ASSESSMENT OF SAMPLING TECHNIQUES AND FISH ASSEMBLAGE STRUCTURE IN LARGE WESTERN RIVER SYSTEMS

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Fisheries Science

in the

College of Graduate Studies

University of Idaho

by

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December 2013

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ABSTRACT

A comparison of sampling techniques and investigation of fish assemblage structure is greatly needed to improve management of western river systems. The objective of this thesis was to compare the efficacy of several gears (hoop nets, boat-mounted electrofishing, benthic trawls) for sampling fish assemblages of western rivers (Green River, Wyoming; Kootenai River, Idaho) and to investigate patterns of fish assemblage shifts in relation to habitat in the Kootenai River. In general, species-specific detectability varied by system and habitat, but was most influenced by gear. Electrofishing and hoop nets had the highest detection probabilities for most species, whereas detectability of most fishes was low with trawls. Transitions in fish assemblage and habitat structure were apparent among river sections in the Kootenai River. This thesis provides information that will improve sampling efficiency and our understanding of factors that structure fish assemblages and populations in coldwater rivers.

ACKNOWLEDGEMENTS

I would first like to thank my advisor, Dr. Michael C. Quist, for his unwavering patience, guidance, and excellent instruction. His involvement throughout my career has instilled a passion for fisheries research, encouraged my active American Fisheries Society involvement, and advanced my development as a fisheries professional. I also appreciate the assistance other committee members (Dr. Kenneth D. Cain, Ryan S. Hardy, Dr. Daniel J. Schill, and Dr. Christopher J. Williams) have provided for this project. I owe a great deal of gratitude to field technicians Christian Brown, Dan Donnelly, Kayla Griffin, John Hansen, Wes Field, Erin Landers, Nick Porter, and Jarrod Yates. Through all of the long commutes to field sites and inclement weather, field technicians made the work enjoyable. I would also like to acknowledge the assistance I received from fellow graduate students Marika Dobos, Zach Klein, Elizabeth Ng, Joshua McCormick, Steve Whitlock, John Walrath, and Carson Watkins. Insight and comments from lab mates have undoubtedly improved this work and their assistance was greatly appreciated. I would also like to thank past graduate students at Iowa State University, particularly Dr. Jesse Fischer, Anthony Sindt, and Timothy Parks, for encouraging my professional growth as an undergraduate and providing me limitless learning opportunities. I also want to acknowledge the support my family has provided through my entire education experience. I would especially like to thank my father and brother for exposing me to the outdoors and conservation at an early age and instilling my passion for natural resources. Most importantly, I would like to extend my gratitude to my wife Sarah. Without her support, sacrifices, and understanding I could not have completed this work.

I also would like to acknowledge Idaho Department of Fish and Game for providing funding for this project. I would like to express my gratitude to employees of Idaho Department of Fish and Game (T.J. Ross, Kathy Gidley, Pete Rust, Wes Ewing, Nick Porter) and Wyoming Game and Fish Department (Robb Keith, Travis Neebling, Darren Rhea, Anna Senecal, Hilda Sexauer) for assistance with planning and conducting field work.

DEDICATION

This thesis is dedicated to my parents, Linda and Jerry Smith.

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CHAPTER 1: GENERAL INTRODUCTION

Freshwater fishes are among North America’s most imperiled fauna (Master 1990) with over 30% of all freshwater fishes classified as imperiled, vulnerable, or extinct (Richter et al. 1997; Jelks et al. 2008). A high proportion of imperiled fishes inhabit North America’s river systems (Galat and Zweimüller 2001), likely a consequence of widespread alterations (e.g., channelization, pollution, watershed land use changes, dam construction) to lotic habitats. As a result of alterations, lotic systems are among the most anthropogenically-influenced ecosystems on the planet (Malmqvist and Rundle 2002).

Large rivers have been modified on a global scale (Dynesius and Nilsson 1994), with over half of the world’s large river systems fragmented by dam construction (Nilsson et al. 2005). In the contiguous United States, only 42 rivers have unaltered flow for greater than 200 km (Benke 1990). Dams have numerous deleterious effects on riverine systems by limiting access to the floodplain, homogenizing instream habitat (Ligon et al. 1995), blocking fish migration (Larineier 2000), and altering hydrologic, thermal, and nutrient regimes (Gregory et al. 2002; Liermann et al. 2012). Consequently, dam construction and operation have altered fish assemblages (Paragamian 2002; Quinn and Kwak 2003; Galat et al. 2005; Quist et al. 2005; Hoagstrom et al. 2007).

Freshwater biodiversity provides many important ecosystem services (e.g., fisheries, storage of genetic information, improved water quality; Hooper et al. 2005; Dudgeon et al. 2006; Cardinale et al. 2011). Consequently, understanding and rapidly evaluating ecosystem quality of freshwater systems is a priority for many management agencies. Fishes are commonly used to assess ecosystem quality (e.g., index of biotic integrity); however, such assessments rely on accurate surveys of the entire fish assemblage (i.e., no undetected species; Karr 1981; Kwak and Freeman 2010). Selection of appropriate sampling techniques with high detection probabilities is an important consideration for biomonitoring surveys (Kwak and Peterson 2007; Bonar et al. 2009). Unfortunately, a paucity of information exists regarding effective sampling techniques for fish assemblages in large riverine systems of western North America. The goals of this research were to (1) evaluate the efficacy of three sampling techniques for fish assemblages and the influence of habitat characteristics on detectability in the Kootenai and Green rivers and (2) describe fish assemblage and population-level relationships with habitat characteristics of a western riverine system.

THESIS ORGANIZATION

This thesis contains four chapters. Chapter two compares sampling techniques for fish assemblages using detection probabilities and investigates the influence of habitat characteristics on detectability. Chapter three evaluates shifts in aquatic habitat and fish assemblage structure along the longitudinal gradient of the Kootenai River of Idaho. Chapter four synthesizes findings from all chapters and presents the general conclusions of my thesis.

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CHAPTER 2: COMPARISON OF ELECTROFISHING, HOOP NETS, AND BENTHIC TRAWLS FOR FISH SURVEYS IN WESTERN NORTH AMERICAN RIVERS

A manuscript to be submitted for publication in the *North American Journal of Fisheries Management*

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ABSTRACT

Research comparing different sampling techniques helps improve the efficiency and efficacy of sampling efforts. We compared the effectiveness of three sampling techniques (small-mesh hoop nets, benthic trawls, boat-mounted electrofishing) for 30 species in the Green (WY, USA) and Kootenai (ID, USA) rivers by estimating detection probabilities (probability of detecting a species given its presence at a site). Electrofishing had the highest detection probabilities for most species, but hoop nets also had high detectability for several species (e.g., adult Burbot *Lota lota*, juvenile Northern Pikeminnow *Ptychocheilus oregonensis*). Benthic trawls had low detection probabilities for most fishes. Gear-specific effects were present for most species indicating large differences in gear efficacy among techniques. In addition to gear effects, habitat characteristics also influenced detectability of fishes. Most species-specific habitat relationships were idiosyncratic and reflected differences in the ecology of the species. Overall, this study provides important information on the effectiveness of various techniques targeting fish assemblages and will help improve future sampling efforts in coldwater river systems.

Freshwater aquatic systems are threatened worldwide and have experienced high rates of biodiversity decline relative to terrestrial systems (Dudgeon et al. 2006; Strayer and Dudgeon 2010). Declines of freshwater fishes have been widely reported with approximately 700 fishes listed as imperiled (endangered, threatened, vulnerable) in North America (Jelks et al. 2008). Unfortunately, extinction rates are expected to increase in future decades (Ricciardi and Rasmussen 1999). Due to widespread declines in aquatic biodiversity, increased effort has been allocated by natural resource agencies to monitor fish assemblages (Noble et al. 2007). In particular, high amounts of effort and multiple sampling techniques will likely be required to monitor large riverine systems as a result of high habitat complexity and diverse fish assemblage structure (Bonar et al. 2009a; Simpkins and Mistak 2010).

Effective management of fish populations and assemblages commonly relies on long-term monitoring programs to detect shifts in population and (or) assemblage structure (Thomas 1996; Magurran et al. 2010). Long-term data are essential for understanding fish population trajectories in response to management actions (e.g., habitat restoration, fishing regulation change) on short and long temporal scales (Noble et al. 2007). Additionally, understanding responses of lotic fish assemblage structure to anthropogenic effects often depend on long-term datasets, as shifts in fish assemblage structure typically occur over large temporal scales (Quist et al. 2005; Hoagstrom et al. 2007; Gido et al. 2010). Long-term monitoring programs can provide valuable information, but few monitoring programs account for imperfect detection probabilities (probability of detecting a species given its presence at a site [$\hat{p}$]; Boulinier et al. 1998; Yoccoz et al. 2001; McKenzie et al. 2006).

Detection probabilities typically vary by gear and by habitat characteristics (Burdick et al. 2008; Schloesser et al. 2012; Haynes et al. 2013). Failure to account for differences in detectability when investigating temporal or spatial trends may confound true patterns and result in erroneous conclusions, particularly if detection probabilities are highly variable over large temporal or spatial scales (Boulinier et al. 1998; Nichols et al. 1998; MacKenzie et al. 2006). Understanding and accounting for imperfect detectability allows managers to obtain more accurate estimates of fish population trajectories and assemblage composition.

Large rivers generally have high habitat complexity and biodiversity, particularly in warmwater systems (Guy et al. 2009; Paukert and Galat 2010; Simpkins and Mistak 2010). As a result, several techniques are commonly used for single species and fish assemblage surveys in warmwater rivers (Guy et al. 2009). For instance, Guy et al. (2009) recommend the use of eight standardized gears including bag seines, large-mesh benthic trawls, small-mesh benthic trawls, boat-mounted electrofishing, drifted trammel net, and three types of hoop nets (small-, medium-, large-mesh) for the collection of fishes in warmwater river systems. The reason for multiple gears is that many techniques are specialized and only sample a single species or functional group effectively. For example, hoop nets and low-pulse electrofishing are used to sample ictalurids (Channel Catfish *Ictalurus punctatus*, Blue Catfish *I. furcatus*) in large warmwater rivers, but they often collect few other species (Holland and Peters 1992; Buckmeier and Schlechte 2009). However, other techniques (boat-mounted electrofishing) have been reported to sample the majority of fish assemblages in warmwater river systems (Neebling and Quist 2011). In addition to research on gear efficacy, sampling effort recommendations for representative fish assemblage surveys have also been investigated in warmwater systems (Angradi 2006; Neebling and Quist 2011). For example, Neebling and Quist (2011) recommend electrofishing a minimum of 2,500 m and conducting 42 small-mesh benthic trawl hauls (50 m long) to effectively survey fish assemblages in Iowa's non-wadeable rivers.

Although a limited amount of research comparing different sampling gears has been conducted in warmwater systems, even less research has focused on sampling fish assemblages in coldwater rivers (Pugh and Schramm 1998; Lapointe et al. 2006; Neebling and Quist 2011; Schloesser et al. 2012). Of the research conducted in large coldwater rivers, general gear recommendations include boat- or raft-mounted electrofishing, seines, gill nets, and snorkeling (Curry et al. 2009). Similar to warmwater systems, electrofishing surveys are common and assumed to sample the majority of species in coldwater systems (Hughes and Herlihy 2007; Maret et al. 2007). However, additional guidance regarding gear selectivity would improve sampling efficiency and management of coldwater river systems.

Multiple-gear sampling designs are often necessary to collect representative samples of fish assemblages in coldwater and warmwater rivers (Curry et al. 2009; Guy et al. 2009). However, multiple-gear sampling designs cost more than surveys using a single technique and complicate data standardization (Nobel et al. 2007; Curry et al. 2009; Quist et al. 2009). Due to potential drawbacks of using multiple sampling gears, comparing sampling techniques is critical for determining the most efficient and effective use of resources.

The goal of this study was to investigate differences in detectability among techniques and fishes in large rivers of western North America. Specific objectives were to determine which species were sampled with different gears and to evaluate relationships between detectability and habitat characteristics.

METHODS

Study area

This study was conducted in the Green and Kootenai rivers, two large river systems in the western United States. The Green River has a drainage basin of approximately 117,000 km² and a length of 1,175 km (Vanicek 1970) with its headwaters originating in the Wind River Mountain Range of Wyoming (Cooper et al. 1999). The Green River is the largest tributary of the Colorado River, flowing through Wyoming, Utah, and Colorado before its confluence with the Colorado River at Canyonlands National Park, Utah. Much of the Green River watershed is located in the Rocky Mountain and Wyoming Basin ecoregions, with primary land use consisting of agriculture (e.g., grazing, production of livestock forage), mining (e.g., coal, uranium, petroleum), recreation, and logging (Green River Basin 2010). In addition to land use alterations, several impoundments have been constructed in the Green River and include Flaming Gorge Dam (construction completed in 1962), Fontenelle Dam (1964), Meeks Cabin Dam (1971), and Stateline Dam (1979; Green River Basin Water Plan 2001).

The Kootenai River has an international watershed of approximately 45,600 km², residing in both the United States and Canada (Knudson 1994). Headwaters of the Kootenai River are located in Kootenay National Park, British Columbia, Canada. From its headwaters, the Kootenai River flows south into the United States, first entering Montana and then Idaho, before returning to British Columbia and entering the Columbia River near Castlegar, British Columbia. Land use in the watershed includes logging, agriculture, mining, and some industrial facilities (e.g., fertilizer production, municipal waste facilities; Richards 1997). However, much of the anthropogenically-altered land uses occur in the lower reaches of the river, leaving headwaters relatively pristine. In addition to altered land use and levee construction, completion of Libby Dam at Libby, Montana arguably had the largest influence on the Kootenai River system. Libby Dam was completed in 1972 by the U.S. Army Corps of Engineers and impounds nearly 148 km of the Kootenai River, forming Lake Koocanusa (Whitfield and Woods 1982). Completion of Libby Dam has had deleterious effects on the riverine ecosystem downstream, being directly implicated in the collapse of at least two fisheries: Burbot *Lota lota* (Paragamian et al. 2000) and White Sturgeon *Acipenser transmontanus* (Paragamian et al. 2001).

Reach selection and field sampling

Sampling in the Green River occurred at 28, 500-m long reaches during the summers (June - August) of 2012 and 2013. Forty-five reaches (500 m) were surveyed in the Kootenai River during the summers (June - August) of 2012 and 2013 and fall (September - October) of 2012. Each reach was subdivided into two 250-m subsections (hereafter referred to as a sampling site). All reaches sampled in a season were resampled at least once and many (74%) were resampled three or four times in a single season. All resampling efforts occurred within six weeks of initial surveys, but resampling events for most reaches

(> 80%) were completed within one week. Each reach was assumed to be demographically closed between season-specific sampling periods.

Fish were sampled using three gears (hoop nets, benthic trawl, boat-mounted electrofishing; see below for additional descriptions). Once sampling reaches were identified, one of the 250-m sites (randomly selected) was sampled with small-mesh hoop nets and the remaining site was sampled with a modified-Missouri benthic trawl. Electrofishing sampled bank habitat along the entire reach. In total, we used four small-mesh hoop nets, four trawl hauls, and two 250-m electrofishing runs in each sample reach for every sampling event. Active gears (i.e., electrofishing, trawls) sampled reaches first; passive gears (i.e., hoop nets) were set following completion of active sampling.

Hoop nets are a passive sampling gear commonly used in rivers to capture a variety of fishes (Guy et al. 2009). We used small-mesh hoop nets in an attempt to retain small-bodied fishes. Hoop nets used in this study had an overall length of 3.7 m and were covered with 6.3-mm bar measure knotless delta style mesh. Nets had six, 60-cm diameter circular steel hoop frames to keep nets open while fishing. Two throats (10 cm minimum diameter) were located between the second and fourth, and fourth and sixth hoop frames. Four hoop nets were deployed following electrofishing and trawling. Nets were baited with local non-game fishes (e.g., *Catostomus* spp.) and fished for approximately 12 hrs.

The modified Missouri River benthic trawl is an effective gear for small-bodied and juvenile fishes (i.e., < 300 mm) in riverine habitats (Herzog et al. 2005; Neebling and Quist 2011). 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 bar measure delta style, knotless mesh). 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. A chain (5-mm link diameter) was attached to the 3.7-m footrope to maintain contact with the bottom at all times. Due to differences in depth, length of towlines (2.2 cm twisted nylon rope) varied by river system (Green River towline length = 20.0 m, Kootenai River towline length = 30.5 m) to ensure that trawls were fished along the bottom. Otter doors (61 cm × 30.5 cm) were attached to the trawl and prevented the collapse of the trawl while deployed. Trawls were deployed off the bow and pulled downstream. Nets were fished 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, the trawl haul was replicated. A global positioning system receiver (Lowrance, Tulsa, OK) was used to measure distance sampled and measurement started once the trawl was fully deployed. Distance traveled with the trawl fully deployed was used as a measure of effort.

Electrofishing is a common and effective fish sampling method in both lentic and lotic systems (Guy et al. 2009; Miranda and Boxrucker 2009). Electrofishing gear consisted of an Infinity model electrofisher (Midwest Lake Electrofishing Systems, Inc., Polo, MO) and a 5,000 W Honda generator (American Honda Motor Co., Inc., Torrance, CA). Electrofishing power output was standardized to 2,750 – 3,250 W (Miranda 2009). Two netters were stationed near the bow of the boat to collect fish. Dip nets used to collect fish had 6.3-mm knotless mesh. Pulsed-DC electrofishing effort was conducted during the day.

