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Nutrient Restoration of a Large, Impounded, Ultra-Oligotrophic Western River to Recover Declining Native Fishes

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Abstract

Declines in many fish populations in large, western rivers have been primarily attributed to the anthropogenic reduction of nutrient inputs and subsequent impacts to the food web. The largest known river fertilization program was implemented starting in 2005 on the Kootenai River in northern Idaho to restore resident fisheries. Annual electrofishing surveys were conducted at multiple sites in Idaho and Montana before and during nutrient addition to evaluate assemblage and population-level responses. Although few responses in fish assemblage structure were observed, the addition of liquid ammonium polyphosphate fertilizer (3 μg/L) to the Kootenai River increased fish abundance and biomass over the 20-km stretch of river downstream of the treatment site. Increases were most notable in Largescale Suckers *Catostomus macrocheilus,* Mountain Whitefish *Prosopium williamsoni*, and Rainbow Trout *Oncorhynchus mykiss* populations, although increases in catch and biomass were detected for nearly all fish species. The Kootenai River is approximately 30 times larger in discharge than other rivers that have been experimentally fertilized and provides compelling evidence that the mitigation of nutrient declines in rivers of similar size can result in positive influences on the fish populations where primary and secondary production are limiting growth, survival, and recruitment. However, results from our study also highlight the importance of completing evaluations across varying levels of biological organization (e.g., assemblage and population) and over biologically relevant timeframes.

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Anthropogenic reduction of nutrient inputs into aquatic systems primarily occurs from nutrient abatement or the construction of dams for flood control or hydropower (Ney 1996). The reduction in nutrients has long been recognized as a concern for aquatic communities (Ney 1996; Stockner et al. 2000). Dams trap sediment and nutrients, and multiple dams compound the negative effects to downstream fish populations through reduced primary production (Ney 1996). Unlike reductions in marine-derived nutrients experienced by many lotic systems across the Pacific Northwest (Thomas et al. 2003), cultural oligotrophication in systems not influenced by marine-derived nutrients requires perpetual mitigation to increase and sustain adequate primary production (Stockner and Ashley 2003).

Primary production is the foundation of food webs and is often limited by the availability of nutrients, specifically nitrogen (N) and phosphorus (P) in freshwater ecosystems (Minshall 1978; Thomas et al. 2003; Dodds and Smith 2016). Fluctuations in the availability of N and P often influence autotrophic production (Grimm and Fisher 1986; Peterson et al. 1993) and consequently may affect rate functions of various fish populations (Chapman 1966; Slaney and Northcote 1974; Dill et al. 1981). As such, novel mitigation programs have been developed to restore fisheries and ecosystems affected by oligotrophy using a holistic resource management model that addresses factors limiting growth, survival, and recruitment of fishes.

Mitigation for anthropogenic oligotrophication and the associated declines in abundance, biomass, and biodiversity of aquatic communities has been successfully performed via stream or lake fertilization (Stockner and Ashley 2003). The goal of aquatic fertilization programs is often to bolster fish abundance via bottom-up mechanisms. The conceptual model is as follows: increased N and P levels result in increases in phytoplankton and periphyton accrual rates, followed by increases in macroinvertebrate biomass and abundance, which are then followed by positive responses in fish abundance, growth, survival, and recruitment (Ward and Slaney 1988; Mundie et al. 1991; Perrin and Richardson 1997; Johnston et al. 1999). Over the past two decades, nutrient supplementation programs have been initiated across the northwestern United States to mitigate for nutrient losses from diminished Pacific salmon *Oncorhynchus* spp. stocks or from the construction of dams (Stockner and Ashley 2003).

One such river that has experienced a substantial reduction in nutrient levels over the past 50 years is the Kootenai River, a large, seventh-order river that originates in southeastern British Columbia, Canada, and flows through northwestern Montana and northern Idaho. Historically, nutrient input into the lower portion of the system was dramatically reduced with the construction of Libby Dam in 1972 (Figure 1; Snyder and Minshall 1996).

