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Microhabitat use of native fishes in the Kootenai River: A fine-scale evaluation of large-scale habitat rehabilitation efforts

Philip R. Branigan[1] | Michael C. Quist[2] | Bradley B. Shepard[3] | Susan C. Ireland[4]

[1] Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho, USA

[2] U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho, USA

[3] B.B. Shepard and Associates, Livingston, Montana, USA

[4] Fish and Wildlife Department, Kootenai Tribe of Idaho, Bonners Ferry, Idaho, USA

Correspondence
Phil Branigan, Idaho Department of Fish and Game, 1414 E. Locust Ln., Nampa, Idaho 83686, USA.
Email: phil.branigan@idfg.idaho.gov

Abstract

Fish and microhabitat data were collected at 542 prepositioned electrofishing sites (surface area of each site = 4 m^2) in the Kootenai River, Idaho, during 2014 and 2015 to evaluate small-scale habitat use by fishes, as it relates to large-scale habitat rehabilitation efforts. Samples were collected from a 12-km braided segment of river that had received localized habitat rehabilitation treatments since 2011. Fish and microhabitat data were collected to investigate habitat drivers related to the occurrence and relative abundance of fishes. Each sampling location was selected at random and characterized as "treated" (i.e., rehabilitated) or "untreated" based on proximity to habitat treatments. Fishes sampled from backwaters composed 71% of the overall catch and 84% of the catch from locally untreated areas of the river. Species-specific regression models suggested that water depth and current velocity influenced the occurrence and abundance of fishes. In particular, shallow habitats with low current velocities were important for small-bodied native fishes and likely serve as important rearing areas for juvenile fish. These habitat conditions typically characterize backwater and channel-margin habitats that are vulnerable to anthropogenic perturbation. Prioritizing process-based rehabilitation of these areas in large, regulated rivers would allow natural channel-forming processes for the benefit of native fishes.

KEYWORDS

fisheries management, habitat rehabilitation, microhabitat use, prepositioned electrofishing

1 | INTRODUCTION

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

Changes in habitat quality and quantity have been identified as primary drivers associated with the decline of freshwater fish populations across North America (Nilsson, Reidy, Dynesius, & Revenga, 2005; Reidy Liermann, Nilsson, Roberson, & Ng, 2012; Ricciardi & Rasmussen, 1999). Large floodplain rivers are dynamic freshwater ecosystems that exhibit a wide variety of hydrologic conditions, connectedness, and local habitat characteristics. Most large river ecosystems are composed of a suite of lotic, lentic, and off-channel macrohabitats (i.e., main channel, side channels, backwaters, and oxbows) that develop through changes in water quantity. Many riverine fishes rely on the presence of diverse habitats created by seasonal inundation (i.e., seasonal flood events; Welcomme, 1979), but diverse habitats are generally absent in human-modified river systems due to the direct and indirect effects of water development. Dams and their impoundments are considered among the greatest threats to floodplain river

ecosystem function. In addition to flood attenuation, dams have been implicated in restricting nutrient and sediment delivery, homogenizing channels, and altering thermal and discharge regimes (Baxter, 1977; Dynesius & Nilsson, 1994; Nilsson et al., 2005). Furthermore, levees constructed alongside rivers serve to confine flow and disconnect rivers from their floodplains, limiting the development of off-channel habitats. Collectively, dams and levees limit connections between aquatic and terrestrial environments, create movement barriers for fishes, and decrease aquatic habitat complexity (Ward & Stanford, 1995). Water resource development has been shown to cause declines in fluvial fish populations (Paragamian, 2002; Quist, Hubert, & Rahel, 2005) and is associated with river fragmentation and the loss of critical backwater habitat (Dodrill et al., 2015; Freeman, Bowen, Bovee, & Irwin, 2001; Gore & Shields, 1995).

