountain whitefish was negatively related to average depth, likely reflecting increased occurrence in the shallow braided section of the Kootenai River. In general, most of the influential habitat characteristics (e.g. depth and proportion of cobble or boulder substrate) were reflective of species ecology and the river section where they were most common. Results of the hurdle regressions further emphasized differences in habitat and fish structure along the longitudinal gradient of the Kootenai River.

Our research indicates differences in fish assemblage and habitat structure among river sections in the Kootenai River. A general pattern of species addition was apparent, with the greatest species richness in areas of high habitat complexity. Species addition patterns were also related to increased occurrence of non-native fishes in lower river sections. In addition to assemblage investigations, species-specific population relationships with habitat characteristics indicated that habitat use varied by species. Despite the difficulties of investigating relationships among fishes and aquatic habitat in large river systems, an

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understanding of these relationships will be important in preserving biodiversity and restoration of imperilled rivers of western North America.

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## APPENDIX

## TOTAL FISH SAMPLING EFFORT ORGANIZED BY REACH AND TECHNIQUE IN THE KOOTENAI RIVER, IDAHO. A COORDINATE FOR THE UPPER TERMINUS OF EVERY SAMPLE REACH IS PROVIDED

| | | Gear | | |
|---|---|---|---|---|
| Latitude | Longitude | Electro fishing (s) | Hoop net (net-night) | Trawl (haul) |
| **Canyon** | | | | |
| 48°41′05.13″N | −116°07′22.22″W | 1265 | 12 | 12 |
| 48°41′21.84″N | −116°08′01.44″W | 1298 | 12 | 12 |
| 48°42′53.31″N | −116°08′34.20″W | 1892 | 12 | 12 |
| 48°42′56.42″N | −116°09′23.51″W | 2311 | 12 | 12 |
| 48°42′51.98″N | −116°10′42.72″W | 1675 | 12 | 12 |
| **Braided** | | | | |
| 48°41′46.90″N | −116°12′10.23″W | 1821 | 12 | 12 |
| 48°42′32.00″N | −116°13′20.52″W | 2046 | 12 | 12 |
| 48°42′07.90″N | −116°14′27.33″W | 1578 | 12 | 12 |
| 48°42′07.28″N | −116°15′17.80″W | 1596 | 12 | 12 |
| 48°41′42.43″N | −116°16′15.79″W | 1198 | 8 | 8 |
| 48°41′46.28″N | −116°18′07.22″W | 1989 | 8 | 8 |
| **Meander** | | | | |
| 48°41′50.53″N | −116°20′13.02″W | 2871 | 12 | 12 |
| 48°42′07.74″N | −116°21′06.12″W | 3376 | 12 | 12 |
| 48°42′16.36″N | −116°22′14.70″W | 1811 | 8 | 8 |
| 48°49′45.07″N | −116°22′42.90″W | 3224 | 12 | 12 |
| 48°48′21.47″N | −116°22′48.52″W | 2260 | 8 | 8 |
| 48°47′39.54″N | −116°22′55.94″W | 4476 | 12 | 12 |
| 48°45′40.02″N | −116°23′15.59″W | 3737 | 12 | 12 |
| 48°44′12.16″N | −116°23′02.27″W | 2004 | 8 | 8 |
| 48°46′28.78″N | −116°23′23.39″W | 2975 | 12 | 12 |
| 48°49′47.29″N | −116°23′33.63″W | 3735 | 12 | 12 |
| 48°49′07.72″N | −116°23′36.83″W | 2075 | 8 | 8 |
| 48°50′31.40″N | −116°23′59.04″W | 2153 | 8 | 8 |
| 48°49′26.90″N | −116°23′06.82″W | 3920 | 12 | 12 |
| 48°42′33.04″N | −116°23′07.19″W | 3410 | 12 | 12 |
| 48°51′37.09″N | −116°24′00.63″W | 3495 | 12 | 12 |
| 48°44′21.08″N | −116°24′11.94″W | 2327 | 8 | 8 |
| 48°45′11.22″N | −116°24′17.71″W | 2539 | 8 | 8 |
| 48°47′17.64″N | −116°24′19.71″W | 2006 | 8 | 8 |
| 48°46′55.93″N | −116°24′28.46″W | 2260 | 8 | 8 |
| 48°52′07.52″N | −116°24′37.19″W | 2934 | 12 | 12 |
| 48°53′49.01″N | −116°24′43.84″W | 2905 | 12 | 12 |
| 48°54′37.62″N | −116°24′55.90″W | 2311 | 12 | 12 |
| 48°52′28.31″N | −116°25′02.14″W | 3169 | 12 | 12 |
| 48°52′46.39″N | −116°25′22.73″W | 2291 | 8 | 8 |
| 48°53′14.82″N | −116°25′06.13″W | 2162 | 8 | 8 |
| 48°54′42.54″N | −116°26′08.27″W | 1825 | 12 | 12 |
| 48°56′09.14″N | −116°29′14.62″W | 2451 | 12 | 12 |
| 48°56′38.61″N | −116°30′12.91″W | 2341 | 12 | 12 |
| 48°56′55.20″N | −116°30′26.31″W | 3254 | 12 | 12 |
| 48°57′31.95″N | −116°31′14.26″W | 3243 | 12 | 12 |
| 48°58′11.41″N | −116°31′38.47″W | 3065 | 12 | 12 |
| 48°58′42.73″N | −116°32′09.95″W | 2831 | 12 | 12 |