In addition, levy construction for flood control and agriculture isolated floodplain habitats that once contributed seasonal nutrient inputs to the lower river (Northcote 1973; Woods 1982). After construction of Libby Dam, the reservoir created by the dam (Lake Koocanusa) retained approximately 65% of P and 25% of N (Woods 1982), resulting in ultra-oligotrophic conditions (Carlson trophic state index of 0–40) downstream (Carlson and Simpson 1996; Ashley et al. 1997; Schindler et al. 2011). Cultural oligotrophication of the Kootenai River resulted in substantial reductions in periphyton, macroinvertebrate, and fish production, particularly in the Idaho section of the river (Paragamian 2002; Snyder and Minshall 2005).

The sequestration of nutrients upstream of Libby Dam was implicated as the major cause for reduced densities of Rainbow Trout *O. mykiss gairdneri*, as well as many other native fish species, in the Idaho portion of the Kootenai River (Paragamian et al. 2000, 2001; Paragamian 2002). Although the Rainbow Trout fishery was regarded as the most important sport fishery in the Idaho portion of the river (Paragamian 1995a; Walters 2003), post-dam densities averaged only 50 fish/km (4.5 fish/ha) by the mid-1990s (Paragamian 1995b; Downs 2000; Walters and Downs 2001) compared to similar regional rivers, which exhibited three- to fourfold greater densities (Spokane River; Bennett and Underwood 1988). Similar to Rainbow Trout, reductions in the densities of other native fish species, such as Mountain Whitefish *Prosopium williamsoni*, Largescale Suckers *Catostomus macrocheilus*, and Redside Shiner *Richardsonius balteatus*, were documented (Paragamian 2002; Hardy 2008). Other native fish species, such as Kootenai River White Sturgeon *Acipenser transmontanus*, Bull Trout *Salvelinus confluentus*, and Burbot *Lota lota*, have also declined due to changes in environmental conditions, including nutrient dynamics (Hardy et al. 2015).

To mitigate for the effects of anthropogenic oligotrophication caused by Libby Dam, a nutrient restoration program was implemented starting in 2005 by the Kootenai Tribe of Idaho and the Idaho Department of Fish and Game (Holderman and Hardy 2004; Minshall et al. 2014). This restoration program marked a substantial cooperative venture by the two entities to implement the largest stream fertilization program in the world to date. Our study focused on fish assemblage and population-level effects in response to experimental nutrient additions in the Idaho section of the Kootenai River. Although stream fertilization studies have been performed in Canada (Peterson et al. 1993; Deegan et al. 1997; Larkin et al. 1999; Slavik et al. 2004), most studies have occurred in small to medium streams. Comparatively few studies have experimentally supplemented nutrient regimes of large rivers that were historically void of marine-derived nutrients, and even fewer studies have involved oligotrophic rivers (Dodds 2006; Minshall et al. 2014). Thus, our study provides
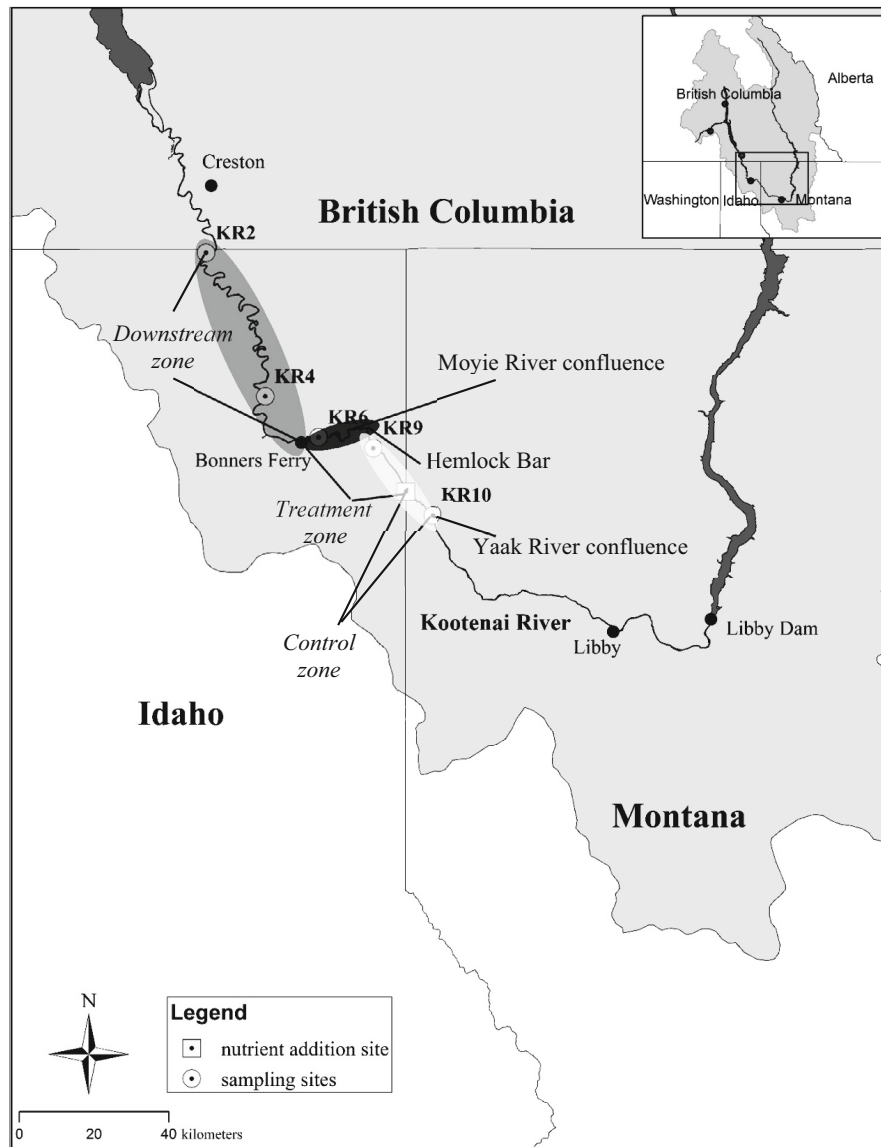
FIGURE 1. Map of the study area in the Kootenai River, Idaho. Shown are Libby Dam, the treatment site, sampling sites (KR2, KR4, etc.), and river zones. The shaded area denotes the Kootenai River watershed. The light-gray shaded area denotes the "downstream" geomorphic reach, the dark-gray shaded area denotes the "braided" geomorphic reach, and the white shaded area denotes the "canyon" geomorphic reach.