With an increasing focus on species conservation (e.g., Schloesser et al., 2012; Theiling et al., 1999), lotic systems have become a target for restoration and rehabilitation projects in an attempt to mitigate the effects of anthropogenic disturbance (Bernhardt et al., 2005; Gore & Shields, 1995; Lake, Bond, & Reich, 2007). Placement of large woody habitat features and other engineered structures (e.g., dikes and riprapped shoreline) in rivers and streams has become one of the most common techniques used to improve fish habitat (Madejczyk, Mundahl, & Lehtinen, 1998; Roni, Beechie, Pess, & Hanson, 2015; Schloesser et al., 2012). Another common rehabilitation technique is the creation or reconnection of off-channel habitat units that provide areas of shallow water and reduced current velocity (e.g., side channels and backwaters; Roni et al., 2002). Engineered structures and channel units are designed to meet the ecological needs for many riverine fishes by providing diverse and dynamic physical habitats that function similar to premodified conditions. In particular, engineered structures and channel units increase habitat complexity by decreasing current velocity and dispersing flow, thereby allowing sediment deposition, nutrient exchange, and localized fluctuations in water temperature (Cushman, 1985; Kauffman, Beschta, Otting, & Lytjen, 1997; Roni et al., 2002). Large river fish assemblages have been shown to respond favourably to habitat rehabilitation efforts, as observed through the use of engineered features (Grift et al., 2003; Phelps, Tripp, Herzog, & Garvey, 2015).

The Kootenai River is a large river that has experienced habitat alterations and improvements. The river originates in British Columbia, Canada, and flows into the United States passing through the states of Montana and Idaho. In Idaho, approximately 20,230 ha of floodplain habitat was eliminated due to shoreline and instream modifications (Kootenai Tribe of Idaho, KTOI, 2009). The construction of Libby Dam, a large hydroelectric power facility located near Libby, Montana, was completed in 1972 and has altered historic flow, temperature, and nutrient regimes (Knudson, 1994; Woods, 1982). Consequently, shifts in fish assemblage structure downstream of Libby Dam have been reported, including population declines of at least two species of conservation concern: Burbot *Lota lota* and White Sturgeon *Acipenser transmontanus* (Paragamian, Kruse, & Wakkinen, 2001; Paragamian, Whitman, Hammond, & Andrusak, 2000).

Declines in native fish populations of the lower Kootenai River (i.e., downstream of Libby Dam) have motivated efforts to improve aquatic habitat (Duke et al., 1999; KTOI, 2009; Paragamian, 2012; Paragamian & Hansen, 2009). The Kootenai Tribe of Idaho and their collaborators initiated a large-scale and long-term habitat rehabilitation programme to enhance existing habitat to benefit native fishes at all life stages (KTOI, 2009). Since 2011, several localized habitat rehabilitation treatments have been implemented in a 12-km braided segment of the river (KTOI, 2009). Some of the primary rehabilitation projects include treatments designed to disperse flow, create floodplain and off-channel habitats, increase substrate heterogeneity and create complex instream habitats by adding woody structures. The habitat rehabilitation programme has an adaptive management component that relies on monitoring to assess the effectiveness of each project and the cumulative effects of multiple projects on habitat characteristics and fish populations. Information from this monitoring is used to modify the locations and designs of future habitat rehabilitation efforts.

We evaluated fine-scale habitat associations of fishes in a large, modified western river with regard to large-scale habitat rehabilitation efforts. The specific objective of this study was to identify microhabitat features associated with the occurrence and relative abundance of fishes at all life stages. Results from this study will inform the design and location of future engineered habitat features in the Kootenai River and serve as a model for other large, regulated floodplain river systems.

2 | METHODS

2.1 | Study area

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

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

2.2 | Field sampling

Microhabitat associations of fishes were assessed using a prepositioned areal electrofishing device (PAED; Bain, Finn, & Booke, 1985, Dauwalter, Wenger, & Gardner, 2014). A PAED consisted of a cathode and anode that were powered by a Smith-Root LR-24 backpack electrofishing unit (Smith-Root Inc.; Vancouver, Washington) positioned on shore. The electrodes were constructed with a 9.1 m length of insulated tinned-copper wire that terminated in a plug (Midwest Lakes Electrofishing Systems; Polo, Missouri). The insulated wire was joined to a length of 4.8-mm-diameter stainless steel aircraft cable that remained exposed to complete the electrical circuit. The cathode was constructed with 6.1 m of stainless steel aircraft cable, and the anode used 3.4 m. A wire rope clip secured a loop for the anode, producing a circle (surface area = 0.80 m^2).