Effort was randomly allocated to one bank for the upstream sampling site and alternated to the other bank for the downstream site. Electrofishing was initiated in the uppermost portion of the reach and sampled fish with a single pass (approximately 250 m) in a downstream direction. Fish catch was enumerated at the completion of electrofishing for every sample site. Effort was recorded as the number of seconds with electricity being applied to the water.

Fishes were identified in the field, but if fishes were unable to be accurately identified, voucher specimens were collected and identified in the laboratory. Following identification, all fish were measured (total length; mm), enumerated, and released at a location away from the subsequent sample sites.

An evaluation of aquatic habitat was completed for every reach and was modeled after Neebling and Quist (2011), U.S. Environmental Protection Agency non-wadeable river protocols (Flotermersch et al. 2006), and Wilhelm et al. (2005). Some habitat variables were assumed to be constant in a season (e.g., bank type, substrate composition; hereafter referred to as site-scale variables), whereas other variables likely varied for each sampling event (e.g., discharge, temperature; hereafter referred to as sample-scale variables). Sample-scale habitat characteristics were collected at the completion of each sampling event (water temperature [°C], water clarity [m], conductivity [µS/cm]). Average daily discharge (m^3/s) was acquired from U.S. Geological Survey gaging stations.

In addition to sample-scale covariates, we collected site-scale habitat characteristics for each reach. 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 each transect were measured for depth, velocity, and substrate composition (Neebling and Quist 2011). Water depth was recorded using a Lowrance depth finder (Lowrance, Tulsa, OK). In depths less than 1 m, mean water column velocities were measured at 60% of the depth using an electromagnetic flow meter (modified from Kaufmann et al. 1999; Flotermersch et al. 2001; Neebling and Quist 2011; Marsh-McBirney, Loveland, CO). If depth was greater than 1 m, mean water column velocity was recorded at 20% and 80% of the depth. Bottom velocity measurements were collected 8 cm from the bottom. Substrate composition was classified 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), or bedrock (modified from Orth and Maughan 1982).

Statistical analysis

To reduce the risk of multicollinearity, Spearman's correlation coefficient was used to investigate potential relationships among habitat variables. In general, the most ecologically relevant 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; Table 2.1). However, some variables deemed ecologically important were highly correlated, but were both included because they likely influenced detectability via different mechanisms. For example, average depth and the proportion of large substrate were highly correlated ($\hat{\rho}$ = -0.76), but likely influenced occupancy and detectability differently.

Occupancy models were used to investigate gear-specific detection probabilities of fishes and relationships among detection probabilities and habitat characteristics. Occupancy models use information on detection and non-detection to estimate site occupancy (probability of sites being occupied; $\hat{\psi}$) and account for imperfect detectability (MacKenzie et al. 2002; MacKenzie et al. 2006). To account for imperfect detectability, sampling must be replicated (spatially or temporally) in a period of demographic closure. Occupancy models estimate the probability of observing each detection history (i.e., binary code indicating the detections or non-detections of a species at a site through repeated surveys) based a series of detection or non-detection information (MacKenzie et al. 2002; MacKenzie et al. 2006; Burdick et al. 2008). For example, given that a species is present, the probability of observing a detection history consisting of two sampling events takes the form of:

$$\mathrm{Pr}(h) = \hat{\psi}(\hat{p}_1)(1\text{-}\hat{p}_2)$$

where $\mathrm{Pr}(h)$ is the probability of the detection history, $\hat{\psi}$ is the probability of occupancy, and $\hat{p}$ indicates whether a species was sampled or not (1-$\hat{p}$) during each sampling event (MacKenzie et al. 2006; Burdick et al. 2008; Williams 2010). Maximum likelihood is then used to estimate parameters given the observed data (MacKenzie et al. 2006; Burdick et al. 2008).

Fish species were classified as small- or large-bodied fishes (median total length of adults for a species ≥ 200 mm) because differences in length may influence habitat use, gear selectivity, and detection probabilities (Argent and Kimmel 2005; Bonar et al 2009b; Schloesser et al. 2012; Haynes et al. 2013). Occupancy models for large-bodied fishes were separated by life history stage, specifically length at maturity. Although we were not explicitly interested in life history stage, categorizing fish as juveniles or adults provided an objective way to separate fishes into groups while using information on their ecology. Approximate lengths at maturity were obtained from the literature and used to classify large-bodied fish as juvenile or adult (Appendix). Some species were not detected with all sampling techniques. Consequently, detection histories were used from only techniques that detected a particular species or life history stage at least once in a system and season.

Single-season models were constructed in three stages for each species (small-bodied fishes) or life history stage (large-bodied fishes) with a naïve occupancy estimate ≥ 0.10 (MacKenzie et al. 2005; modified from Schloesser et al. 2012). We first determined which habitat characteristics most influenced occupancy rates and held those covariates constant for remaining model states (J. Nichols, Patuxent Wildlife Research Center, personal communication). This helped minimize additional variation not attributed to detectability in the occupancy models. The second stage compared models with constant versus gear-specific detection probabilities. The final stage used the top candidate model (i.e., lowest AIC_c value [Akaike's Information Criterion adjusted for small sample size]) from the second stage to investigate relationships between detectability and habitat covariates. Seven to fifteen candidate models were constructed for each species based on *a priori* hypotheses to investigate relationships between detectability and habitat covariates (Burnham and Anderson 2002).

Overdispersion was assessed using global models (model containing the most parameters (Burnham and Anderson 2002). However, due to a reduced sample size in the fall season, simple candidate models were constructed (i.e., a single habitat explanatory variable). Consequently, overdispersion for candidate model sets with no global model was evaluated with the best-fitting model (Burnham and Anderson 2002). An overdispersion parameter (variance inflation factor; $\hat{c}$) was estimated using a Pearson chi-square statistic and parametric bootstrap (1,000 iterations; MacKenzie and Bailey 2004; MacKenzie et al. 2006). If $\hat{c}$ was greater than one, data were likely either overdispersed or there was a lack of model fit and estimated model variance was adjusted with $\hat{c}$ (Burnham and Anderson 2002; MacKenzie et al. 2006). If species were detected at every event at each occupied site (i.e., perfect detectability), a standard error estimate of detectability could not be calculated. Occupancy models were fit using program PRESENCE (Hines 2006).

Candidate models were ranked using AIC_c adjusted for small sample size (AIC_c; Burnham and Anderson 2002). A conservative estimate of effective sample size (i.e., total number of reaches) was used to adjust for small sample size. If overdispersion ($\hat{c} > 1$) was present, quasi-AIC_c ($QAIC_c$) was used to rank candidate models (Burnham and Anderson 2002). Additionally one additional parameter was added to the total number of parameters 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

Two-hundred and twenty-three sampling events occurred at 28 reaches in the Green River (Figure 2.1) and 45 reaches in Kootenai River (Figure 2.2) in the summers of 2012 and 2013 (Kootenai and Green rivers) and fall of 2012 (Kootenai River only). A total of 11,676 individuals consisting of 30 species and nine families was sampled. Two federally listed species (Bull Trout *Salvelinus confluentus*, White Sturgeon) were collected in the Kootenai River. Additionally, three species of high conservation concern in Idaho and Wyoming were collected: Flannelmouth Sucker *Catostomus latipinnis* (Species of Concern in Wyoming), Leatherside Chub *Lepidomeda copei* (Species of Concern in Wyoming), and Burbot (Imperiled Species in Idaho).

Electrofishing collected four unique species (i.e., a species not collected with other techniques) in the Green River (Figure 2.3) and five unique species in the Kootenai River (Figure 2.4). Hoop nets detected one unique species in the Green River (Fathead Minnow *Pimephales promelas*). Trawls failed to detect any unique species in either river system. Electrofishing collected the majority of individuals (percentage of total catch = 82%), followed by hoop nets (11%), and trawls (7%).

Gear-specific detectability in the Green River was greatest with electrofishing for adult White Sucker *Catostomus commersonii* (0.70 ± 0.05) and Common Carp *Cyprinus carpio* (0.68 ± 0.13), and with hoop nets for adult Burbot (0.61 ± 0.06). Similarly, detection probabilities in the Kootenai River were highest with electrofishing for juvenile Peamouth *Mylocheilus caurinus* ($\hat{p}$ ± standard error [NA = not available]; 1.00 ± NA), adult Mountain Whitefish *Prosopium williamsoni* (1.00 ± NA), and adult Largescale Sucker *Catostomus* *macrocheilus* (0.87 ± 0.03; Table 2.2). Detection probabilities with hoop nets in the Kootenai River were highest for juvenile (0.86 ± 0.04) and adult (0.46 ± 0.05) Northern Pikeminnow *Ptychocheilus oregonensis*. Overall, detection probabilities among systems were greatest with electrofishing for 86% of small-bodied species, 85% of juvenile large-bodied fishes, and 92% of adult large-bodied fishes. Detectability of the trawl was low for most species (< 0.10) and was highest for Longnose Dace *Rhinichthys cataractae* (0.44 ± 0.06) in the Green River and juvenile Mountain Whitefish in the Green (0.24 ± 0.17) and Kootenai (0.38 ± 0.05) rivers.

Gear-specific effects on detectability were apparent for most species or species-life history stage combinations that were sampled with at least two techniques (Table 2.3). Occupancy models of most small-bodied (100%), juvenile large-bodied (60%), and adult large-bodied fishes (100%) had more support with gear-specific models than constant detectability models in the Green River. Similarly, gear-specific models had more support than constant detectability models for 80% of small-bodied, 100% of juvenile large-bodied, and 100% of adult large-bodied fishes in the summer in the Kootenai River. Gear-specific models also had more support than constant detectability models for most small-bodied (66%), juvenile large-bodied (60%), and adult large-bodied fishes (50%) in the fall sampling of the Kootenai River.

Although detectability of many fishes was best predicted solely with gear covariates, environmental characteristics were also related to detectability of some fishes in the Green River. For instance, detectability of juvenile Rainbow Trout and juvenile Mountain Whitefish were positively related to water velocity, whereas detection probabilities of Utah

Chub, adult Brown Trout, adult Burbot, and Mottled Sculpin were negatively related to velocity (Table 2.3). Other variables, such as the coefficient of variation in velocity were related similarly (i.e., negatively) to the detectability of juvenile salmonids (e.g., Mountain Whitefish, Rainbow Trout *Oncorhynchus mykiss*). Site-specific covariates were influential for more species than sample-scale covariates in the Green River. However, one sample covariate, water temperature, influenced detectability of numerous species.

Similar to the Green River, occupancy models for samples in the summer season in the Kootenai River indicated variable effects of environmental characteristics on detectability. Average depth and the proportion of cobble or boulder substrate appeared in top models for many species (Table 2.3). Specifically, depth was positively related to detectability of adult Longnose Sucker *Catostomus catostomus*, adult Cutthroat Trout *Oncorhynchus clarkii*, Torrent Sculpin *Cottus rhotheus*, and cyprinids (adult Peamouth, juvenile Northern Pikeminnow), and negatively related to detectability of adult Largescale Sucker, Brown Bullhead *Ameiurus nebulosus*, and several adult salmonids (Kokanee *Oncorhynchus nerka*, Mountain Whitefish, Rainbow Trout). The proportion of cobble or boulder substrate was negatively related to detectability of most fishes (juvenile Northern Pikeminnow, juvenile Longnose Sucker, adult Longnose Sucker, adult Cutthroat Trout, Yellow Perch *Perca flavescens*), but positive relationships were apparent for Brown Bullhead and adult Mountain Whitefish. Sample covariates (discharge, water clarity) were selected among top candidate models for summer samples in the Kootenai River for several fishes. Specifically, discharge was positively related to detectability of adult Peamouth, juvenile Largescale Sucker, juvenile Longnose Sucker, juvenile Rainbow Trout, adult

Cutthroat Trout, and adult Kokanee, but was negatively related to detectability of Yellow Perch, juvenile Northern Pikeminnow, and adult Burbot. Negative relationships between water clarity and detectability were observed for Pumpkinseed *Lepomis gibbosus*, Yellow Perch, juvenile Longnose Sucker, adult Longnose Sucker, adult Kokanee, adult Rainbow Trout, and adult Cutthroat Trout; however, a positive relationship was observed for adult Mountain Whitefish.

Habitat characteristics appeared to have less of an effect on detection probabilities in the fall compared to summer in the Kootenai River (i.e., fewer top models contained environmental characteristics). Of the top models that contained habitat covariates, important site-specific variables included water velocity, depth, and the proportion of cobble or boulder substrate (Table 2.3). Detection probabilities were negatively related to water velocity for juvenile Largemouth Bass *Micropterus salmoides*, juvenile Mountain Whitefish, and juvenile Largescale Sucker, but positively related to adult Largescale Suckers, adult Kokanee, and juvenile Rainbow Trout. Depth was positively related to detectability of juvenile Northern Pikeminnow and Yellow Perch. Detectability of juvenile Rainbow Trout and adult Rainbow Trout were positively related to the proportion of cobble or boulder substrate, whereas negative relationships were discovered for Yellow Perch and adult Mountain Whitefish. Sample-scale covariates were important in explaining detectability of Brown Bullhead and juvenile Mountain Whitefish in the fall season.

DISCUSSION

Sampling techniques used in our study have been used to sample fish assemblages in warmwater and coldwater rivers of North America (Curry et al. 2009; Guy et al. 2009). However, differences in detectability among species and life history stages were apparent among techniques. Our comparison of sampling techniques using detection probabilities provides important information for future sampling in both systems and presents an application of occupancy models for gear comparison investigations.

Occupancy models can be an effective method for comparing sampling techniques. Historically, different sampling techniques have been compared by estimating catchability (proportion of the population sampled with one unit of effort); however, catchability requires unbiased estimates of abundance (Peterson and Paukert 2009). Abundance can be difficult to estimate with reasonable precision in riverine systems due to high connectivity and habitat complexity (Speas et al. 2004; Peterson and Paukert 2009). Comparisons may also be made using relative abundance estimates (e.g., catch-per-unit-effort), but due to differences in measures of effort, particularly between active and passive gears, results are difficult to interpret (Peterson and Paukert 2009). We argue that the use of occupancy models and detectability (comparisons are made among gears using probabilities) is advantageous over traditional comparison methods.

Previous research indicates electrofishing is an effective method for monitoring fish assemblages in large river systems (Pugh and Schramm 1998; Lapointe et al. 2006; Mercado-Silva and Escandon-Sandoval 2008; Neebling and Quist 2011). Neebling and Quist (2011) found that electrofishing sampled the greatest number of species compared to trawl and seine techniques in Iowa's non-wadeable rivers. Similarly, Mercado-Silva and Escandon-Sandoval (2008) reported greater estimates of species richness, diversity, and biomass with electrofishing compared to seines in the San Francisco River, Mexico. Results from our research are similar for western riverine systems where electrofishing not only collected the majority of individuals, but sampled most detected species and nine unique species between the two river systems. However, despite high catch rates and detection of all species in the current study with electrofishing, detectability was higher with other gears for some fishes.

Hoop nets are a passive sampling technique that is commonly used to collect fishes (e.g., ictalurids, cyprinids) in both warmwater (Pugh and Schramm 1998; Lapointe et al. 2006) and coldwater (Stone 2010) lotic systems (Guy et al. 2009). Tillma et al. (1997) found that baited hoop nets were highly effective for sampling Channel Catfish and Flathead Catfish *Pylodictis olivaris* in a small tributary of the Missouri River. Hoop nets collected most species and detected two unique species (bighead carp *Hypophthalmichthys nobilis*, black crappie *Pomoxis nigromaculatus*) compared to electrofishing in the lower Mississippi River, Mississippi (Pugh and Schramm 1998). Four unique species were collected with hoop nets in the Detroit River, Ontario and hoop nets were an important supplement to the other gears (e.g., electrofishing, seines; Lapoint et al. 2006). Results of our study support the observation that hoop nets and electrofishing are complementary in fish assemblage surveys of western rivers.

Modified Missouri benthic trawls are effective for sampling small-bodied benthic fishes in non-wadeable Midwestern rivers (Herzog et al. 2005; Neebling and Quist 2011).

Neebling and Quist (2011) found that trawls collected the greatest number of individuals and the most species (73% of species observed) as part of a gear comparison study (boat-mounted electrofishing, benthic trawls, seines) in non-wadeable Iowa rivers. Herzog et al. (2009) collected several rare, small-bodied fishes (e.g., Shoal Chub *Macrhybopsis hyostoma*, River Darter *Percina shumardi*) in Minnesota rivers with a benthic trawl. In our study, trawls had low detection probabilities for most species (< 0.10) and did not sample any unique species. Water clarity varied by system and season, but was generally in excess of 2 m. Consequently, net avoidance due to high water clarity is a likely mechanism for the low efficacy observed in our study. Similar negative relationships between water clarity and catch have been reported for benthic trawls in large lentic systems (Duijse et al. 1992). Thus, benthic trawls in western rivers with high water clarity may contribute little to fish assemblage surveys.