important information on restoring fish populations in large rivers that have experienced significant impacts from nutrient loss as a result of water development.

The Kootenai River fertilization has been extensively assessed, and the current analysis complements studies involving broader evaluations of trophic-level responses to nutrient addition, including those reported on periphyton and macroinvertebrate biomass and abundance in the Kootenai River (Holderman et al. 2009; Hoyle 2012; Minshall et al. 2014). In addition, our study also adds to a study by Watkins et al. (2017) that described the effects of nutrient additions on the growth, survival, and recruitment of Mountain Whitefish and Largescale Suckers. Our

evaluations are unique in that they lend more detailed information on the population-level effects (i.e., density, biomass, and species associations) of nutrient addition for native fish populations within the Kootenai River system. In this study, we evaluated the hypothesis that fish assemblage structure, abundance, and biomass for native focal species (i.e., Rainbow Trout, Mountain Whitefish, and Largescale Sucker) would increase with the addition of nutrients over the treatment period.

Study Area

The Kootenai River flows south from its headwaters in Kootenay National Park in southeastern British

Columbia, Canada, through northwestern Montana, where it enters Lake Koocanusa, the reservoir formed by Libby Dam (Figure 1). The river then flows northwest into the panhandle of Idaho, then north into British Columbia to form Kootenay Lake, and finally enters the Columbia River at Castlegar, British Columbia. The Kootenai River is the second-largest tributary of the Columbia River and third largest in drainage size (i.e., approximately 50,000 km²; Bonde and Bush 1975). Historically, peak discharges of the Kootenai River were greater than 2,832 m³/s, which is now generally moderated by Libby Dam (i.e., rarely exceeds 1,700 m³/s). The study area was comprised of approximately 106 km of the river flowing through the panhandle of Idaho, along with one control site near the Yaak River confluence in Montana (Figure 1).