Fish and habitat surveys were conducted in 4 m^2 sites within the braided segment of the Kootenai River, Idaho, during summers and autumns of 2014 and 2015. Sites were randomly selected and sampled from areas <1.5 m deep to allow capture of immobilized fish by a dip netter wearing chest waders. Accordingly, conclusions drawn from this evaluation are limited by the constraints of the PAED, but sites were surveyed only when the PAED could effectively sample the area. A sampling event began by deploying the anode. Next, the cathode was positioned approximately 1-m downstream of the anode to ensure consistent electrical fields among sites. Each site remained undisturbed for a minimum of 30 min before electrifying the equipment. The time delay between deploying and electrifying the equipment (i.e., PAED "set time") allows fishes to recolonize the area and assume normal behaviour and habitat use (Branigan, Quist, Shepard, & Ireland, 2018; Dauwalter et al., 2014). Following the set time, PAEDs were electrified by applying pulsed DC (500–800 W, 60 Hz) for 20 s. A single netter collected all immobilized fishes with a dip net (6-mm mesh). Operators ensured that fishes were not frightened into the immobilization zone while approaching each site. Captured fishes were identified to species; measured (total length, mm); and released downstream to avoid recapture in subsequent sites. Unidentified fish were preserved in 10% formalin and transported to the University of Idaho. Overall, 542 sites were sampled during 2014 (n = 217) and 2015 (n = 325).

After fish were collected and processed, microhabitat characteristics were measured for each site. Given that we used pulsed DC to electrify the PAEDs, fishes were immobilized beyond the confines of the 0.80-m^2 anode ring. Therefore, we collected habitat data within a 2 m^2 quadrat (surface area = 4 m^2) centred on the anode. This area fully encompassed the immobilization zone of the PAED and served as the unit of inference for this evaluation. The quadrat was oriented perpendicular to the water current, such that three transects 2 m in length were created and positioned upstream, downstream, and bisecting the circular anode. Water depth, bottom current velocity, mean column current velocity, and substrate type were measured at 0%, 20%, 40%, 50%, 60%, 80%, and 100% of the length of each transect. Current velocity was measured with a portable velocity metre (Flo-Mate Model 2000; Marsh-McBirney Inc.; Loveland, Colorado); mean column current velocity was measured at 60% of the water depth when depth was <0.75 m and at 20% and 80% of the depth and averaged when depth was >0.75 m (Buchanan & Somers, 1969). The dominant substrate type at each transect point was classified based on a modified Wentworth scale as silt-clay (<0.064 mm diameter), sand (0.064 $\leq$ 3 mm), gravel (3 $\leq$ 16 mm), pebble (16 $\leq$ 65 mm), cobble (65 $\leq$ 257 mm), or boulder (>257 mm; Cummins, 1962).

Instream cover features were also measured at each site. Instream cover was defined as any structure within the quadrat that had an area $\geq$0.04 m^2 along any two planes of dimension. Cover types consisted of submerged aquatic vegetation, emergent aquatic vegetation, branch complex, single log, log complex, bank roots, rootwad, stump, single boulder, boulder complex, and riprap. The area of each cover feature in the quadrat was calculated as the product of length of the longest axis and the average of three evenly spaced width measurements oriented perpendicular to the length measurement (Sindt, Quist, & Pierce, 2012).

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

2.3 | Habitat and fish assemblage structure

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

Due to marked differences in catch between backwaters and channels (see results), differences in fish assemblage structure among the habitat types were evaluated using permutational multivariate analysis of variation (PERMANOVA). A Bray–Curtis dissimilarity measure was used for PERMANOVA analyses using adonis function from the Vegan package in Program R (Oksanen et al., 2015).

2.4 | Species-specific habitat associations

Species-specific habitat relationships using occurrence (i.e., presence–absence) and count data (i.e., relative abundance) were assessed with hurdle models. Hurdle models are a two-stage regression, whereby the first stage predicts the probability of a species presence using logistic regression (binomial response variable) and the second stage predicts the relative abundance of a species using non-zero count data

(e.g., negative-binomial error distribution; Martin et al., 2005). This modelling approach allows the factors that influence a species presence to be modelled separately from those influencing relative abundance (Wenger & Freeman, 2008).