The effect of gear on detectability was present for most species. In general, gear-specific or constant detectability models had more support than models incorporating environmental covariates. Gear effects are not surprising, as gear biases have been previously reported for a variety of passive (Hubert et al. 2012) and active (Hayes et al. 2012; Reynolds and Koltz 2012) sampling techniques (Bonar et al. 2009a). Gear biases are likely related to species ecology and explain differences in species-specific detection probabilities among techniques. For example, detectability of adult White Sucker in the Green River varied among techniques (gear, detection probability; electrofishing, 0.70; hoop nets, 0.12; trawls, 0.09). Our results are similar to Fischer (2012), who compared detection probabilities of seven sampling techniques for fish assemblages in reservoirs and natural lakes in the midwestern region of the United States. Fischer (2012) found species-specific detection probabilities varied among gears. For instance, detectability of black bullhead *Ameiurus melas* was low for most gears (< 0.40), but was highest for fyke nets (~0.80). Schloesser et al. (2012) reported similar findings. Specifically, they reported large differences in detectability of seven imperiled Missouri River fishes among three gears (i.e., trammel nets, gill nets, otter trawls) in a portion of the Missouri River (Iowa, Nebraska, Kansas, Missouri). Results of our research support previous work indicating species-specific detection probabilities vary greatly by gear and differences are likely related to gear biases and species ecology. Consequently, our findings underscore the importance of investigating gear-specific detection probabilities in an effort to improve gear selection and sampling efficiency for future fish assemblage surveys.

Although detectability of many fishes in the present study was best explained by gear, relationships with some environmental characteristics were apparent although their effects were highly variable. Most relationships with species-specific detection probabilities and habitat characteristics were idiosyncratic and reflected differences in the ecology of collected species. For instance, detectability of Longnose Dace in the Green River was negatively related to depth and likely reflects the benthic habitat affinities of the species (Mullen and Burton 1995). Additionally, detection probabilities of juvenile Largescale Sucker and juvenile Rainbow Trout in summer samples from the Kootenai River were positively related to discharge. Increased discharge in the Kootenai River resulted in inundated terrestrial vegetation along river margins. Catostomids (e.g., Razorback Sucker *Xyrauchen texanus*; Modde et al. 2001; Quist and Spiegel 2012) and salmonids (e.g., Chinook Salmon *Oncorhynchus tshawytscha;* Sommer et al. 2001) commonly use floodplain habitats and inundated vegetation. Greater detection in inundated vegetation may also be an artifact of increased sampling efficiency in shallow, low velocity habitats (Reynolds and Kolz 2012). Overall, depth and the proportion of cobble or boulder substrate had widespread effects on the detectability of fishes. For example, depth effects were selected among the top candidate models for over half of the species in the summer season of the Kootenai River samples. Depth has previously been reported to influence sampling efficiency (Reynolds and Kolz 2012). Bayley and Austen (2002) reported negative relationships between electrofishing catchability and depth for various lentic fishes (e.g., Bluegill *Lepomis macrochirus*) in Illinois lakes. Negative relationships between capture probabilities of Smallmouth Bass *Micropterus dolomieu* and mean thalweg depth have been reported for Oklahoma streams (Dauwalter and Fisher 2007). High proportions of large substrate may also influence detectability through several mechanisms including reduced sampling efficiency from snagged nets or difficulties netting immobilized fishes (Herzog et al. 2009; Guy et al. 2009; Reynolds and Kolz 2012). However, a higher proportion of large substrate may improve sampling efficiency due to increases in electrofishing power density in rocky substrates and by concentrating fishes (Speas et al. 2004; Reynolds and Kolz 2012

The effect of habitat characteristics on detection probabilities varied by life history stage for some species in the Kootenai and Green rivers. For example, detectability was positively related to temperature for juvenile Mountain Whitefish, but temperature was negatively related to the detection of adult Mountain Whitefish in the Green River. Reduced ability of fish to avoid capture at lower water temperatures (reduced metabolism and [or] escape behaviors) with electrofishing techniques could be one mechanism for the inverse relationship with temperature for adults (Reynolds and Kolz 2012). Speas et al. (2004) proposed a similar mechanism to explain a negative relationship between catchability of large (> 250 mm) Rainbow Trout and temperature in the Colorado River, Arizona. A positive relationship with detectability and temperature for juveniles could be related to an increased susceptibility of juveniles as their total length increased through the summer. Size-related biases are common for most sampling techniques and increased total length generally increases susceptibility for most gears (Bonar et al. 2009a; Reynolds and Kolz 2012; Hubert et al. 2012). For instance, total length of Smallmouth Bass was positively related to the probability of electrofishing capture in small lotic systems of Oklahoma (Dauwalter and Fisher 2007). Dolan and Miranda (2003) reported that an increase in total length greatly influenced electrofishing efficiency in a series of laboratory studies. Although detectability of some life stages were related to habitat in a different manner, habitat relationships were similar for some species. For example, detectability of both juvenile and adult Longnose Sucker was related to water clarity in the Kootenai River. Water clarity has been reported to influence catch of fishes with our gears (Bonar et al. 2009a; Guy et al. 2009; Hubert et al. 2012; Reynolds and Kolz 2012). Stone (2010) reported a positive relationship with hoop net catch of native fishes in the Colorado River and water clarity. However, electrofishing efficiency may be negatively related to water clarity in systems with traditionally high water clarity (Dewey 1992; Reynolds and Kolz 2012).

System-specific effects of detectability and habitat characteristics on fishes were apparent between the Kootenai and Green rivers. For example, the effect of depth on detectability varied by river system, with depth effects common in the Kootenai River and rare in the Green River. The effect of depth may be minimized in the Green River due to low average (< 1 m) and little variation in depths. In contrast, large differences in depth were observed (up to 11 m among sites in some reaches) among sample reaches in the Kootenai River. Large variation of depths in the Kootenai River system might explain relationships with average depth and detection probabilities. Additionally, water clarity was related to the detection probabilities of several species in the Kootenai River, whereas detectability of only one species (adult White Sucker) was related to water clarity in the Green River. Water clarity is commonly related to the catch of active and passive techniques, but due to low average depth (< 1 m) and high water clarity (> 1.5 m) in the Green River, the fact that few relationships were observed is not surprising (Hubert et al. 2012; Reynolds and Kolz 2012). Overall, the effect of environmental characteristics on detectability varied by system and a highly detailed investigation of system-specific habitat effects is likely required to fully understand the idiosyncrasies among gears, seasons, and species. Nevertheless, gears with the greatest detectability were generally consistent for species and families across river systems.

Our research confirms differences in detectability among gears and fishes, and illustrates the importance of understanding species-specific detection probabilities. General trends regarding gear efficacy appear consistent for species and families. However, differences in fish assemblage structure and habitat characteristics suggest that further investigations focusing on the influence of habitat on detectability are needed in other systems. An understanding of detection probabilities and the influence of environmental characteristics will allow managers to improve sampling designs and efficiency.

ACKNOWLEDGEMENTS

We thank C. Brown, D. Donnely, W. Field, K. Griffin, J. Hansen, E. Landers, N. Porter, J. Walrath, C. Watkins, S. Whitlock, and J. Yates for assistance with field research. We also thank C. Gidley, P. Rust, and T.J. Ross of Idaho Department of Fish and Game and R. Keith, T. Neebling, D. Rhea, A. Senecal, and H. Sexauer of Wyoming Game and Fish Department for assistance planning and implementing field work. Assistance with occupancy models was received from J. Nichols of the Patuxent Wildlife Research Center. Funding for the project was provided by Idaho Department of Fish and Game. Additional support was provided by the U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the U.S. Geological Survey, University of Idaho, and Idaho Department of Fish and Game, and Wildlife Management Institute. This project was conducted under the University of Idaho Institutional Animal Care and Use Committee Protocol 2011-33. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 2.1. Mean and standard error (in parentheses) of sample- and site-scale habitat variables collected from 72 reaches on the Kootenai and Green rivers during 2012 and 2013. Variables were used to investigate relationships between occupancy and detectability of fishes with single-season occupancy models.

		System and season		
		Green River	Kootenai River	
Variable	Description	Summer	Summer	Fall
Bank_{Bo}	Percentage of bank consisting of large substrate (i.e., cobble, boulder; %)	27.70 (4.57)	15.92 (3.10)	23.60 (7.36)
Bank_{Veg}	Percentage of bank consisting of vegetation (%)	56.50 (5.03)	38.80 (4.63)	18.00 (8.36)
Clarity	Mean Secchi disk depth (m)	1.82 (0.03)	2.78 (0.01)	4.03 (0.27)
$\text{Clarity}_{\text{Max}}$	Factor (Secchi disk depth was greater than max depth in reach)	0.58 (0.05)	0.03 (0.01)	0.13 (0.07)
CV_{Vel}	Mean coefficient of variation in water column velocity	0.39 (0.02)	0.37 (0.03)	0.47 (0.03)
Depth	Mean depth (m)	0.83 (0.03)	6.49 (0.33)	4.39 (0.59)
Q	Mean discharge (m^3/s)	35.30 (2.14)	701.98 (16.41)	222.90 (11.46)
$\text{Substrate}_{\text{Co-Bo}}$	Percentage of substrate consisting of cobble and boulder (%)	42.10 (6.40)	10.10 (3.10)	20.90 (10.8)
Temp	Mean temperature (°C)	13.11 (0.26)	14.60 (0.13)	12.45 (0.61)
Vel_{Avg}	Mean water column velocity (m/s)	0.75 (0.03)	0.54 (0.05)	0.53 (0.12)
Vel_{Sub}	Mean substrate velocity (m/s)	0.59 (0.02)	0.35 (0.04)	0.35 (0.10)

Table 2.2. Estimated detection probability ($\hat{p}$) of taxa organized by river system, season, taxa, and life history stage. Only occupancy models for large-bodied species (median total length of adults for a species ≥ 200 mm) were separated by life stage (i.e., juvenile, adult). Sampling techniques include electrofishing (EF), hoop nets (HN), and trawl (TR). Standard error of detectability was adjusted by the variance inflation factor and is presented in parentheses. Standard error could not be calculated for species that were detected at every sampling event and is indicated by (NA). A hyphen indicates that detection probabilities were unable to be calculated because no fish were sampled with the respective technique(s).

	Detection probability ($\hat{p}$)		
Taxa and life history stage	EF	HN	TR
Green River – Summer			
Cyprinidae			
Common Carp			
Adult	0.68 (0.13)	-	-
Longnose Dace	0.27 (0.05)	0.09 (0.03)	0.44 (0.06)
Utah Chub	0.12 (0.12)	-	-
Catostomidae			
Flannelmouth Sucker			
Adult	0.24 (0.10)	0.03 (0.03)	-
White Sucker			
Juvenile	0.45 (0.08)	0.12 (0.04)	0.02 (0.02)
Adult	0.70 (0.05)	0.12 (0.04)	0.09 (0.03)
Salmonidae			
Brown Trout			
Juvenile	0.29 (0.09)	0.03 (0.03)	0.07 (0.04)
Adult	0.34 (0.08)	0.02 (0.01)	0.05 (0.03)
Cutthroat Trout			
Juvenile	0.11 (0.14)	0.04 (0.06)	0.04 (0.06)
Adult	0.30 (0.08)	0.03 (0.02)	0.01 (0.01)
Mountain Whitefish			
Juvenile	0.31 (0.19)	0.04 (0.07)	0.24 (0.17)
Adult	0.48 (0.08)	-	0.04 (0.02)
Rainbow Trout			
Juvenile	0.42 (0.09)	0.08 (0.04)	0.04 (0.03)
Adult	0.54 (0.07)	0.05 (0.03)	0.06 (0.03)
Gadidae			
Burbot			
Juvenile	0.19 (0.14)	0.19 (0.14)	-
Adult	0.12 (0.09)	0.61 (0.14)	-
Cottidae			
Mottled Sculpin	0.27 (0.07)	0.01 (0.01)	0.10 (0.04)

Table 2.2 cont'd.

Kootenai River – Summer			
Cyprinidae			
Northern Pikeminnow			
Juvenile	0.78 (0.05)	0.86 (0.04)	0.02 (0.01)
Adult	0.69 (0.05)	0.46 (0.05)	-
Peamouth			
Juvenile	0.78 (0.18)	0.06 (0.10)	-
Adult	0.80 (0.06)	-	-
Redside Shiner	0.63 (0.06)	0.40 (0.05)	-
Catostomidae			
Largescale Sucker			
Juvenile	0.57 (0.07)	0.10 (0.03)	0.02 (0.02)
Adult	0.87 (0.03)	-	-
Longnose Sucker			
Juvenile	0.36 (0.11)	0.07 (0.04)	-
Adult	0.39 (0.09)	0.01 (0.01)	-
Ictaluridae			
Brown Bullhead	0.05 (0.04)	0.14 (0.08)	-
Salmonidae			
Cutthroat Trout			
Adult	0.08 (0.03)	-	-
Kokanee			
Juvenile	0.44 (0.09)	-	0.01 (0.02)
Adult	0.29 (0.13)	-	-
Mountain Whitefish			
Juvenile	0.57 (0.05)	0.03 (0.01)	0.38 (0.05)
Adult	0.68 (0.05)	0.01 (0.01)	0.01 (0.01)
Rainbow Trout			
Juvenile	0.43 (0.14)	-	-
Adult	0.24 (0.09)	0.02 (0.02)	-
Gadidae			
Burbot			
Adult	-	0.12 (0.03)	-
Cottidae			
Torrent Sculpin	0.55 (0.05)	0.11 (0.03)	0.02 (0.02)
Centrarchidae			
Pumpkinseed	0.26 (0.12)	0.05 (0.03)	-
Percidae			
Yellow Perch	0.40 (0.14)	0.07 (0.05)	-

Table 2.2 cont'd.

Kootenai River – Fall			
Cyprinidae			
Northern Pikeminnow			
Juvenile	0.71 (0.33)	0.49 (0.35)	-
Adult	0.37 (0.12)	0.21 (0.10)	-
Peamouth			
Juvenile	1.00 (NA)	0.13 (0.12)	-
Adult	0.33 (0.13)	0.05 (0.05)	-
Redside Shiner	0.63 (0.10)	0.29 (0.10)	0.04 (0.04)
Catostomidae			
Largescale Sucker			
Juvenile	0.58 (0.10)	-	0.08 (0.06)
Adult	0.79 (0.08)	-	-
Longnose Sucker			
Juvenile	0.67 (0.22)	-	-
Adult	0.53 (0.29)	-	-
Ictaluridae			
Brown Bullhead	0.25 (0.16)	0.12 (0.10)	-
Salmonidae			
Kokanee			
Adult	0.08 (0.06)	-	-
Mountain Whitefish			
Juvenile	0.72 (0.11)	-	0.24 (0.10)
Adult	1.00 (NA)	-	0.20 (0.24)
Rainbow Trout			
Juvenile	0.36 (0.21)	-	0.09 (0.09)
Adult	0.45 (0.11)	0.30 (0.10)	-
Gadidae			
Burbot			
Juvenile	0.04 (0.03)	0.04 (0.03)	-
Cottidae			
Slimy Sculpin	0.63 (0.18)	-	0.09 (0.09)
Torrent Sculpin	0.83 (0.07)	-	0.21 (0.08)
Centrarchidae			
Largemouth Bass			
Juvenile	0.53 (0.29)	-	-
Pumpkinseed	0.80 (0.14)	0.22 (0.13)	0.04 (0.06)
Percidae			
Yellow Perch	0.34 (0.25)	-	0.11 (0.12)

Table 2.3. Candidate models investigating the effect of sample- and site-scale habitat characteristics on detection probabilities ($\hat{p}$) for fishes in the Kootenai and Green rivers. Probability of occupancy ($\hat{\psi}$) was included with each model. Only occupancy models for large-bodied species were separated by life history stage (i.e., juvenile, adult). Akaike's Information Criterion (AIC$_c$) or quasi-Akaike's Information Criterion (QAIC$_c$) adjusted for small sample size was used to rank candidate models. Total number of parameters (*K*), model weight (w_i), and two times the log-likelihood (*-2Log(l)*) are included. The global model or model with the best fit (models with only single habitat covariates due to small sample size) out of each candidate set is italicized. Model fit was evaluated with the variance inflation factor ($\hat{c}$). Candidate models for juvenile Peamouth in the fall season of the Kootenai River did not converge on maximum likelihood estimates and are not included. Direction of effect for each habitat covariate is also indicated (positive [+], negative [-]). An asterisk next to a species name or life history stage indicates collection with only one technique in the season and system.

Taxa and life history stage	Model name	AIC$_c$ or QAIC$_c$	Δ AIC$_c$ or QAIC$_c$	*K*	w_i	*-2Log(l)*	$\hat{c}$
	Green River – Summer						
Cyprinidae							
Common Carp							
Adult*	$\hat{\psi}(., -\mathrm{Vel}_{\mathrm{Avg}}), \hat{p}(., -\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}})$	45.88	0.00	4	0.49	36.14	
	$\hat{\psi}(., -Vel_{Avg}), \hat{p}(., +Depth, +Temp, +Vel_{Avg})$	50.94	5.06	6	0.08	34.94	0.94
Longnose Dace							
	$\hat{\psi}(.), \hat{p}(\mathrm{Gear}, -\mathrm{Depth}, +\mathrm{Vel}_{\mathrm{Sub}})$	255.22	0.00	6	0.32	239.22	
	$\hat{\psi}(.), \hat{p}(Gear, -Clarity, -Depth, +Vel_{Sub})$	256.06	0.84	7	0.21	236.46	0.18
Utah Chub*							
	$\hat{\psi}(., -\mathrm{Depth}), \hat{p}(.)$	35.54	0.00	3	0.34	28.54	
	$\hat{\psi}(., -\mathrm{Depth}), \hat{p}(., -\mathrm{Vel}_{\mathrm{Avg}})$	35.82	0.28	4	0.30	26.08	
	$\hat{\psi}(., -\mathrm{Depth}), \hat{p}(., +\mathrm{Clarity})$	36.23	0.69	4	0.24	26.49	
	$\hat{\psi}(., -Depth), \hat{p}(., -Vel_{Avg}, +CV_{Vel})$	38.75	3.21	5	0.07	26.02	0.65

Table 2.3 cont'd.