The Montana and Idaho portions of the Kootenai River below Libby Dam can be separated into three distinct geomorphic habitat types. Directly below the dam, the river flows through a narrow canyon segment characterized by steep canyon walls, high gradient, and cobble and boulder substrates. In this segment of the river, the channel has an average gradient of 0.6 m/km and the velocities are often greater than 0.8 m/s. Downstream from the canyon segment, a braided transition segment extends from the Moyie River to the town of Bonners Ferry (Figure 1). Downstream from the braided transition segment, velocities slow to less than 0.4 m/s, gradient reduces to 0.02 m/km, the channel deepens, and the river meanders through the Kootenai Valley (Snyder and Minshall 2005). Studies have documented that both abiotic conditions and biotic communities at all trophic levels differ among the distinct geomorphic habitat reaches in the Kootenai River (Minshall et al. 2014; Smith et al. 2016).

METHODS

Nutrient addition (treatment).— We added agricultural-grade ammonium polyphosphate ([NH_4, $P_2O_5]_n$; 10-34-0) and urea ammonium nitrate ($CO[NH_2]_2NH_4NO_3$; 32-0-0) liquid fertilizer from approximately June 1 to September 30 in 2005–2017 at a single location near the Idaho–Montana border (Figure 1). Nutrients were applied at rates ensuring that the epilimnetic dissolved inorganic nitrogen : total dissolved phosphorus ratio remained greater than 10:1 on a weight : weight basis throughout the growing season (Ashley and Stockner 2003). Nutrient addition began in 2005 to reach 1.5 µg/L of total dissolved phosphorus and increased to 3.0 µg/L from 2006 to 2017 to achieve the targeted treatment concentration. After 2006, fertilizer was precisely applied to achieve the target N:P ratio. However, 32-0-0 was seldom added since dissolved inorganic nitrogen was typically above the desired target throughout the growing season. To remain consistent with previous evaluations of lower trophic levels (Minshall et al. 2014; Shafii et al. 2021),

we chose to include 2005 as a prenutrient addition year in our analysis. Fertilizer was applied to the river via a gravity-flow system with the aid of low-flow pumps designed to dose at loading rates directly proportional to the daily discharge rates of the Kootenai River at the application site. River flow was determined daily at an on-site U.S. Geological Survey gauging station (12305000 at Leonia, Idaho) to aid in pump calibrations.

Field sampling.— Biological sampling sites for the study were established to gather fisheries and lower-trophic-level data prior to and after the addition of nutrients. Our study only evaluated the effects of nutrient addition on resident fishes. Additional trophic level results were reported by Minshall et al. (2014) and Hoyle et al. (2014). Fish populations were annually surveyed at five sampling sites (Figure 1). The control site (KR10) was located in the Montana portion of the Kootenai River (i.e., upstream from the nutrient addition site), termed the "control zone." Site KR10 was located approximately 10 river kilometers (rkm) upstream from the nutrient addition site. Two sites (KR9 and KR6) were located within the "treatment zone" of the river, which was upstream from the town of Bonners Ferry, Idaho, but immediately downstream from the nutrient addition site. Site KR9 was located approximately 10 rkm downstream from the nutrient addition site, and site KR6 was located approximately 20 rkm downstream from the nutrient addition site. Two additional sites were located downstream from Bonners Ferry, in the "downstream zone" of the river. Site KR4 was located approximately 45 rkm downstream from the nutrient addition site, and site KR2 was approximately 100 rkm downstream from the nutrient addition site (Figure 1).

Boat electrofishing was conducted during August and September from 2002 to 2017 at the five standardized sampling sites. All sites were sampled using a jet boat equipped with a Coffelt VVP-15 (Coffelt Manufacturing, Inc., Flagstaff, Arizona) electroshocker powered by a 5,000-W Honda generator. Electrofishing settings were typically set to generate 6–8 A at 175–200 V. The sampling crew consisted of two netters and one boat driver. Each site was divided into six equal subsections of 333 m, with 150 m separating each to ensure that each subsection was independent of the next. The sampling design resulted in 1 km of electrofishing occurring on both the left and right banks of the river for a total of 2 km of sampling per site. A single pass was made through each subsection, starting with downstream sections first to ensure that no fish drifted into areas that had not yet been sampled. After each subsection was sampled, the elapsed sampling time was recorded and collected fishes were identified to species, measured (TL, mm), and weighed (g). Specific population indices that were estimated include catch per unit of effort (CPUE; number of fish/min of electrofishing) and abundance by weight as biomass per unit of effort (BPUE;

kg of fish/min of electrofishing). For all analyses, 2002–2005 were considered "pretreatment" years and 2006–2017 were considered "treatment" years.