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

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

Thirteen to 16 *a priori* candidate models were developed for each modelling stage for fishes that satisfied sample size requirements associated with each habitat type. Habitat treatment was coded as a binary categorical variable. Interactions with habitat treatment were evaluated by including interactive models in each candidate set using two habitat variables: woody cover and fine substrate. Given the high number of small-bodied fishes sampled, age categories were used to model Age-0 fish separately from those estimated to be older than Age 0. Empirical length-at-age data from the Kootenai River were used to estimate ages of Largescale Sucker, *Catostomus macrocheilus*, and Mountain Whitefish, *Prosopium williamsoni*, (M.C. Quist, unpublished data). Length criteria from Pearsons, Li, and Lamberti (1992) were used to estimate age for Longnose Dace, *Rhinichthys cataractae*; Redside Shiner, *Richardsonius balteatus*; and Torrent Sculpin, *Cottus rhotheus*. Candidate models were ranked using Akaike's information criterion adjusted for small sample size (AIC_c; Burnham & Anderson, 2002). The model with the smallest AIC_c value from each candidate set was considered to be the top model, but models within two AIC_c units of the top model were also considered plausible (Burnham & Anderson, 2002).

3 | RESULTS

A total of 1,447 native fish representing four families and eight species collected from 542 prepositioned electrofishing samples. Data collected in 2014 and 2015 were combined because preliminary regression analyses indicated similar patterns in habitat use between years. Differences were observed in the proportion of sites occupied and in the number of fish captured between backwater and channel habitats for Age-0 fish and those older than Age-0. Age-0 fish occurred in a much higher proportion of backwater sites than channel sites, and many more Age-0 fish were captured in backwater sites than in channel sites (Figure 1). Fishes sampled from backwater habitats accounted for 71% of the overall catch and 84% of the catch from untreated areas of the river. Of those fishes sampled from backwaters, 89% were estimated as Age 0. Fish older than Age 0 were slightly more abundant than Age-0 fish and occupied a higher proportion of sites in channels than backwater areas. Largescale Sucker was the most abundant Age-0 fish species sampled from both channel and backwater habitats, whereas Age-0 Longnose Dace were found in moderate abundance (Figure 2). Other Age-0 fishes were sampled at contrasting levels of abundance between channels and backwaters. Species occurrence and counts of fishes older than Age 0 varied across channel and backwater habitats. Redside Shiner was most abundant in backwaters, whereas Torrent Sculpin was most abundant in channels. The

TABLE 1 Summary statistics for habitat variables measured at 542 prepositioned electrofishing sites on the Kootenai River, Idaho, during the summers (May–August) and autumns (October–November) of 2014 and 2015

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

Note. CV: coefficient of variation. Habitat variables were separated by habitat type (i.e., backwater or channel).

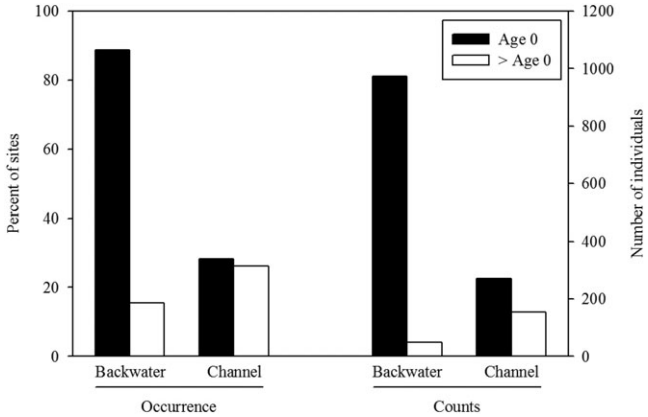

FIGURE 1 Summary of fish occurrence and abundance by estimated age and habitat type (i.e., backwater or channel) from 542 prepositioned electrofishing sites on the Kootenai River, Idaho, during 2014 and 2015. A total of 141 sites was sampled in backwater habitats; 401 sites were sampled from channel habitats