Catostomidae							
Flannelmouth Sucker							
Adult	$\hat{\psi}(., \text{-Substrate}_{\text{Co-Bo}}), \hat{p}(\text{Gear})$	61.62	0.00	4	0.40	51.88	
	$\hat{\psi}(., \textit{-Substrate}_{\textit{Co-Bo}}), \hat{p}(\textit{Gear, +Clarity, -CV}_{\textit{Vel}})$	66.72	5.10	6	0.04	50.72	0.51
Catostomidae							
White Sucker							
Juvenile	$\hat{\psi}(., \text{+CV}_{\text{Vel}}), \hat{p}(\text{Gear})$	167.62	0.00	5	0.33	154.89	
	$\hat{\psi}(., \text{+CV}_{\text{Vel}}), \hat{p}(\text{Gear, +Substrate}_{\text{Co-Bo}})$	168.87	1.25	6	0.18	152.87	
	$\hat{\psi}(., \textit{+CV}_{\textit{Vel}}), \hat{p}(\textit{Gear, +Depth, -Vel}_{\textit{Avg}})$	174.25	6.63	7	0.01	154.65	0.19
Adult	$\hat{\psi}(.), \hat{p}(\text{Gear, -Clarity, -Clarity}_{\text{Max}})$	204.93	0.00	6	0.81	188.93	
	$\hat{\psi}(.), \hat{p}(\textit{Gear, -Clarity, -Depth, -Vel}_{\textit{Avg}})$	218.96	14.03	7	0.00	199.36	0.31
Salmonidae							
Brown Trout							
Juvenile	$\hat{\psi}(., \text{-CV}_{\text{Vel}}), \hat{p}(\text{Gear})$	57.14	0.00	5	0.39	130.42	
	$\hat{\psi}(., \textit{-CV}_{\textit{Vel}}), \hat{p}(\textit{Gear, +CV}_{\textit{Vel}}\textit{, -Substrate}_{\textit{Co-Bo}}\textit{, +Vel}_{\textit{Avg}})$	68.29	11.15	9	0.00	127.71	3.17
Adult	$\hat{\psi}(., \text{-Substrate}_{\text{Co-Bo}}), \hat{p}(\text{Gear})$	134.51	0.00	5	0.36	121.78	
	$\hat{\psi}(., \text{-Substrate}_{\text{Co-Bo}}), \hat{p}(\text{Gear, -Vel}_{\text{Avg}})$	135.35	0.84	6	0.24	119.35	
	$\hat{\psi}(., \textit{-Substrate}_{\textit{Co-Bo}}), \hat{p}(\textit{Gear, -CV}_{\textit{Vel}}\textit{, -Depth, -Vel}_{\textit{Avg}})$	142.83	8.32	8	0.01	119.25	0.24
Cutthroat Trout							
Juvenile	$\hat{\psi}(.), \hat{p}(., \text{+Temp})$	50.59	0.00	3	0.34	43.59	
	$\hat{\psi}(.), \hat{p}(.)$	52.42	1.83	2	0.14	47.94	
	$\hat{\psi}(.), \hat{p}(., \textit{+Depth, -Substrate}_{\textit{Co-Bo}}\textit{, +Temp})$	55.22	4.63	5	0.03	42.49	0.01

Table 2.3 cont'd.

Salmonidae							
Cutthroat Trout							
Adult	$\hat{\psi}(.), \hat{p}(\mathrm{Gear})$	132.70	0.00	4	0.31	122.96	
	$\hat{\psi}(.), \hat{p}(Gear, -Clarity, -CV_{Vel}, -Depth)$	142.09	9.39	7	0.01	122.49	0.05
Mountain Whitefish							
Juvenile	$\hat{\psi}(., +\mathrm{Vel}_{\mathrm{Avg}}), \hat{p}(., +\mathrm{Temp})$	186.52	0.00	4	0.20	176.78	
	$\hat{\psi}(., +\mathrm{Vel}_{\mathrm{Avg}}), \hat{p}(., -\mathrm{CV}_{\mathrm{Vel}})$	187.07	0.55	4	0.16	177.33	
	$\hat{\psi}(., +\mathrm{Vel}_{\mathrm{Avg}}), \hat{p}(.)$	187.37	0.85	3	0.13	180.37	
	$\hat{\psi}(., +\mathrm{Vel}_{\mathrm{Avg}}), \hat{p}(., +\mathrm{Vel}_{\mathrm{Avg}})$	187.86	1.34	4	0.10	178.12	
	$\hat{\psi}(., +Vel_{Avg}), \hat{p}(., -Depth, +Substrate_{Co\text{-}Bo}, +Temp)$	189.76	3.24	6	0.04	173.76	0.24
Adult	$\hat{\psi}(., +\mathrm{Vel}_{\mathrm{Sub}}), \hat{p}(\mathrm{Gear}, -\mathrm{Temp})$	129.46	0.00	5	0.98	116.73	
	$\hat{\psi}(., +Vel_{Sub}), \hat{p}(Gear, +CV_{Vel}, +Substrate_{Co\text{-}Bo})$	139.73	10.27	6	0.01	123.73	0.11
Rainbow Trout							
Juvenile	$\hat{\psi}(.), \hat{p}(\mathrm{Gear}, +\mathrm{Vel}_{\mathrm{Avg}})$	146.92	0.00	5	0.31	134.19	
	$\hat{\psi}(.), \hat{p}(\mathrm{Gear}, -\mathrm{CV}_{\mathrm{Vel}})$	147.47	0.55	5	0.23	134.74	
	$\hat{\psi}(.), \hat{p}(Gear, -CV_{Vel}, -Depth, +Vel_{Avg})$	152.30	5.11	7	0.02	132.43	0.53
Adult	$\hat{\psi}(., +\mathrm{CV}_{\mathrm{Vel}}), \hat{p}(\mathrm{Gear})$	171.22	0.00	5	0.29	158.49	
	$\hat{\psi}(., +\mathrm{CV}_{\mathrm{Vel}}), \hat{p}(\mathrm{Gear}, -\mathrm{Temp})$	173.09	1.87	6	0.11	157.09	
	$\hat{\psi}(., +CV_{Vel}), \hat{p}(Gear, -Clarity, -CV_{Vel}, -Depth)$	180.59	9.37	8	0.00	157.01	0.29

Table 2.3 cont'd.

Gadidae							
Burbot							
Juvenile	$\hat{\psi}(.,\ -\mathrm{Vel}_{\mathrm{Sub}}),\ \hat{p}(.)$	36.32	0.00	3	0.18	29.32	
	$\hat{\psi}(.,\ -\mathrm{Vel}_{\mathrm{Sub}}),\ \hat{p}(.,\ +\mathrm{Temp})$	37.12	0.80	4	0.12	27.38	
	$\hat{\psi}(.,\ -\mathrm{Vel}_{\mathrm{Sub}}),\ \hat{p}(.,\ -\mathrm{Vel}_{\mathrm{Sub}})$	37.32	1.00	4	0.11	27.58	
	$\hat{\psi}(.,\ -Vel_{Sub}),\ \hat{p}(.,\ +CV_{Vel},\ +Depth,\ +Temp)$	41.19	4.87	6	0.01	25.19	0.87
Adult	$\hat{\psi}(.),\ \hat{p}(\mathrm{Gear})$	40.57	0.00	3	0.32	168.02	
	$\hat{\psi}(.),\ \hat{p}(\mathrm{Gear},\ -\mathrm{Vel}_{\mathrm{Sub}})$	40.05	1.48	4	0.15	159.81	
	$\hat{\psi}(.),\ \hat{p}(Gear,\ -Vel_{Sub},\ +Temp)$	45.15	4.58	6	0.03	158.86	5.45
Cottidae							
Mottled Sculpin							
	$\hat{\psi}(.),\ \hat{p}(\mathrm{Gear},\ -\mathrm{Q})$	162.28	0.00	5	0.43	149.55	
	$\hat{\psi}(.),\ \hat{p}(\mathrm{Gear},\ -\mathrm{Vel}_{\mathrm{Sub}})$	163.30	1.02	5	0.26	150.57	
	$\hat{\psi}(.),\ \hat{p}(Gear,\ -Clarity,\ +Substrate_{Co\text{-}Bo},\ -Vel_{Sub})$	166.41	4.13	7	0.07	146.44	0.12
	Kootenai - Summer						
Cyprinidae							
Northern Pikeminnow							
Juvenile	$\hat{\psi}(.),\ \hat{p}(\mathrm{Gear},\ +\mathrm{Depth},\ -\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}})$	216.44	0.00	5	0.51	202.11	
	$\hat{\psi}(.),\ \hat{p}(\mathrm{Gear},\ -\mathrm{Q},\ -\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}})$	217.04	0.60	5	0.38	202.71	
	$\hat{\psi}(.),\ \hat{p}(Gear,\ -Clarity,\ -CV_{Vel},\ +Depth)$	220.51	4.07	7	0.07	203.31	0.45
Adult	$\hat{\psi}(.,\ -\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}),\ \hat{p}(\mathrm{Gear},\ -\mathrm{CV}_{\mathrm{Vel}})$	258.75	0.00	5	0.73	247.13	
	$\hat{\psi}(.,\ -Substrate_{Co\text{-}Bo}),\ \hat{p}(Gear,\ -Clarity,\ -CV_{Vel},\ -Depth)$	264.17	5.42	7	0.05	246.97	0.90

Table 2.3 cont'd.

Cyprinidae							
Peamouth							
Juvenile	$\hat{\psi}(.,\ +\text{Depth}),\ \hat{p}(\text{Gear})$	18.32	0.00	4	0.32	156.94	
	$\hat{\psi}(.,\ +Depth),\ \hat{p}(Gear,\ -Clarity,\ +Depth,\ +Bank_{Veg})$	26.48	8.16	8	0.01	146.20	23.43
Adult*	$\hat{\psi}(.,\ -Substrate_{Co\text{-}Bo}),\ \hat{p}(.,\ +Depth,\ +Q,\ +Bank_{Veg})$	76.06	0.00	7	0.75	68.87	1.17
Redside Shiner							
	$\hat{\psi}(.),\ \hat{p}(\text{Gear})$	233.64	0.00	3	0.32	303.19	
	$\hat{\psi}(.),\hat{p}(Gear,\ +Bank_{Bo},\ -CV_{Vel},\ -Q)$	241.16	7.52	7	0.01	302.35	1.32
Catostomidae							
Largescale Sucker							
Juvenile	$\hat{\psi}(.),\ \hat{p}(\text{Gear},\ +\text{Q})$	223.95	0.00	5	0.42	212.33	
	$\hat{\psi}(.),\ \hat{p}(Gear,\ +Clarity,\ -CV_{Vel},\ +Depth)$	230.81	6.85	7	0.03	213.60	0.60
Adult	$\hat{\psi}(.,\ +\text{Bank}_{\text{Veg}}),\ \hat{p}(.,\ -\text{Depth},\ +\text{Bank}_{\text{Veg}})$	91.91	0.00	5	0.50	80.29	
	$\hat{\psi}(.,\ +\text{Bank}_{\text{Veg}}),\ \hat{p}(.,\ +\text{VegBank})$	93.74	1.83	4	0.20	84.69	
	$\hat{\psi}(.,\ +Bank_{Veg}),\ \hat{p}(.,\ +Q,\ -Depth,\ +Bank_{Veg})$	93.82	1.91	6	0.20	79.49	0.78

Table 2.3 cont'd.

Catostomidae							
Longnose Sucker							
Juvenile	$\hat{\psi}(.), \hat{p}(\text{Gear, -Clarity})$	114.78	0.00	4	0.20	105.73	
	$\hat{\psi}(.), \hat{p}(\text{Gear})$	115.20	0.42	3	0.16	108.58	
	$\hat{\psi}(.), \hat{p}(\text{Gear, +Q})$	115.97	1.19	4	0.11	106.92	
	$\hat{\psi}(.), \hat{p}(\text{Gear, -Temp})$	116.25	1.47	4	0.10	107.20	
	$\hat{\psi}(.), \hat{p}(\text{Gear, -Substrate}_{\text{Co-Bo}})$	116.78	2.00	4	0.08	107.73	
	$\hat{\psi}(.), \hat{p}(Gear, -Depth, +Q, -Bank_{Veg})$	121.00	6.22	6	0.01	106.67	0.76
Adult	$\hat{\psi}(.), \hat{p}(\text{Gear, -Clarity})$	113.60	0.00	4	0.25	127.47	
	$\hat{\psi}(.), \hat{p}(\text{Gear})$	113.92	0.32	3	0.21	131.09	
	$\hat{\psi}(.), \hat{p}(\text{Gear, -Bank}_{\text{Veg}})$	115.23	1.63	4	0.11	129.51	
	$\hat{\psi}(.), \hat{p}(\text{Gear, -Substrate}_{\text{Co-Bo}})$	115.34	1.74	4	0.10	129.65	
	$\hat{\psi}(.), \hat{p}(\text{Gear, +Depth})$	115.41	1.81	4	0.10	129.73	
	$\hat{\psi}(.), \hat{p}(Gear, -Clarity, +CV_{Vel}, +Depth)$	117.77	4.17	7	0.03	128.50	1.25
Ictaluridae							
Brown Bullhead							
	$\hat{\psi}(\text{., +CV}_{\text{Vel}}), \hat{p}(.)$	71.62	0.00	3	0.23	65.00	
	$\hat{\psi}(\text{., +CV}_{\text{Vel}}), \hat{p}(\text{., +Substrate}_{\text{Co-Bo}})$	72.05	0.43	4	0.19	63.00	
	$\hat{\psi}(\text{., +CV}_{\text{Vel}}), \hat{p}(\text{., -Depth})$	73.09	1.47	4	0.11	64.04	
	$\hat{\psi}(\text{., +CV}_{\text{Vel}}), \hat{p}(\text{., +Bank}_{\text{Bo}})$	73.25	1.63	4	0.10	64.20	
	$\hat{\psi}(., +CV_{Vel}), \hat{p}(., -CV_{Vel}, +Depth, +Substrate_{Co-Bo})$	76.82	5.20	6	0.02	62.49	0.53

Table 2.3 cont'd.

Salmonidae						
Cutthroat Trout						
Adult*	$\hat{\psi}(., -\mathrm{Bank}_{\mathrm{Veg}}), \hat{p}(.)$	48.60	0.00	3	0.23	41.98	
	$\hat{\psi}(., -\mathrm{Bank}_{\mathrm{Veg}}), \hat{p}(., -\mathrm{Clarity})$	49.39	0.79	4	0.15	40.34	
	$\hat{\psi}(., -\mathrm{Bank}_{\mathrm{Veg}}), \hat{p}(., +\mathrm{Depth})$	49.87	1.27	4	0.12	40.82	
	$\hat{\psi}(., -\mathrm{Bank}_{\mathrm{Veg}}), \hat{p}(., -\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}})$	50.27	1.67	4	0.10	41.22	
	$\hat{\psi}(., -\mathrm{Bank}_{\mathrm{Veg}}), \hat{p}(., -\mathrm{CV}_{\mathrm{Vel}})$	50.29	1.69	4	0.09	41.24	
	$\hat{\psi}(., -\mathrm{Bank}_{\mathrm{Veg}}), \hat{p}(., +\mathrm{Q})$	50.54	1.94	4	0.08	41.49	
	$\hat{\psi}(., -\mathit{Bank}_{\mathit{Veg}}), \hat{p}(., -\mathit{Clarity}, +\mathit{Depth}, +\mathit{Bank}_{\mathit{Veg}})$	54.40	5.80	6	0.01	40.07	0.80
Kokanee						
Juvenile	$\hat{\psi}(., -\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}), \hat{p}(\mathrm{Gear})$	114.61	0.00	4	0.39	128.73	
	$\hat{\psi}(., -\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}), \hat{p}(\mathrm{Gear}, -\mathrm{Bank}_{\mathrm{Veg}})$	116.51	1.90	5	0.15	127.72	
	$\hat{\psi}(., -\mathit{Substrate}_{\mathit{Co\text{-}Bo}}), \hat{p}(\mathit{Gear}, +\mathit{CV}_{\mathit{Vel}}, +\mathit{Depth}, -\mathit{Bank}_{\mathit{Veg}})$	121.88	7.27	8	0.01	127.06	1.15
Adult*	$\hat{\psi}(., +\mathit{Substrate}_{\mathit{Co\text{-}Bo}}), \hat{p}(., -\mathit{Clarity}, -\mathit{CV}_{\mathit{Vel}}, -\mathit{Depth})$	81.56	0.00	7	0.22	73.37	1.14
	$\hat{\psi}(., +\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}), \hat{p}(.)$	81.65	0.09	3	0.21	82.76	
	$\hat{\psi}(., +\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}), \hat{p}(., +\mathrm{Bank}_{\mathrm{Bo}})$	81.74	0.18	4	0.20	79.94	
	$\hat{\psi}(., +\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}), \hat{p}(., +\mathrm{Q})$	83.18	1.62	4	0.10	81.58	
	$\hat{\psi}(., +\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}), \hat{p}(., -\mathrm{CV}_{\mathrm{Vel}})$	83.31	1.75	4	0.09	81.72	
	$\hat{\psi}(., +\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}), \hat{p}(., -\mathrm{Clarity})$	83.53	1.97	4	0.08	81.97	
Mountain Whitefish						
Juvenile	$\hat{\psi}(.), \hat{p}(\mathrm{Gear})$	338.06	0.00	4	0.24	329.01	
	$\hat{\psi}(.), \hat{p}(\mathit{Gear}, -\mathit{Depth}, +\mathit{Q}, -\mathit{Substrate}_{\mathit{Co\text{-}Bo}})$	344.82	6.76	7	0.01	327.62	0.66

Table 2.3 cont'd.