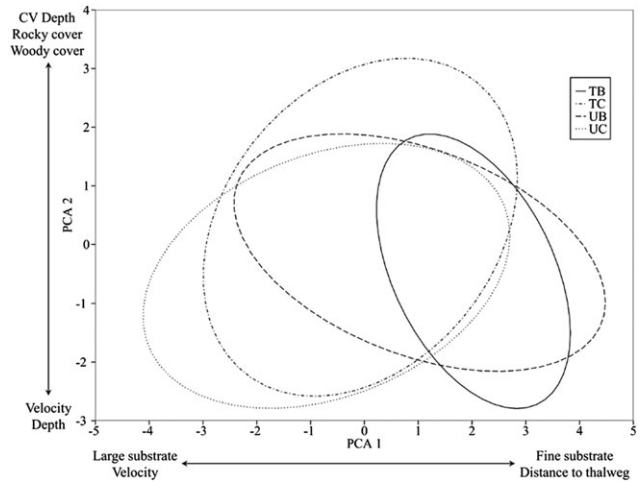

FIGURE 3 Principal component ordination of habitat characteristics measured at 541 prepositioned electrofishing sites in the Kootenai River in summers (May–August) and autumns (October–November) of 2014 and 2015. The first principal component axis (PCA 1) explained 20.51% of the variation and the second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

PERMANOVA analyses using occurrence and count data indicated that the fish assemblage differed significantly between backwater and channel habitats ($p < 0.001$).

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

Models predicting the occurrence of fishes were fit for three species sampled from backwaters and four species from channels (Table 2). Nearly all plausible models included a negative relationship with depth and (or) current velocity. Presence of Age-0 Largescale Sucker and Longnose Dace were positively related to the proportion of large substrate and negatively related to mean depth. Torrent

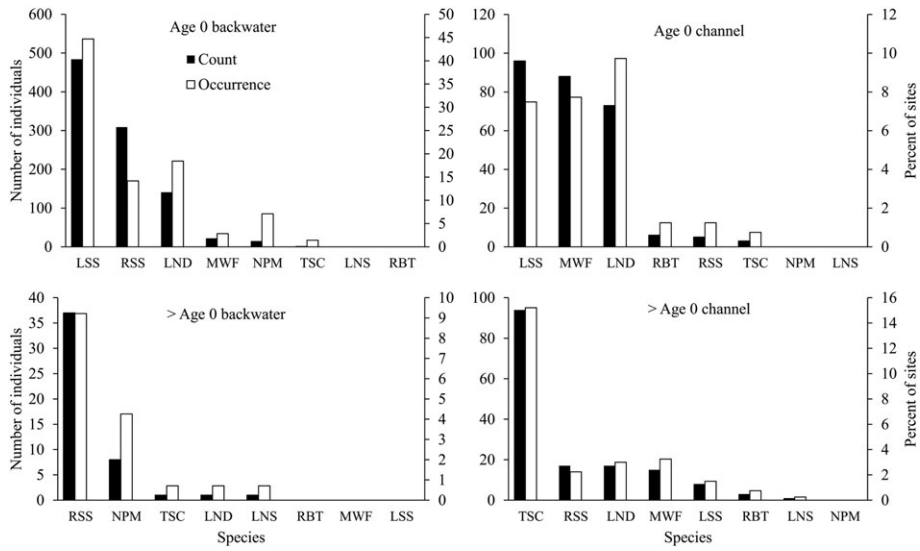

FIGURE 2 Summary of species occurrence and abundance for Age-0 and >Age-0 fish sampled from 542 sites on the Kootenai River, Idaho, during 2014 and 2015 (LND: Longnose Dace; LNS: Longnose Sucker; LSS: Largescale Sucker; MWF: Mountain Whitefish; NPM: Northern Pikeminnow; RBT: Redband Trout; RSS: Redside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

TABLE 2 Top binomial logistic regression models used to evaluate the occurrence of fishes in backwaters and channels from the Kootenai River during 2014 and 2015

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

Note. Akaike's information criterion (AIC_c) adjusted for small sample size was used to rank models; only models with a $\Delta AIC \leq 2$ from each candidate set are included. Models in italics indicate the global model used for respective candidate sets. Effect of model covariates are indicated as (positive [+], negative [−]).

Sculpin older than Age 0 displayed similar habitat associations and were positively related to the presence of woody cover. Presence of Age-0 Mountain Whitefish was negatively related to woody cover except at treated sites where the relationship with woody cover was positive. Although Redside Shiner satisfied sample size requirements for modelling purposes, models generated using occurrence data consistently exhibited poor fit (Table 2).

Top models explaining the relative abundance of fishes sampled from backwaters and channels differed from those associated with the occurrence of a particular species, but several plausible models included a negative relationship with depth and (or) current velocity (Table 3). In backwater habitats, the relative abundance of Age-0 Largescale Sucker and Redside Shiner were negatively related to the proportion of large substrate and mean depth. Age-0 Longnose Dace were negatively related to mean current velocity. Fishes sampled from channel habitats had different relationships with microhabitat characteristics than fishes sampled from backwaters. Relative abundance of Age-0 Largescale Sucker was positively related to the proportion of fine substrate. Relative abundance of Age-0 Mountain Whitefish was also positively related to the proportion of fine substrate but only when sampled from treated sites. Age-0 Longnose Dace were abundant in shallow areas and low current velocities. Relative abundance of Torrent Sculpin greater than Age 0 was positively related to rocky cover features (e.g., riprapped shorelines and boulders).

4 | DISCUSSION

Fish assemblage structure differed between backwaters and channels of the Kootenai River, but similar patterns in habitat use emerged. Our analyses indicated that occurrence and abundance of several Age-0 fish species were positively related to shallow, slow current velocity (SSCV) habitats. Shallow water provides refuge from predation by larger bodied fishes that typically avoid shallow habitats due to their vulnerability to terrestrial predators (Power, 1984; Schlosser, 1987). Habitats characterized by slow current velocities offer refuge from swift currents that may displace small fishes (Ottaway & Clarke, 1981). Furthermore, areas of reduced flow might also provide conditions necessary for phytoplankton and zooplankton production, both of which serve as food resources for small-bodied or young fishes (Nunn, Harvey, & Cowx, 2007a, 2007b; Spaink, Ietswaart, & Roijackers, 1998). In concert, shallow habitats with slow current velocities warm quickly and can extend the growth season for fishes (Ward & Stanford, 1995). The importance of SSCV habitats for small-bodied fishes has been demonstrated in small unimpounded streams (Watkins, Doherty, & Copp, 1997) and in a large unimpounded river (Reinhold, Bramblett, Zale, Roberts, & Poole, 2016). Unfortunately, the formation of SSCV habitats is often dramatically reduced in systems where channelization and flow regulation occur (Bowen, Bovee, & Waddle, 2003; Poff et al., 1997), as has occurred in the Kootenai River system.

TABLE 3 Top linear regression models used to evaluate the relative abundance of fishes in backwaters and channels from the Kootenai River during 2014 and 2015

Habitat type	Species	Estimated age	Model name	AIC_c	ΔAIC_c	K	w_i	R^2
Backwater								
	Largescale Sucker	0	$-Sub_{Large}$, −Depth, $-Vel_{MC}$	308.04	0.00	4	0.65	0.09
	Longnose Dace	0	$-Vel_{MC}$	119.22	0.00	2	0.56	0.05
	Redside Shiner	0	$-Sub_{Large}$	102.57	0.00	2	0.55	0.17
			$-Sub_{Large}$, −Depth	103.65	1.09	3	0.32	0.19
Channel								
	Largescale Sucker	0	$+Sub_{Fine}$, $-Cover_{Wood}$	101.82	0.00	3	0.57	0.12
	Longnose Dace	0	−Depth, $-Vel_{MC}$	94.52	0.00	3	0.35	0.11
			$+Sub_{Large}$, −Depth, $-Vel_{MC}$	95.02	0.40	4	0.29	0.14
	Mountain Whitefish	0	$-Sub_{Fine}$, −TRT, +TRT × Sub_{Fine}	90.70	0.00	4	0.71	0.15
	Torrent Sculpin	>0	$+Cover_{Rock}$	101.57	0.00	2	0.99	0.22

Note. Akaike's information criterion (AIC_c) adjusted for small sample size was used to rank models; only models with a $\Delta AIC \leq 2$ from each candidate set are included. Effect of model covariates are indicated as (positive [+], negative [−]).