Salmonidae							
Mountain Whitefish							
Adult	$\hat{\psi}(.), \hat{p}(\text{Gear}, +\text{Clarity}, -\text{Depth})$	156.94	0.00	6	0.34	142.61	
	$\hat{\psi}(.), \hat{p}(\text{Gear}, -\text{Depth})$	158.05	1.11	5	0.19	146.43	
	$\hat{\psi}(.), \hat{p}(\text{Gear}, -\text{Depth}, +\text{Substrate}_{\text{Co-Bo}})$	158.74	1.80	6	0.14	144.41	
	$\hat{\psi}(.), \hat{p}(\mathit{Gear}, -\mathit{Bank}_{Bo}, +\mathit{Clarity}, -\mathit{Depth})$	159.56	2.62	7	0.10	142.14	0.64
Rainbow Trout							
Juvenile*	$\hat{\psi}(., -\text{Substrate}_{\text{Co-Bo}}), \hat{p}(., +\text{Q})$	85.04	0.00	4	0.23	85.16	
	$\hat{\psi}(., -\text{Substrate}_{\text{Co-Bo}}), \hat{p}(.)$	85.87	0.83	3	0.15	89.11	
	$\hat{\psi}(., -\text{Substrate}_{\text{Co-Bo}}), \hat{p}(., +\text{Bank}_{\text{Bo}}, +\text{Q})$	86.92	1.88	5	0.09	84.20	
	$\hat{\psi}(., -\mathit{Substrate}_{Co\text{-}Bo}), \hat{p}(., +\mathit{Bank}_{Bo}\ +\mathit{Depth}, +\mathit{Q})$	89.42	4.38	7	0.03	83.78	1.16
Adult	$\hat{\psi}(.),\hat{p}(\text{Gear}, -\text{Clarity}, -\text{Depth})$	143.64	0.00	5	0.25	132.02	
	$\hat{\psi}(.),\hat{p}(\mathit{Gear}, -\ \mathit{Bank}_{Bo}, -\mathit{Clarity}, -\mathit{Depth})$	144.05	0.41	6	0.20	129.72	0.90
Gadidae							
Burbot							
Adult*	$\hat{\psi}(., +\text{Depth}), \hat{p}(.)$	73.87	0.00	3	0.38	73.89	
	$\hat{\psi}(., +\text{Depth}), \hat{p}(., +\text{Bank}_{\text{Veg}})$	74.84	0.97	4	0.24	72.07	
	$\hat{\psi}(., +\text{Depth}), \hat{p}(., -\text{Q})$	75.81	1.94	4	0.15	73.18	
	$\hat{\psi}(., +\mathit{Depth}), \hat{p}(., +\mathit{Depth}, -\mathit{Substrate}_{Co\text{-}Bo}, +\mathit{Temp})$	82.44	8.57	7	0.01	74.37	1.14

Table 2.3 cont'd.

Cottidae							
Torrent Sculpin							
	$\hat{\psi}$(.), $\hat{p}$(Gear, -CV$_{Vel}$)	209.43	0.00	5	0.24	196.93	
	$\hat{\psi}$(.), $\hat{p}$(Gear)	209.86	0.43	4	0.20	200.26	
	$\hat{\psi}$(.), $\hat{p}$(Gear, -Substrate$_{Co\text{-}Bo}$)	210.65	1.22	5	0.13	198.15	
	$\hat{\psi}$(.), $\hat{p}$(Gear, +Depth)	210.95	1.52	5	0.11	198.45	
	$\hat{\psi}$(.), $\hat{p}$(Gear, +Bank$_{Bo}$, +Clarity, +Depth)	216.78	7.35	7	0.01	197.69	0.72
Centrarchidae							
Pumpkinseed							
	$\hat{\psi}$(.), $\hat{p}$(Gear)	85.93	0.00	3	0.26	117.63	
	$\hat{\psi}$(.), $\hat{p}$(Gear, -Bank$_{Veg}$)	87.54	1.61	4	0.12	116.16	
	$\hat{\psi}$(.), $\hat{p}$(Gear, -Clarity)	87.62	1.69	4	0.11	116.27	
	$\hat{\psi}$(.), $\hat{p}$(Gear, -CV$_{Vel}$, -Depth, -Substrate$_{Co\text{-}Bo}$)	93.53	7.60	7	0.01	116.79	1.53
Percidae							
Yellow Perch							
	$\hat{\psi}$(.), $\hat{p}$(Gear)	90.41	0.00	3	0.25	83.79	
	$\hat{\psi}$(.), $\hat{p}$(Gear, -Clarity)	91.21	0.80	4	0.17	82.16	
	$\hat{\psi}$(.), $\hat{p}$(Gear, +Depth)	92.05	1.64	4	0.11	83.00	
	$\hat{\psi}$(.), $\hat{p}$(Gear, -Substrate$_{Co\text{-}Bo}$)	92.33	1.92	4	0.10	83.28	
	$\hat{\psi}$(.), $\hat{p}$(Gear, +Bank$_{Veg}$)	92.36	1.95	4	0.09	83.31	
	$\hat{\psi}$(.), $\hat{p}$(Gear, -Q)	92.38	1.97	4	0.09	83.67	
	$\hat{\psi}$(.), $\hat{p}$(Gear, -Clarity, -CV$_{Vel}$, +Depth)	95.92	5.51	6	0.01	81.59	0.79

Table 2.3 cont'd.

	Kootenai River - Fall						
Cyprinidae							
Northern Pikeminnow							
Juvenile	$\hat{\psi}(.), \hat{p}(., -Vel_{Sub})$	65.87	0.00	3	0.49	56.44	0.69
	$\hat{\psi}(.), \hat{p}(., +\mathrm{Depth})$	66.16	0.29	3	0.43	56.73	
Adult	$\hat{\psi}(., +\mathrm{Vel}_{\mathrm{Avg}}), \hat{p}(.)$	58.97	0.00	3	0.49	49.54	
	$\hat{\psi}(., +Vel_{Avg}), \hat{p}(., -Depth, +Q)$	68.03	9.06	5	0.01	46.03	0.64
Peamouth							
Adult	$\hat{\psi}(., -\mathrm{Vel}_{\mathrm{Avg}}), \hat{p}(\mathrm{Gear})$	51.61	0.00	4	0.89	36.94	
	$\hat{\psi}(., -Vel_{Avg}), \hat{p}(Gear, -Clarity, -CV_{Vel})$	68.49	16.88	6	0.01	35.49	0.21
Redside Shiner							
	$\hat{\psi}(.), \hat{p}(\mathrm{Gear})$	83.71	0.00	2	0.78	69.04	
	$\hat{\psi}(.), \hat{p}(Gear, +Bank_{Bo})$	88.54	4.83	5	0.07	66.54	0.73
Catostomidae							
Largescale Sucker							
Juvenile	$\hat{\psi}(.), \hat{p}(\mathrm{Gear})$	45.94	0.00	3	0.62	46.37	
	$\hat{\psi}(.), \hat{p}(Gear, -Depth, -Vel_{Avg})$	56.09	10.15	6	0.01	43.30	1.02
Adult*	$\hat{\psi}(.), \hat{p}(.)$	18.70	0.00	2	0.63	24.56	
	$\hat{\psi}(.), \hat{p}(., -Depth, +Vel_{Avg})$	28.35	9.65	5	0.01	16.83	2.65
Longnose Sucker							
Juvenile	$\hat{\psi}(., -\mathrm{Vel}_{\mathrm{Sub}}), \hat{p}(.)$	27.20	0.00	3	0.48	17.77	
	$\hat{\psi}(., -Vel_{Sub}), \hat{p}(., -CV_{Vel})$	28.80	1.60	4	0.22	14.13	0.82

Table 2.3 cont'd.

Catostomidae							
Longnose Sucker							
Adult*	$\hat{\psi}(.), \hat{p}(.)$	25.16	0.00	2	0.41	19.66	
	$\hat{\psi}(.), \hat{p}(., -Q)$	26.55	1.39	3	0.21	17.12	0.06
Ictaluridae							
Brown Bullhead							
	$\hat{\psi}(.), \hat{p}(.)$	41.24	0.00	2	0.29	35.74	
	$\hat{\psi}(.), \hat{p}(., +\text{Clarity})$	42.05	0.81	3	0.20	32.62	
	$\hat{\psi}(.), \hat{p}(., -\text{CV}_{\text{Vel}})$	42.17	0.93	4	0.19	32.74	
	$\hat{\psi}(.), \hat{p}(., +\text{Depth})$	43.24	2.00	4	0.10	33.81	
	$\hat{\psi}(.), \hat{p}(., +Clarity, -CV_{Vel})$	45.51	4.27	4	0.04	30.84	0.83
Salmonidae							
Kokanee							
Adult*	$\hat{\psi}(.), \hat{p}(.)$	19.27	0.00	2	0.50	13.77	
	$\hat{\psi}(.), \hat{p}(., +Vel_{Avg})$	19.60	0.33	3	0.43	10.17	0.92
Mountain Whitefish							
Juvenile	$\hat{\psi}(.), \hat{p}(Gear, +Q)$	59.86	0.00	4	0.82	45.19	0.35
Adult	$\hat{\psi}(., -\text{Depth}), \hat{p}(.)$	40.22	0.00	3	0.77	30.79	
	$\hat{\psi}(., -Depth), \hat{p}(., -Substrate_{Co\text{-}Bo})$	44.37	4.15	4	0.10	29.70	0.95

Table 2.3 cont'd.

Salmonidae							
Rainbow Trout							
Juvenile	$\hat{\psi}(.), \hat{p}(., +Substrate_{Co\text{-}Bo})$	34.25	0.00	3	0.42	24.82	0.92
	$\hat{\psi}(.), \hat{p}(., +\mathrm{Vel}_{\mathrm{Avg}})$	35.59	1.34	3	0.22	26.16	
	$\hat{\psi}(.), \hat{p}(.)$	36.22	1.97	2	0.16	30.72	
Adult	$\hat{\psi}(., -\mathrm{CV}_{\mathrm{Vel}}), \hat{p}(.)$	64.60	0.00	3	0.62	52.93	
	$\hat{\psi}(., -CV_{Vel}), \hat{p}(., +Substrate_{Co\text{-}Bo})$	66.30	1.70	5	0.26	46.96	1.06
Gadidae							
Burbot							
Juvenile	$\hat{\psi}(.), \hat{p}(., +Vel_{Sub})$	21.59	0.00	3	0.49	12.16	0.47
	$\hat{\psi}(.), \hat{p}(.)$	22.13	0.54	2	0.37	16.63	
Cottidae							
Slimy Sculpin							
	$\hat{\psi}(.), \hat{p}(\mathrm{Gear})$	39.35	0.00	3	0.63	33.10	
	$\hat{\psi}(.), \hat{p}(Gear, +Clarity, -Vel_{Sub})$	51.37	8.84	5	0.01	29.37	0.28
Torrent Sculpin							
	$\hat{\psi}(.), \hat{p}(\mathrm{Gear})$	55.62	0.00	3	0.71	46.19	
	$\hat{\psi}(.), \hat{p}(Gear, -Bank_{Bo})$	59.25	3.63	4	0.12	44.58	0.15
Centrarchidae							
Largemouth Bass							
Juvenile*	$\hat{\psi}(.), \hat{p}(., -Vel_{Avg})$	22.70	0.00	3	0.54	13.27	0.19

Table 2.3 cont'd.

Centrarchidae							
Pumpkinseed							
	$\hat{\psi}(.), \hat{p}(\text{Gear})$	26.84	0.00	4	0.98	58.89	
	$\hat{\psi}(.), \hat{p}(Gear, -Bank_{Bo})$	37.32	10.48	6	0.01	52.56	12.17
Percidae							
Yellow Perch							
	$\hat{\psi}(.), \hat{p}(., -Vel_{Sub})$	31.61	0.00	3	0.32	22.18	0.89
	$\hat{\psi}(.), \hat{p}(.)$	31.99	0.38	2	0.26	26.49	
	$\hat{\psi}(.), \hat{p}(., -\text{Substrate}_{\text{Co-Bo}})$	32.27	0.66	4	0.23	22.84	

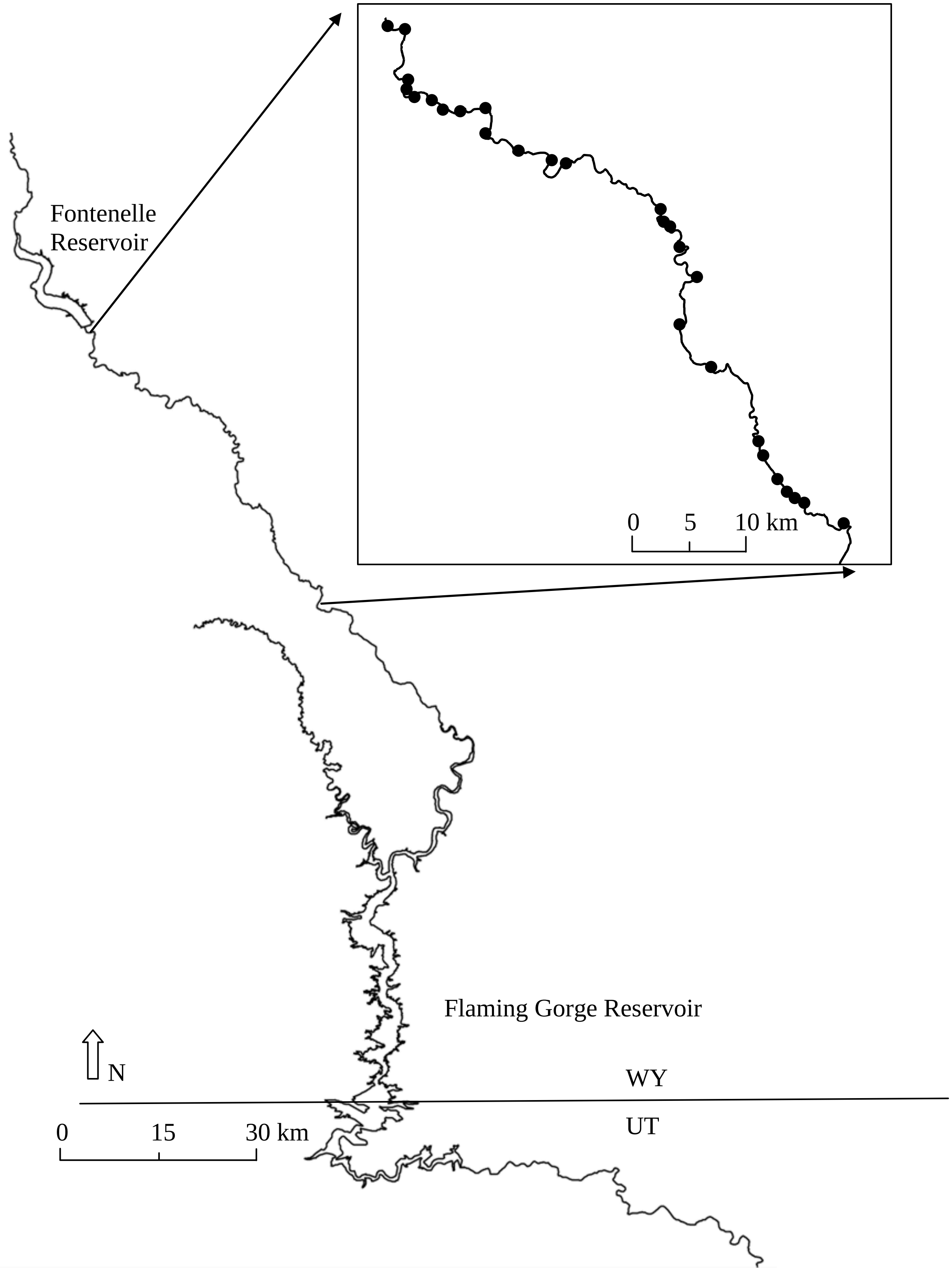

Figure 2.1. Reaches in the Green River (black circles) sampled in 2012 and 2013.

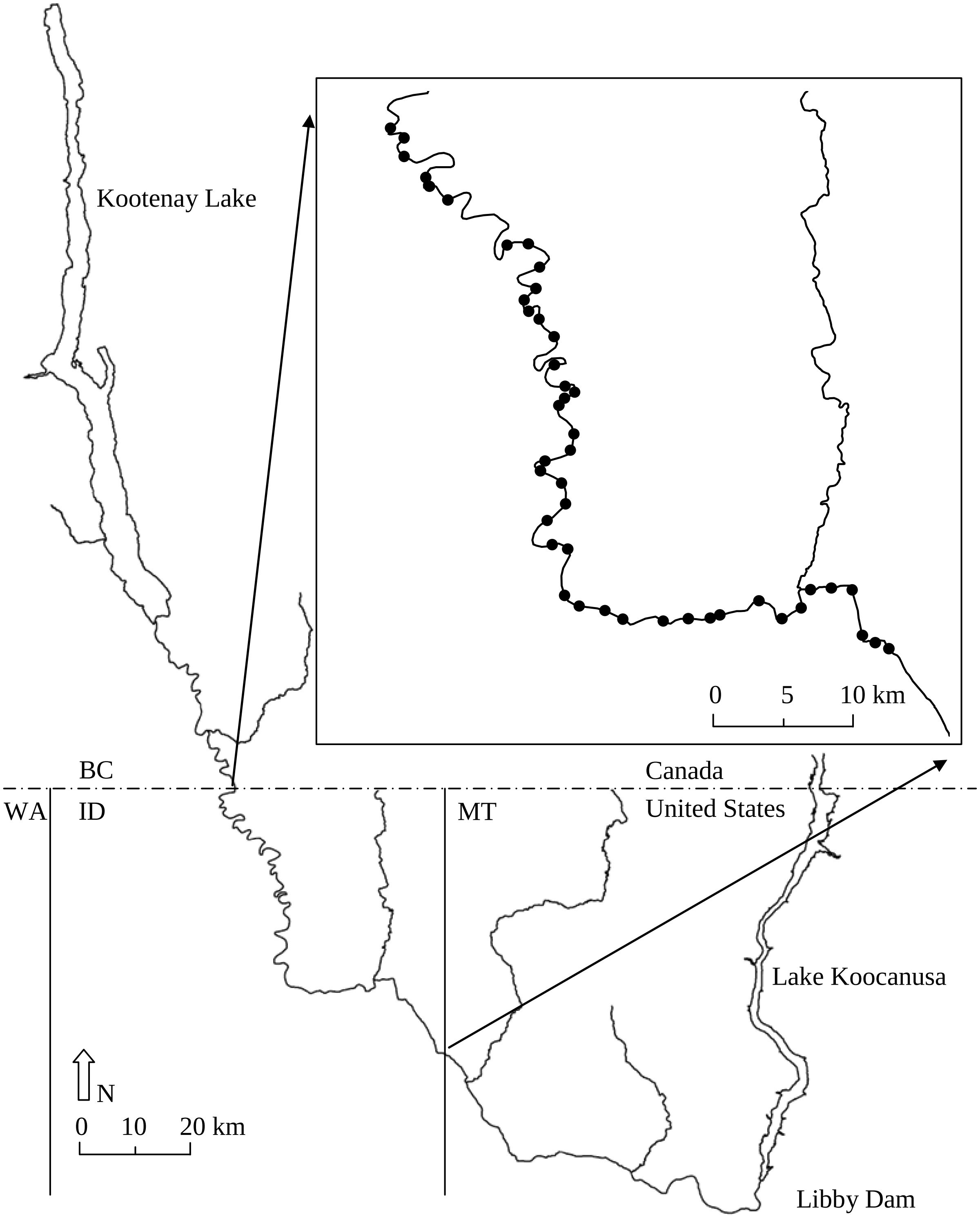

Figure 2.2. Reaches surveyed in the Kootenai River in the summer (2012 and 2013) and fall (2012) seasons.

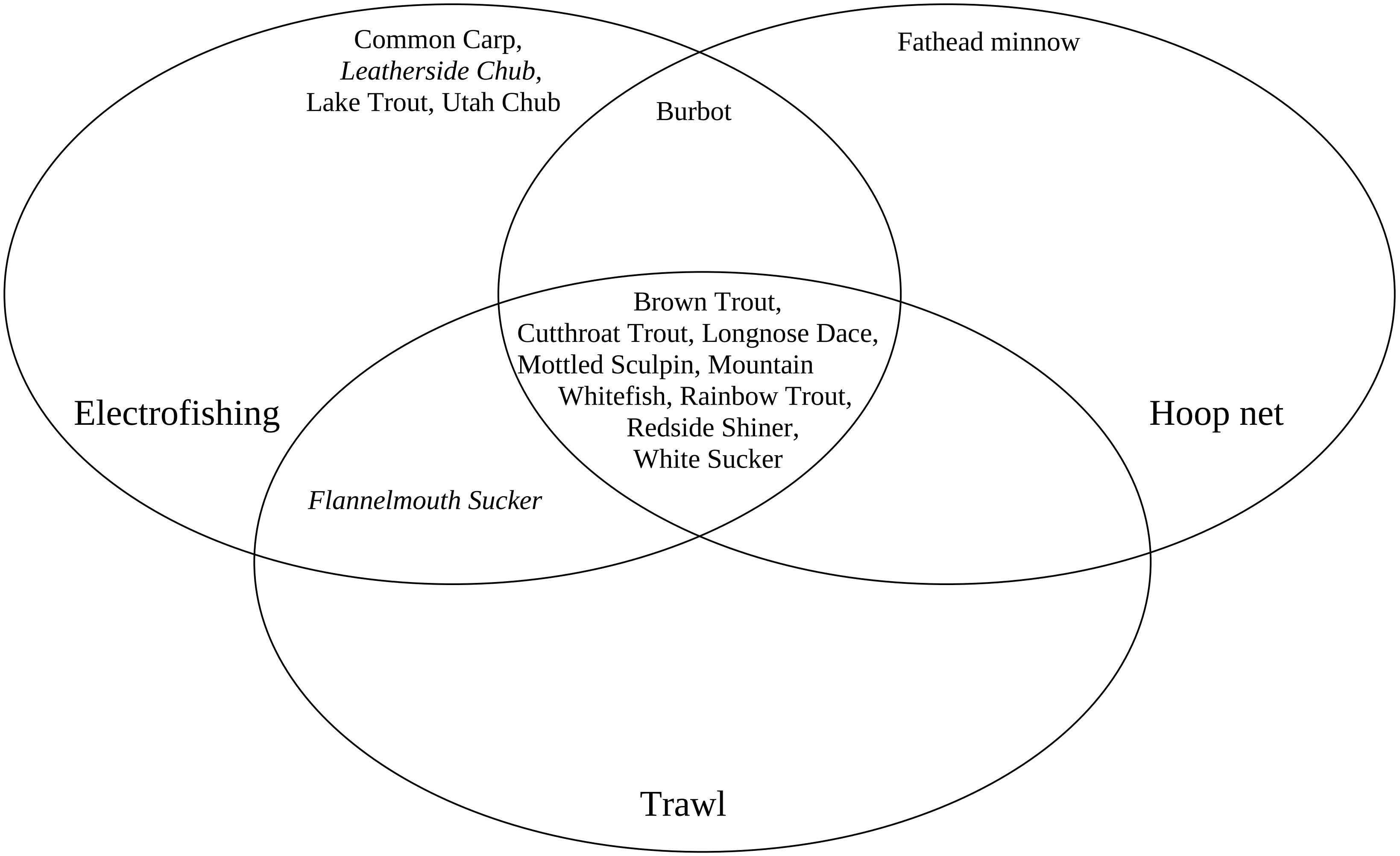

Figure 2.3. Venn diagram of species collected in the Green River in 2012 and 2013. Species in italics are Species of Concern (i.e., Flannelmouth Sucker, Leatherside Chub) in Wyoming.

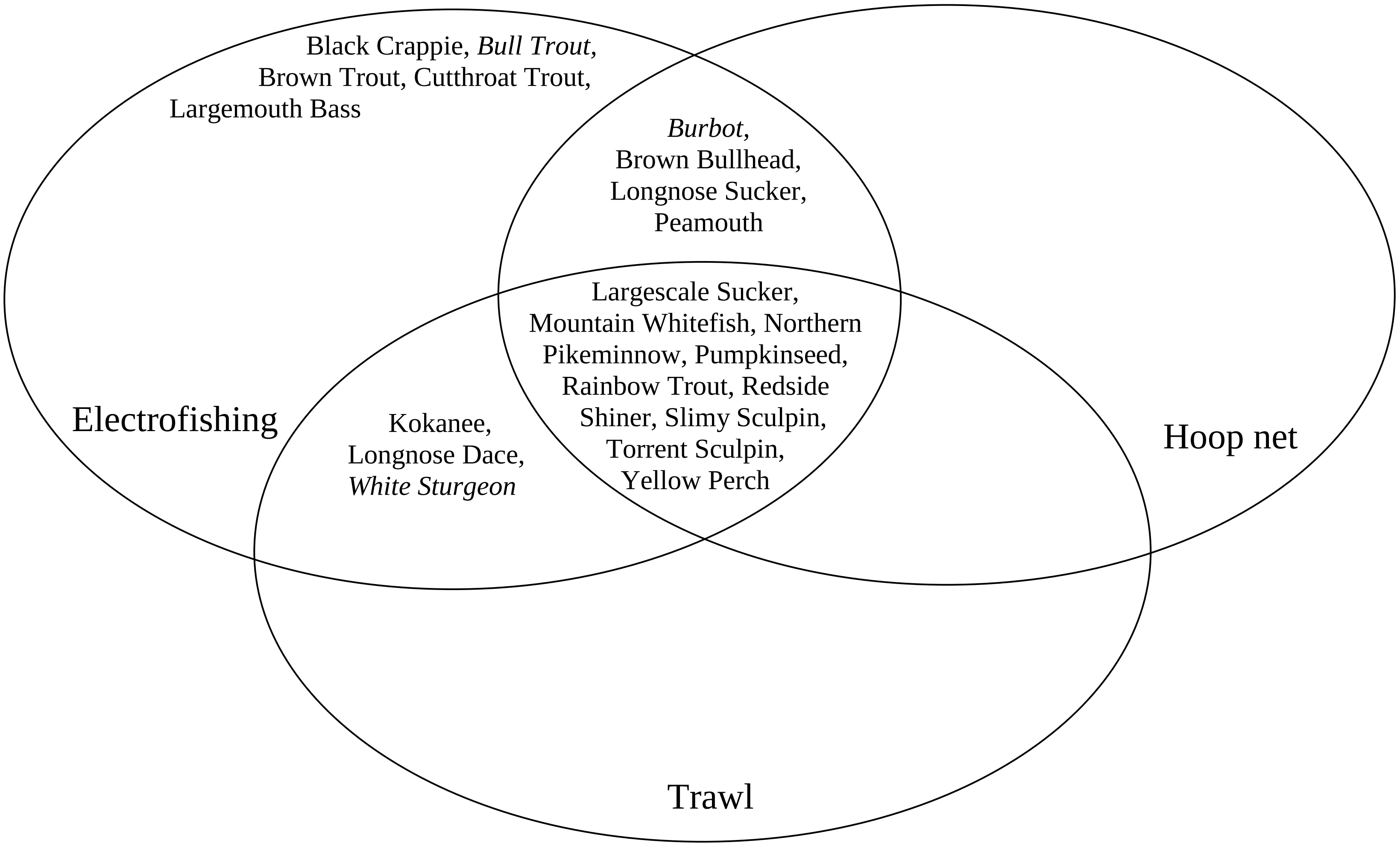

Figure 2.4. Venn diagram of species collected in the Kootenai River in 2012 and 2013. Species in italics are Imperiled Species (i.e., Burbot) in Idaho or receive Federal protection under the Endangered Species Act (i.e., Bull Trout, White Sturgeon).

CHAPTER 3: FISH ASSEMBLAGE STRUCTURE AND HABITAT ASSOCIATIONS IN A LARGE RIVERINE SYSTEM IN A LARGE WESTERN RIVER SYSTEM

A manuscript to be submitted for publication in the *River Research and Applications*

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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, 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. 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.

INTRODUCTION

Lotic systems and their corresponding fish assemblages are highly imperiled due to widespread anthropogenic disturbances (Allen and Flecker, 1993; Søndergaard and Jeppesen, 2007; Hoagstrom *et al.,* 2011). Consequently, factors that influence fish assemblage structure 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, 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).

Longitudinal gradients in fish assemblage structure have been conceptualized as belonging to one of two processes, zonation and addition (Hubert and Rahel, 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 coldwater (salmonid) to warmwater (cyprinid, 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). 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 factors influencing gradients of fish assemblage structure is critical for the conservation of imperiled fishes and preservation of aquatic biodiversity; however, understanding factors regulating processes at the population level are also important.

Fish populations are regulated by internal (e.g., growth) and external factors (e.g., aquatic habitat, 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*, 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; Hoagsrom *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 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, Valez *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 obvious 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, mining; Richards, 1997) and the construction of Libby Dam near Libby, Montana (Knudson, 1994). Construction of Libby Dam was completed in 1972 by the U.S. Army Corps of Engineers for flood control and power generation (Knudson, 1994). Completion of Libby Dam altered natural regimes (i.e., hydrologic, nutrient, thermal; Whitfield and Woods, 1984; Knudson, 1994) and subsequent shifts in fish assemblage structure downstream of Libby Dam have been reported (Paragamian, 2002). Additionally, the operation of Libby Dam has been directly implicated in the decline of native imperiled species (i.e., burbot *Lota lota,* white sturgeon *Acipenser transmontanus*; Paragamian *et al.,* 2000; Paragamian *et al.,* 2001).

The Idaho portion of the Kootenai River has three geomorphic sections (canyon, braided, meander; Fosness and Williams, 2009; Figure 3.1). The canyon section (257 – 312 river kilometer [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, boat-mounted electrofishing) surveyed all reaches repeatedly (2-3 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. 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. Nets had an overall length of 3.7 m and were covered with 6.3-mm bar measure 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 hours. Nets were baited with local non-game fishes (e.g., *Catostomus* spp.). 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 bar measure delta style, knotless mesh). 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 replicated. A global positioning system receiver (Lowrance, Tulsa, OK) was used to measure distance sampled and measurement started once the trawl was fully deployed. Distance (m) traveled 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 (see chapter 2). Electrofishing gear consisted of an Infinity model electrofisher (Midwest Lake Electrofishing Systems, Inc., Polo, MO) and a 5,000 W Honda generator (American Honda Motor Co., Inc., Torrance, CA). Electrofishing power output was standardized to 2,750 – 3,250 W (Miranda, 2009). Two netters were stationed near the bow of the boat to collect fish. Dip nets used to collect fish had 6.3-mm bar knotless mesh. Pulsed-DC electrofishing was conducted during the day. 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. Electrofishing effort was recorded as the distance sampled (m).

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,* 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 3.1). 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). 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). If depth was greater than 1 m, mean water column velocity measures were recorded at 20% and 80% of the depth. 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).

Fish assemblage and habitat structure

A principal component analysis was used to examine correlations among 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 nonmetric multidimensional scaling (NMDS). Nonmetric multidimensional scaling is a robust ordination technique that is widely used to assess fish assemblage relationships (e.g., Helms *et al.*, 2005; Rowe *et al.*, 2009; Ruetz *et al.*, 2007). Fish assemblage composition was investigated using a NMDS with presence-absence data pooled across 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 catch from gears with the greatest detectability (i.e., electrofishing, hoop nets; see chapter 2) were used in analyses of relative abundance data. Differences in assemblage structure among river sections were investigated with a permutational multivariate analysis of variation (PERMANOVA). Permutational multivariate analysis of variance 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 modeling 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 modeling. 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 (see chapter 2). 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). Pseudo R^2 values are analogous to the coefficient of determination in ordinary least squares linear regression, but pseudo R^2 values tend to be lower than traditional coefficient of determination values (Hosmer and Lemshow, 1989). Pseudo R^2 values greater than 0.20 indicate 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 Lemshow, 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, 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 small sample size ($\mathrm{AIC_c}$; Burnham and Anderson, 2002). If overdispersion ($\hat{c} > 1$) was present, quasi-$\mathrm{AIC_c}$ ($\mathrm{QAIC_c}$) 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 $\mathrm{AIC_c}$ or $\mathrm{QAIC_c}$ values (Burnham and Anderson, 2002).

RESULTS

A total of 7,920 fishes including twenty species and nine families was sampled. Three species of high conservation concern were collected: 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 3.2). 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 3.2). The first principal component axis separated the braided and canyon river sections from the meander section (Table 3.3). 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 ($K = 24.1$; $P < 0.001$), and average width ($K = 13.3$; $P = 0.001$).

Stable NMDS ordinations were present for species occurrence (Figure 3.3), electrofishing relative abundance (Figure 3.4), and hoop net relative abundance (Figure 3.5). 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 ($\widehat{r_s}$ = 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 ($\widehat{r_s}$ = 0.35; P < 0.001), proportion of vegetated bank ($\widehat{r_s}$ = 0.16; P = 0.03), coefficient of variation in water velocity ($\widehat{r_s}$ = 0.22; P = 0.006), average depth ($\widehat{r_s}$ = 0.48; P < 0.001), distance from Libby Dam ($\widehat{r_s}$ = 0.52; P < 0.001), and proportion of cobble or boulder substrate ($\widehat{r_s}$ = 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 ($\widehat{r_s}$ = 0.40; P < 0.001), average depth ($\widehat{r_s}$ = 0.42; P < 0.001), distance from

Libby Dam ($\widehat{r_S}$ = 0.44; $P < 0.001$), and the proportion of cobble or boulder substrate ($\widehat{r_S}$ = 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 3.4). In general, the presence of native species (kokanee *Oncorhynchus nerka*, northern pikeminnow, peamouth, 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 3.4). Brown bullhead occurrence was also positively related to the proportion of cobble-boulder bank type and 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).

The second stage of the hurdle regressions indicated that similar relationships with habitat characteristics were apparent for species occurrence and relative abundance (Table 3.5). 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 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 3.5). 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 catch rates. Distance to Libby Dam and the proportion of vegetated bank was negatively related to the relative abundance of pumpkinseed.

DISCUSSION

Biotic (e.g., aquatic vegetation) and abiotic (e.g., elevation, 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, pumpkinseed) was observed. A lack of zonation is likely attributed to minimal elevation and thermal gradients in the Idaho portion of the Kootenai River. 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.