Relationships describing the occurrence and relative abundance of fishes were variable with regard to substrate type. In general, the occurrence of a fish species was positively related to large substrate, whereas relative abundance was negatively related to large substrate. Disentangling the exact mechanism(s) responsible for the observed pattern between fish abundance and substrate type is difficult because flow regulates substrate composition, water residence time, and potential food resources (Allan, 1995; Dodds & Whiles, 2010; Kauffman et al., 1997). For example, backwaters that contained higher proportions of large substrates (e.g., gravel and cobble) were most often lotic channels during periods of high flow prior to being sampled as a backwater. Conversely, backwaters containing a high proportion of fine substrates (e.g., silt and sand) were generally lentic throughout the study. The negative relationship between fish abundance and large substrate may be attributed in part to the observed variation in flow and subsequent substrate characteristics. Alternatively, the relationship may be attributed to greater food availability associated with water residence time. Backwater habitats have been shown to contain twice the amount of organic matter and up to 100 times the amount of zooplankton when compared with channel habitats, largely due to the retention of water (Spaink et al., 1998; Speaker, Moore, & Gregory, 1984; Ward & Stanford, 1995). Regardless of the mechanism, the disproportionately high catch of fish in backwaters suggests that SSCV areas are important for native fish production and are likely serving as nursery habitat for young fish (Copp, 1997a, 1997b; Freeman et al., 2001; Kwak, 1988; Scheidegger & Bain, 1995). In addition, most Age-0 fishes were found in contrasting levels of abundance between channels and backwaters, suggesting that these species display some degree of habitat selection.

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

Habitats characterized by the presence of woody cover features were related to the occurrence of Torrent Sculpin and Mountain Whitefish. Placement of instream woody cover features is one of the primary techniques being used to enhance habitat in the Kootenai River. The occurrence of Torrent Sculpin greater than Age 0 was positively related to woody cover, presumably as a response to predators. Laboratory experiments have shown that Torrent Sculpin congregate in areas with cover when only fine substrates are available but distribute when cobble (i.e., cover) is available (Brusven & Rose, 1981). We found similar results where the relative abundance of Torrent Sculpin was positively related to rocky cover features (e.g., riprap and boulders). In addition to providing cover, wood decreases current velocity

and retains fine sediments and organic material (Speaker et al., 1984). The occurrence and relative abundance of Age-0 Mountain Whitefish was negatively related to woody cover and fine substrate. However, these relationships reversed when the species was sampled from treated sites, which may be related to foraging strategies during early life stages. Chironomid larvae are a major prey item of Age-0 Mountain Whitefish (Stalnaker & Gresswell, 1974) and unlike many macroinvertebrates, chironomid densities are usually highest in fine substrates (Allan, 1995). Although the proposed mechanisms associated with use of wood by Torrent Sculpin and Mountain Whitefish are speculative, these results are of particular interest when applied to the context in the habitat rehabilitation programme because it indicates that small-bodied native fishes are using the engineered habitat features.