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 to 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; Angermier 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, yellow perch). Lionberger and Hubert (2007) attributed downstream species addition patterns to the presence of non-native fishes (common carp *Cyprinus carpio*, walleye *Sander vitreus*, 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, canyon) were characterized by large substrate and fast water velocities, and the fish assemblage was composed of native salmonids (rainbow trout, mountain whitefish), catostomids (largescale sucker), and cyprinids (redside shiner). The meander section was characterized by native cyprinids (northern pikeminnow, peamouth) and non-native species (brown bullhead, largemouth bass *Micropterus salmoides*, pumpkinseed, 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, cutthroat trout) were common in upper river sections; non-native species (e.g., goldfish *Carassius auratus*, yellow bullhead *Ameiurus natalis*, 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, 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 to 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, kokanee) and non-native fishes (i.e., brown bullhead, 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 Allen, 1984; Persson and Eklöv, 1995). Conversely, fine substrates support the growth of aquatic vegetation, and both native (i.e., peamouth, 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, 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, the distance from Libby Dam) appear to be related to river sections. For instance, a positive relationship between northern pikeminnow catch and distance from 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, 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, 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 understanding of these relationships will be important in preserving biodiversity and restoration of imperiled rivers of western North America.

ACKNOWLEDGEMENTS

We thank C. Brown, D. Donnely, W. Field, K. Griffin, J. Hansen, E. Landers, N. Porter, J. Walrath, C. Watkins, S. Whitlock, J. Yates for assistance with field research. We also thank C. Gidley, P. Rust, and T.J. Ross of Idaho Department of Fish and Game for assistance in planning and implementing field work. Funding for the project was provided by Idaho Department of Fish and Game. Additional support was provided by the U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the U.S. Geological Survey, University of Idaho, and Idaho Department of Fish and Game, and Wildlife Management Institute. This project was conducted under the University of Idaho Institutional Animal Care and Use Committee Protocol 2011-33. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 3.1. 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. Habitat variables are organized by river section (braided, canyon, meander). Variables were used to investigate relationships among fish assemblage and populations with habitat characteristics.

		River section		
Variable	Description	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)
Bank_{Veg}	Percentage of bank consisting of vegetation (%)	30.0 (10.3)	44.6 (12.9)	41.7 (6.1)
CV_{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)

Table 3.2. Mean percentage of species composition of catch. 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.

	River section		
Taxa	Braided (*n* = 870)	Canyon (*n* = 551)	Meander (*n* = 6,405)
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)

Table 3.3. Habitat variable loadings from a principal component ordination 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
Bank_{Veg}	Percentage of bank consisting of vegetation (%)	-0.01	-0.56
CV_{Depth}	Mean coefficient of variation in water depth	0.24	0.23
CV_{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

Table 3.4. Candidate models investigating species occurrence using binomial logistic regression. Akaike's Information Criterion (AIC_c) or quasi-Akaike's information criterion ($QAIC_c$) adjusted for small sample size ranked candidate models. The total number of parameters (*K*), model weight (w_i), and two times the negative log-likelihood (-2*Log*(*l*)) are included. Global models or model with the best fit (dispersion parameter, 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 [-]).

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	-Substrate$_{\text{Co-Bo}}$	24.34	0.00	2	0.50	-10.02	0.49	0.35
	+CV$_{\text{Vel}}$, -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	-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	-Substrate$_{\text{Co-Bo}}$, -CV$_{\text{Vel}}$	30.65	0.00	3	0.33	-12.02	0.60	0.42
	-Substrate$_{\text{Co-Bo}}$,	31.80	1.16	2	0.18	-13.75	0.78	0.33
	-CV$_{\text{Vel}}$, +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

Table 3.4 cont'd.

Catostomidae								
Largescale sucker	+Bank$_{Veg}$	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
	+CV$_{Vel}$	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	-Depth, -Substrate$_{Co\text{-}Bo}$	50.52	0.00	4	0.18	-20.73	1.33	0.10
	-Substrate$_{Co\text{-}Bo}$	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
	-Bank$_{Veg}$	51.11	0.59	3	0.13	-22.25	1.39	0.04
	-Bank$_{Co\text{-}Bo}$	52.13	0.16	3	0.08	-22.76	1.42	0.01
	+CV$_{Vel}$, -Substrate$_{Co\text{-}Bo}$	52.39	1.87	4	0.07	-21.67	1.39	0.06
Ictaluridae								
Brown bullhead	+Bank$_{Co\text{-}Bo}$	19.41	0.00	2	0.16	-7.56	0.37	0.07
	-Depth, -Substrate$_{Co\text{-}Bo}$	19.70	0.29	3	0.14	-6.54	0.33	0.19
	+CV$_{Vel}$	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
	-Substrate$_{Co\text{-}Bo}$	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
	+Bank$_{Veg}$	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

Table 3.4 cont'd.

Salmonidae								
Cutthroat trout	-Bank$_{Veg}$	36.94	0.00	2	0.26	-16.32	0.80	0.06
	+Bank$_{Co\text{-}Bo}$	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
	-Bank$_{Veg}$, +Depth	38.80	1.86	3	0.10	-16.09	0.80	0.07
	-Substrate$_{Co\text{-}Bo}$	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	-Substrate$_{Co\text{-}Bo}$	47.94	0.00	3	0.43	-20.66	1.12	0.20
	-Depth, -Substrate$_{Co\text{-}Bo}$	48.96	1.02	4	0.26	-19.96	1.12	0.23
	+CV$_{Vel}$, -Substrate$_{Co\text{-}Bo}$	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	-Bank$_{Veg}$	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
	+Substrate$_{Co\text{-}Bo}$	46.44	0.45	3	0.14	-19.91	1.40	0.02
	-Bank$_{Veg}$	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
	-CV$_{Vel}$	46.93	0.94	3	0.11	-20.16	1.42	0.01
	-Bank$_{Co\text{-}Bo}$	47.05	1.06	3	0.10	-20.22	1.41	0.01
	-Bank$_{Co\text{-}Bo}$, -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

Table 3.4 cont'd.

Gadidae								
Burbot	-Bank$_{\text{Co-Bo}}$	46.52	0.00	3	0.22	-19.95	1.13	0.05
	+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
	-CV$_{\text{Vel}}$	48.50	1.99	3	0.08	-20.94	1.19	0.01
	-Depth, +Distance, +Substrate$_{\textit{Co-Bo}}$	50.76	4.24	5	0.03	-19.57	1.16	0.07
Centrarchidae								
Pumpkinseed	-Substrate$_{\text{Co-Bo}}$	46.59	0.00	3	0.40	-19.99	1.11	0.14
	-Bank$_{\text{Veg}}$, -Substrate$_{\text{Co-Bo}}$	48.08	1.48	4	0.19	-19.51	1.11	0.16
	-Bank$_{\textit{Veg}}$*, -Depth, -Substrate*$_{\textit{Co-Bo}}$	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
	-Substrate$_{\text{Co-Bo}}$	42.16	1.98	2	0.13	-18.93	0.92	0.08
	+Bank$_{\textit{Veg}}$*, +Depth, +Distance*	44.50	4.31	4	0.04	-17.72	0.91	0.14

Table 3.5. Candidate models investigating relative abundance of species in relation to habitat characteristics. Akaike's Information Criterion (AIC_c) or quasi-Akaike's information criterion ($QAIC_c$) adjusted for small sample size ranked 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, 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 [-]).

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	$-CV_{Vel}$, +Distance	128.60	0.00	4	0.58	-59.69	0.70	0.18
	$+Bank_{Veg}$, $-Substrate_{Co\text{-}Bo}$	130.24	3.74	4	0.26	-60.52	0.73	0.17
	+Depth, +Distance, $-Substrate_{Co\text{-}Bo}$	132.33	8.29	5	0.01	-62.51	0.83	0.14
Peamouth	$-Substrate_{Co\text{-}Bo}$	362.01	0.00	4	0.70	-176.38	0.95	0.03
	$+Bank_{Veg}$, *+Depth, +Distance*	371.29	9.28	6	0.01	-178.24	1.11	0.02
Redside shiner	$-Bank_{Veg}$	190.12	0.00	4	0.44	-90.39	1.35	0.02
	$-Bank_{Co\text{-}Bo}$, $+CV_{Vel}$, *-Depth*	197.10	6.99	6	0.01	-91.05	1.50	0.01
Catostomidae								
Largescale sucker	-Depth, $+Bank_{Veg}$	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
	$-CV_{Vel}$, *-Depth, +Distance*	379.16	3.07	5	0.10	-183.72	0.89	0.04

Table 3.5 cont'd.

Longnose sucker	-Bank$_{\text{Co-Bo}}$	120.13	0.00	3	0.21	-56.17	0.85	0.01
	-Substrate$_{\text{Co-Bo}}$	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
	-Bank$_{\text{Veg}}$	121.14	1.00	3	0.13	-56.97	0.89	0.01
	+CV$_{\text{Vel}}$	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, -Bank$_{Veg}$*, -Substrate*$_{Co\text{-}Bo}$	125.11	4.98	5	0.02	-55.89	0.90	0.02
Ictaluridae								
Brown bullhead	*+Substrate*$_{Co\text{-}Bo}$	9.80	0.00	3	0.40	10.10	0.12	-0.40
	-Bank$_{\text{Veg}}$	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	*+CV*$_{Vel}$	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
	+CV$_{Vel}$*, -Depth, -Substrate*$_{Co\text{-}Bo}$	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
	+CV$_{Vel}$*, - Depth, +Substrate*$_{Co\text{-}Bo}$	290.63	5.40	5	0.06	-139.48	0.51	0.18

Table 3.5 cont'd.

Rainbow trout	-Bank$_{Veg}$	108.13	0.00	3	0.19	-50.49	0.49	0.01
	+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
	+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
	+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, +Substrate$_{Co\text{-}Bo}$	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
	+CV$_{Vel}$	-35.48	1.52	3	0.13	22.46	0.12	-0.02
	+Substrate$_{Co\text{-}Bo}$	-35.20	1.80	3	0.11	22.31	0.12	-0.01
	-Depth, -Distance, -Substrate$_{Co\text{-}Bo}$	-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
	-Bank$_{Veg}$	74.04	1.44	4	0.26	-30.52	1.53	0.10
	-Bank$_{Veg}$*, -Depth, -Substrate*$_{Co\text{-}Bo}$	82.38	9.78	6	0.00	-28.19	1.27	0.17
Percidae								
Yellow perch	*+Substrate*$_{Co\text{-}Bo}$	46.94	0.00	3	0.26	-17.47	0.53	0.06
	+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
	+CV$_{Vel}$	48.06	1.12	3	0.15	-18.03	0.61	0.02
	-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

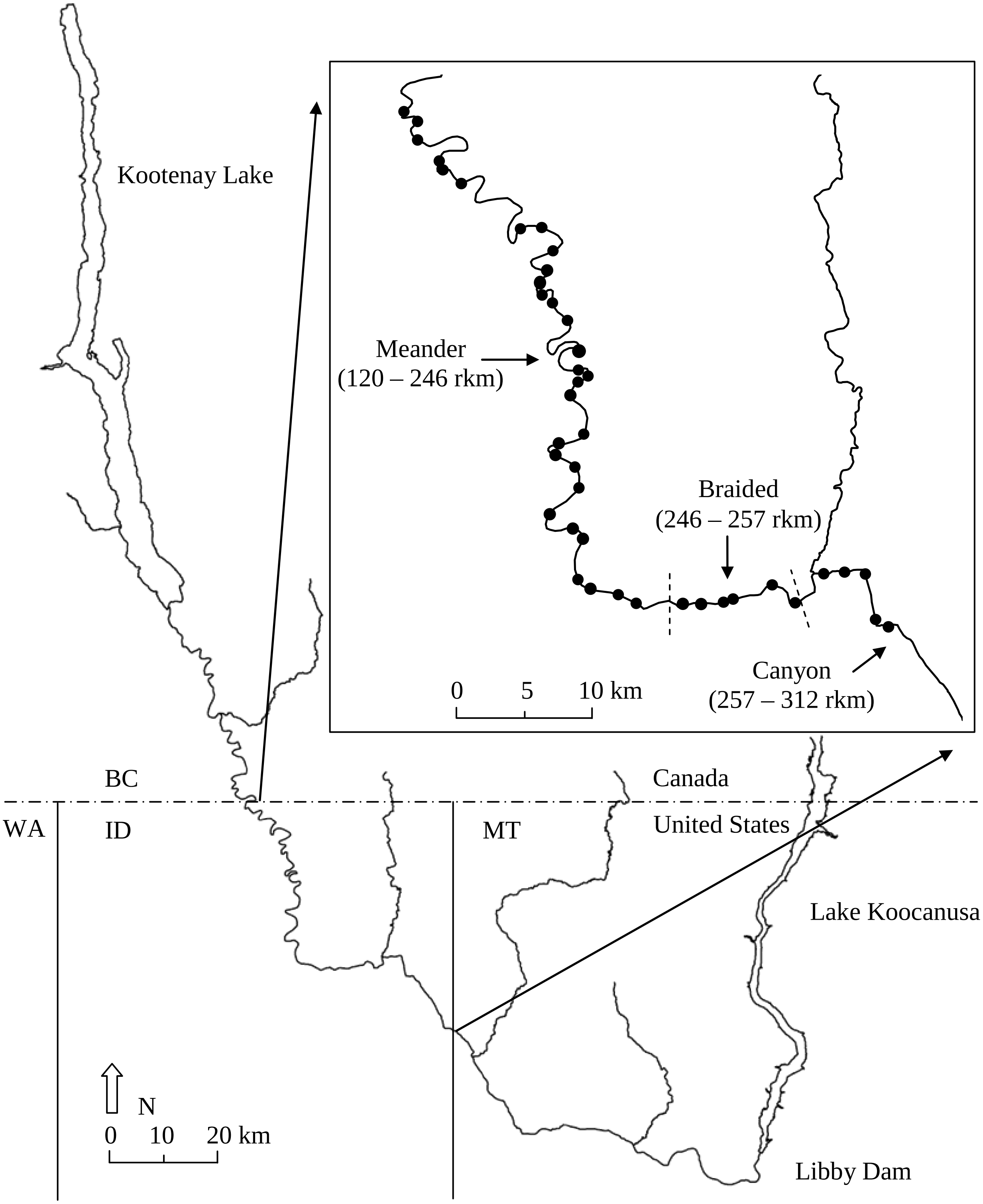


Figure 3.1. Sampling locations (black circles) and river sections (braided, canyon, meander) of the Kootenai River, United States and Canada. River kilometers (rkm) are included for each river section.

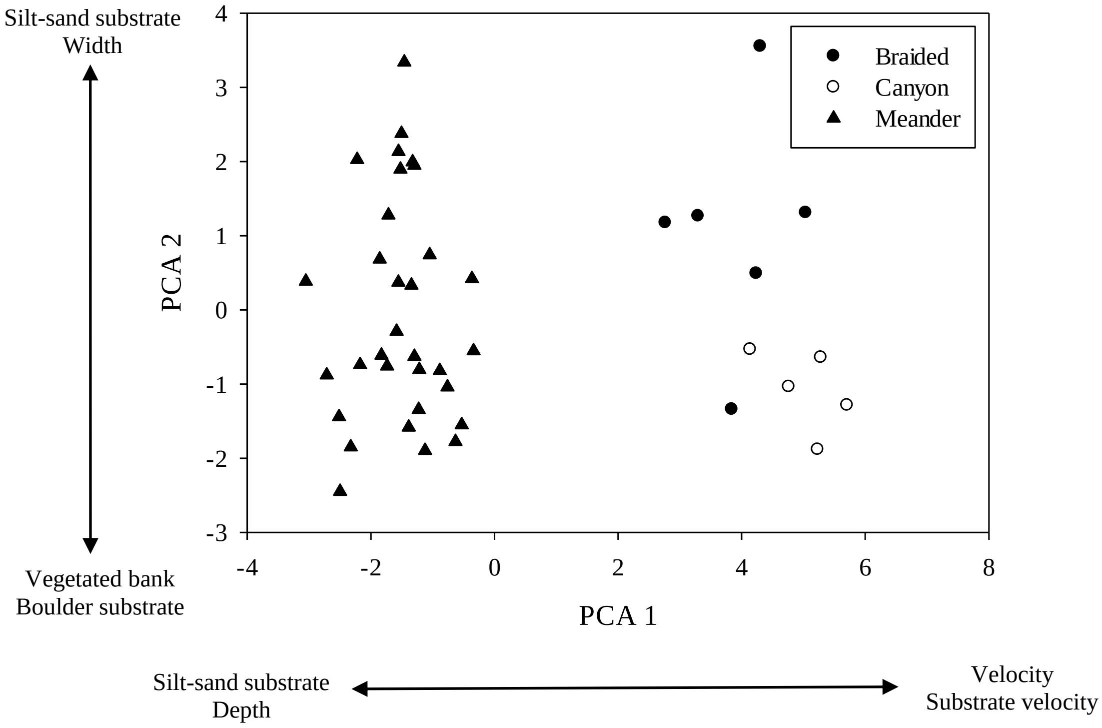


Figure 3.2. Principal component ordination of habitat characteristics measured in the Kootenai River in 2012 and 2013 by river section (braided, canyon, meander). The first principal component axis (PCA 1) explained 48.1% of the variance ($\lambda = 7.22$) and 15.0% of the variance was explained with the second principal component axis (PCA 2; $\lambda = 2.25$).

Figure 3.3. Nonmetric multidimensional scaling ordination (stress = 21.6) of fish assemblage presence-absence data from the Kootenai River organized river section (braided, canyon, 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), 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.

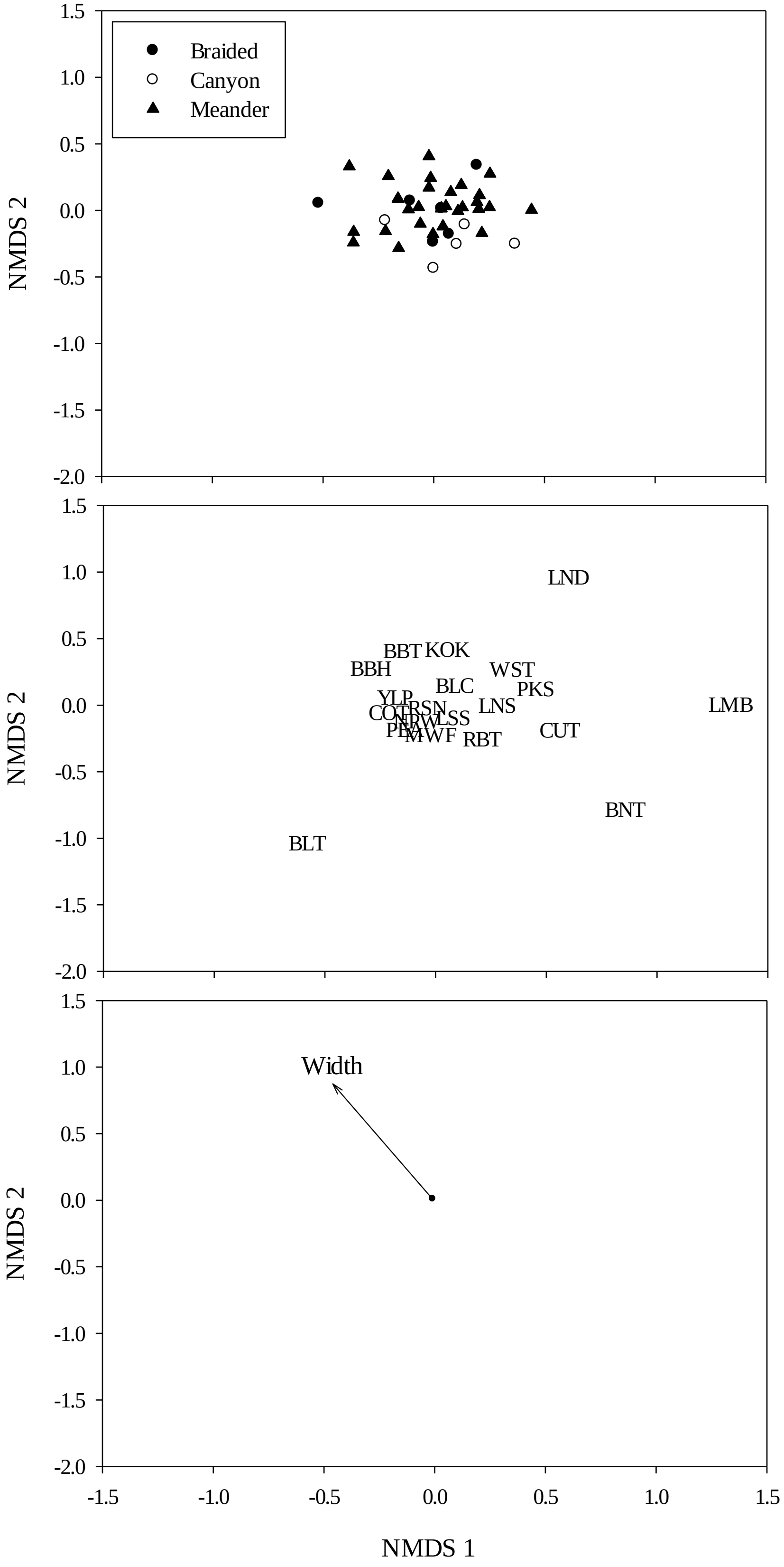

Braided
Canyon
Meander
NMDS 2
NMDS 2
NMDS 2
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
LND
BBT
KOK
BBH
WST
BLC
PKS
YLP
COT
RSN
NRW
LSS
LNS
LMB
PEA
MWF
RBT
CUT
BNT
BLT
Width
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
NMDS 1

Figure 3.4. Nonmetric multidimensional scaling ordination (stress = 12.6) of fish assemblage relative abundance data collected with electrofishing from the Kootenai River organized river section (braided, canyon, 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), yellow perch (YLP). Significant ($P < 0.05$) habitat vectors were fit to the ordination and include proportion of bank consisting of vegetation ($\mathrm{Bank}_{\mathrm{Veg}}$), proportion of cobble-boulder bank ($\mathrm{Bank}_{\mathrm{Co\text{-}Bo}}$), mean coefficient of variation of water velocity ($\mathrm{CV}_{\mathrm{Vel}}$), mean depth (Depth), distance from Libby Dam (Distance), and proportion of substrate consisting of cobble and boulder ($\mathrm{Substrate}_{\mathrm{Co\text{-}Bo}}$).

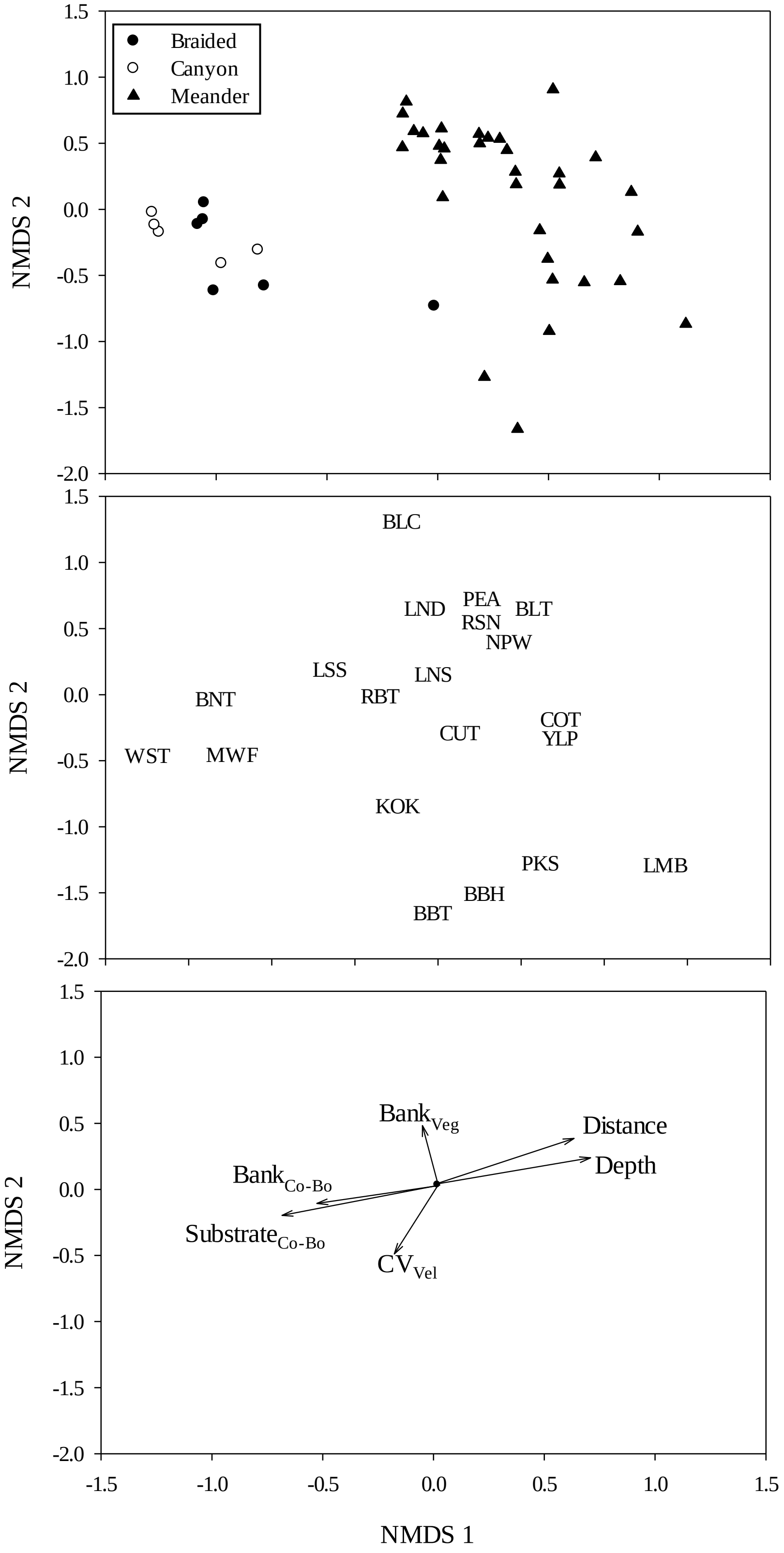
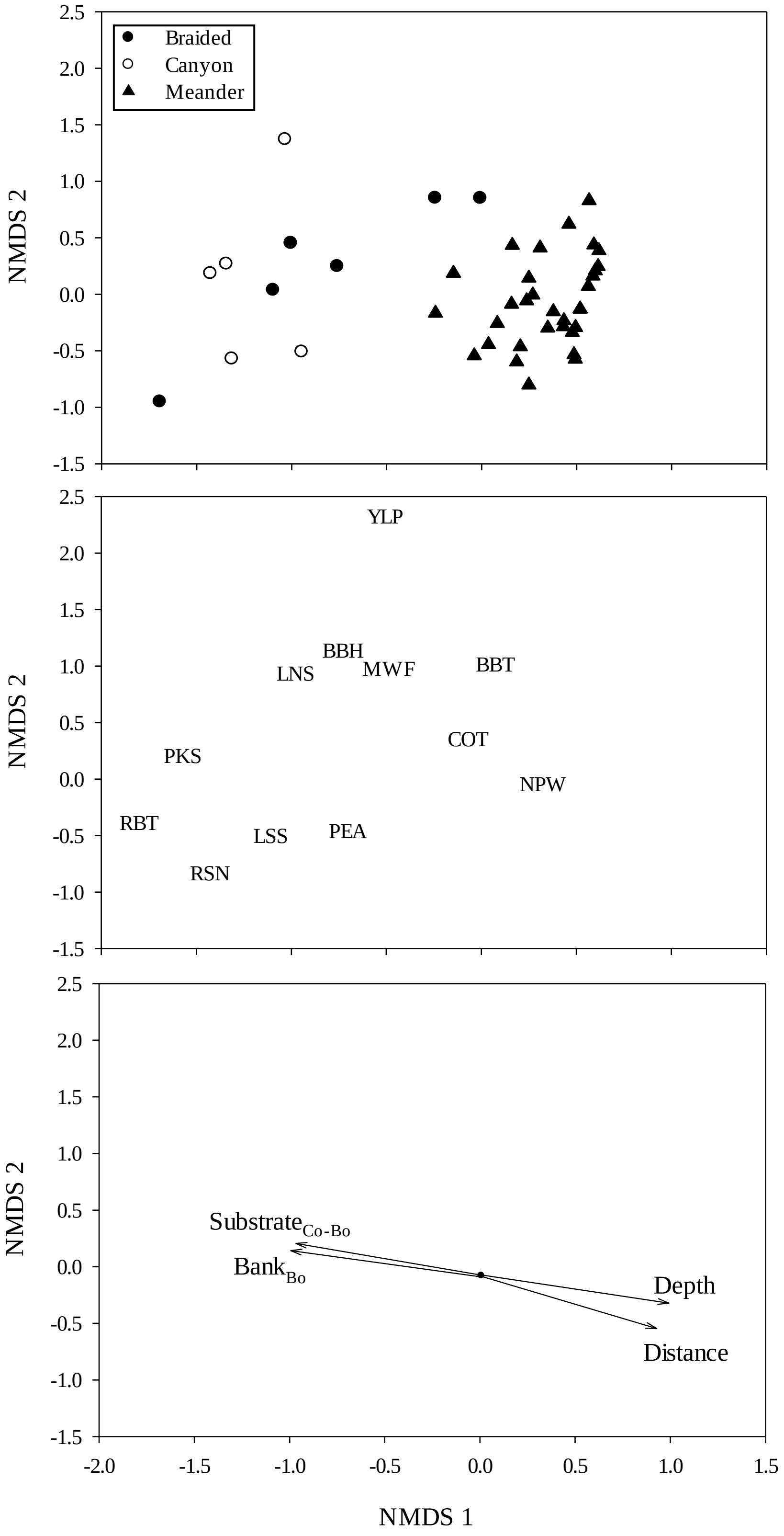

Braided
Canyon
Meander
BLC
LND
PEA
RSN
BLT
NPW
LSS
LNS
BNT
RBT
COT
YLP
CUT
WST
MWF
KOK
PKS
LMB
BBH
BBT
Bank$_{Veg}$
Distance
Depth
Bank$_{Co\text{-}Bo}$
Substrate$_{Co\text{-}Bo}$
CV$_{Vel}$
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
NMDS 2
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
NMDS 1

Figure 3.5. Nonmetric multidimensional scaling ordination (stress = 11.1) of fish assemblage relative abundance data collected with hoop nets from the Kootenai River organized river section (braided, canyon, 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 Libby Dam (Distance), and proportion of substrate consisting of cobble and boulder ($\text{Substrate}_{\text{Co-Bo}}$).


Braided
Canyon
Meander
NMDS 2
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
YLP
BBH
LNS
MWF
BBT
COT
PKS
NPW
RBT
LSS
PEA
RSN
Substrate$_{Co\text{-}Bo}$
Bank$_{Bo}$
Depth
Distance
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
NMDS 1

CHAPTER 4: GENERAL CONCLUSIONS

Non-wadeable river systems have high habitat complexity and support ecologically and recreationally important fishes. Due to the importance of riverine fishes and ecosystems, evaluating and monitoring fishes in western systems should be a high priority. Unfortunately, sampling fishes large rivers is difficult due to high habitat complexity and diverse fish assemblages.

A comparison of three sampling gears was completed in two large rivers in Wyoming and Idaho. Results indicated that significant gear effects were apparent among species and life history stages. Detectability was greatest with electrofishing for most fishes and life history stages. However, hoop nets had greater detection probabilities for adult Burbot and juvenile Northern Pikeminnow. Benthic trawls had low detection probabilities for most species. Consequently, the use of benthic trawls in western systems with high water clarity may result in an inefficient use of resources. Habitat characteristics appeared to have less of an effect on detectability compared to gear type. Understanding the effects of gear, habitat, and life history stage on detectability will improve management of coldwater rivers.

Habitat gradients and fish assemblage structure varied among river sections (braided, canyon, meander) in the Kootenai River. Braided and canyon river sections had similar habitat characteristics and fish assemblages (native salmonids, catostomids, and cyprinids). The meander section was different than the braided and canyon reaches with regard to habitat and fish assemblage structure. Habitat in the meander section was characterized by large proportions of fine substrate, high maximum depths, and low flow velocities. Assemblage composition in the meander section included native (Peamouth, Northern

Pikeminnow) and non-native (Brown Bullhead, Pumpkinseed, Yellow Perch) fishes. Population-level relationships with habitat characteristics varied by species and provided information regarding species ecology and habitat use in the Kootenai River system.

General trends in detectability were apparent between river systems and a gradient of assemblage structure was observed in the Kootenai River. Results of this work provide information regarding gear efficacies and habitat associations of fishes in large western rivers. Future research could better quantify amounts of effort necessary to adequately monitor entire fish assemblages across coldwater systems using a multiple-gear sampling approach. Additionally, further species ecology information could be gained by understanding the habitat associations of fishes across multiple spatial scales. Such information will be important for managing river systems across western North America.

APPENDIX: APPROXIMATE LENGTH AT MATURITY OF LARGE-BODIED FISHES (≥ 200 mm).

Family and common name	Scientific name	Length at maturity (mm)	System	Reference
Cyprinidae				
Common Carp	*Cyprinus carpio*	318	Mid-Murray River, AUS	Brown et al. (2005)
Northern Pikeminnow	*Ptychocheilus oregonensis*	250	St. Joe River, Idaho, USA	Beamsderfer (1992)
			Columbia River, Washington, USA	Gray and Dauble (2001)
Peamouth	*Mylocheilus caurinus*	200	Columbia River, Washington, USA	Gray and Dauble (2001)
Catostomidae				
Flannelmouth Sucker	*Catostomus macrocheilus*	405	Colorado River, Arizona, USA	McKinney et al. (1999)
			Various rivers in the Colorado basin, USA	McAda and Wydoski (1985)
Largescale Sucker	*Catostomus macrocheilus*	330	Columbia River, Washington, USA	Dauble (1986)
Longnose Sucker	*Catostomus catostomus*	265	British Columbia, CAN	Scott and Crossman (1973)
White Sucker	*Catostomus commersonii*	284	Ontario, CAN	Scott and Crossman (1973)
Salmonidae				
Brown Trout	*Salmo trutta*	256	Various rivers, Tennessee, USA	Holbrook and Bettoli (2006)
Cutthroat Trout	*Oncorhynchus clarkii*	150	Little Snake River, Wyoming, USA	Quinlan (1980)
Kokanee	*Oncorhynchus nerka*	160	Kootenay Lake, British Columbia, CAN	Scott and Crossman (1973)
Mountain Whitefish	*Prosopium williamsoni*	235	Kootenai River, Idaho, USA	Meyer et al. (2009)
Rainbow Trout	*Oncorhynchus mykiss*	200	Various systems, USA	Raleigh et al. (1984)
Gadidae				
Burbot	*Lota lota*	280	Various systems, USA and CAN	Scott and Crossman (1973)
			Pavik River, NOR and RUS	Amundsen et al. (2003)
Centrarchidae				
Largemouth Bass	*Micropterus salmoides*	300	Various systems, USA	Bennett et al. (1991)