The fish assemblage of Kootenai River has been evaluated at multiple spatial and temporal scales to assess the effect of habitat rehabilitation on the entire fish assemblage and population abundance of a few targeted fish species. Previous evaluations of the Kootenai River have established that fish assemblages differed among geomorphic sections (Smith et al., 2016) and among main- and side-channels (Watkins et al., 2015). Our study further suggests that fish assemblages differ between backwater and channel habitats. The spatial scale assessed in our study was useful for obtaining species-specific microhabitat data, but 52% of our samples contained no fish. Fish may be absent from samples for several reasons (e.g., abiotic pressures, biotic interactions, and gear avoidance), but sampling such a small relative space may be an underlying cause. Due to limitations of the sampling equipment, we could only sample fishes and habitat from wadeable areas of the river (depth < 1.5 m), which could bias our results to favour SSCV conditions. However, our sampling protocol was applied identically throughout this study, and a site was surveyed only when the location was conducive for effective PAED sampling. Our results clearly indicate the importance of backwaters for small-bodied fishes and the logistic and linear regression models highlight the significance of other SSCV habitats (e.g., channel margins). Wolter, Buijse, and Parasiewicz (2016) suggested that the most relevant spatiotemporal scale to evaluate fish populations occurs at the reach scale because a variety of permanent and temporary hydraulic units are available at that spatial scale, which is generally associated with a species' home range. Despite the limitations of our sampling gear, over 1,400 individuals representing eight species were sampled following the protocol. This highlights the applicability of the sampling scale in a large river system to some extent but emphasizes the importance of evaluating and monitoring fish populations across multiple spatial scales (Fausch, Torgersen, Baxter, & Li, 2002; Sindt et al., 2012).

The current study emphasizes the importance of SSCV habitats to juvenile and small-bodied fishes in a large river system such as the Kootenai River. Relationships with substrate and instream habitat structures were important for a few species in this study, but shallow areas with reduced flow appear to serve as a major driver of habitat use for small-bodied fishes in this floodplain river system. The significance of SSCV habitats for small-bodied fishes has been reported in other large floodplain river systems that have experienced a wide range of anthropogenic disturbances (Love, Phelps, Tripp, & Herzog, 2017; Nannini, Goodrich, Dettmers, Soluk, & Wahl, 2012; Reinhold et al., 2016). However, the availability of SSCV habitats is dependent on flow (Bowen et al., 2003; Reinhold et al., 2016), and these conditions may be entirely absent in regulated floodplain river systems as a result of water development. The lack of SSCV areas in other large river systems has prompted their artificial development for the benefit of native fishes. For example, a variety of approaches (e.g., notching dikes) have been used to create new SSCV habitats in the Missouri River to provide refuge for small-bodied and juvenile native fishes (Papanicolaou, Elhakeem, Dermisis, & Young, 2011; Ridenour, Starostka, Doyle, & Hill, 2009; Schloesser et al., 2012). Engineered SSCV habitats in the Mississippi River, United States, and Huntspill River, United Kingdom, have resulted in increased abundance and diversity of Age-0 fishes when compared with main channel areas (Barko, Herzog, Rabik, & Scheibe, 2004: Langler & Smith, 2001). In addition to engineered features, the significance of SSCV habitats for small-bodied fishes has been observed in the relatively undisturbed Yellowstone River, United States, establishing baseline importance of these areas for systems that may have experienced substantial anthropogenic alteration (Reinhold et al., 2016).

River restoration is a multibillion dollar industry (Bernhardt et al., 2005), yet most programs fail to monitor or evaluate biological responses to the improvements (Kondolf & Micheli, 1995; Roni et al., 2002). The results of this study and those conducted in other large floodplain rivers emphasize the importance of SSCV habitats as an integral component of habitat rehabilitation. Incorporating SSCV habitats into the design of habitat enhancement efforts would benefit several fish species of the Kootenai River. In particular, backwaters appear to be important for native fish production and likely provide prey for piscivorous fishes, some of which are species of conservation concern (White Sturgeon; Burbot; and Bull Trout, *Salvelinus confluentus*). Low-velocity floodplain habitat is scarce in the Kootenai River system, but the abundance of fish sampled from backwaters suggests that they may serve as a vestige of the historical floodplain. Hydrologic connectivity has become an important focus of ecological restoration (e.g., Kondolf et al., 2006), and process-based rehabilitation is currently underway in the Kootenai River to recover lost linkages. Prioritizing the conservation and enhancement of backwaters and other SSCV areas (e.g., channel margins and side channels) in regulated rivers would enable natural channel forming processes for the benefit of native fishes. The observed differences in the relationships between occurrence and relative abundance of fishes with regard to substrate type warrants further investigation. Such inquiry may elucidate potential mechanisms that govern fish assemblage structure in SSCV habitats and further guide the design of rehabilitation activities.

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ORCID

Philip R. Branigan http://orcid.org/0000-0003-3799-0573

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