Fish assemblage.— Fish assemblage relationships were evaluated following methods similar to those described by Kwak and Peterson (2007) using nonmetric multidimensional scaling (NMDS). Bray–Curtis dissimilarity values were calculated using presence–absence (i.e., species occurrence) data that included all sites, years, and fish species. In addition, Bray–Curtis dissimilarity values were calculated using CPUE data and BPUE data from all sites, years, and fish species. Data were pooled across sites within respective river zones and across years within respective pretreatment and treatment periods. Resulting dissimilarity matrices were used to run three separate NMDS analyses. One NMDS analysis was run using the species occurrence dissimilarity matrix, one was run using the CPUE dissimilarity matrix, and one was run using the BPUE dissimilarity matrix. Differences in fish assemblage structure (i.e., by zone, period, and the interaction of zone and period) were evaluated using a permutational multivariate ANOVA (PERMANOVA) for each of the dissimilarity matrices (species occurrence, CPUE, and BPUE). Bray–Curtis dissimilarity matrices were calculated using the Vegdist function, and NMDS and PERMANOVA were done using the MetaMDS and Adonis functions, respectively, in the vegan package (Oksanen et al. 2020) and program R (R Core Team 2021).

Abundance and biomass.— We used generalized mixed-effects models to estimate the effects of nutrient addition on both CPUE and BPUE of fish populations in the Kootenai River. Our analysis followed a before–after–control–impact (BACI) sampling design (Stewart-Oaten et al. 1986). The objective of the analysis was to estimate how CPUE and BPUE were influenced by period (i.e., pretreatment and treatment) within each sampling zone (i.e., control, treatment, and downstream). Every model included fixed effects to estimate the mean effect of each period and zone. We also included random-intercept effects in each model to account for natural variation between sampling sites and years. Separate analyses were run for each focal indicator species as well as a model with aggregated species-specific data (i.e., total fish). The three focal indicator species were Mountain Whitefish, Largescale Sucker, and Rainbow Trout. The three species were chosen as focal indicator fish due to their abundance in the river and the hypothesis that they would most notably respond to nutrient additions. More specifically, we evaluated whether abundance and trends in CPUE and BPUE of these three focal species would increase with the addition of nutrients over the treatment period.

Catch–abundance model.— The general model structure for estimating relative abundance was

$$\log[\lambda_{tj(i)}] = \boldsymbol{\beta^{CPUE}} \boldsymbol{X_{tj(i)}} + \alpha_{j(i)}^{CPUE} + \gamma_t^{CPUE} + \log[E_{tj(i)}],$$

$$y_{tj(i)} \sim NegBinom[\lambda_{tj(i)}, \phi^{CPUE}],$$

$$\alpha_{j(i)}^{CPUE} \sim N(0, \sigma_\alpha^{2\ CPUE}),$$

$$\gamma_t^{CPUE} \sim N(0, \sigma_\gamma^{2\ CPUE}),$$

where $\lambda_{tj(i)}$ is the estimated mean CPUE at subsection i in site j during year t; $\boldsymbol{\beta^{CPUE}}$ is a vector of estimated parameters, $\boldsymbol{X_{tj(i)}}$ is a vector of BACI predictor variables; $\alpha_{j(i)}^{CPUE}$ is a nested random effect on baseline CPUE from subsection i within site j; γ_t^{CPUE} is the year-specific random effect on the baseline CPUE; $E_{tj(i)}$ is a constant offset to account for the observed amount of effort (i.e., minutes of electrofishing) during a specific survey; $y_{tj(i)}$ is the observed total number of fish captured; $\sigma_\alpha^{2\ CPUE}$ is the estimated variance parameter for the subsection-level random effect nested within each site; and $\sigma_\gamma^{2\ CPUE}$ is the estimated variance for the year-based random effect. The vector of BACI predictor variables, $\boldsymbol{X_{tj(i)}}$, consisted of indicator variables to represent the zone-level effect (i.e., control, treatment, and downstream zones), the nutrient period effect (pretreatment or treatment), and the interaction between zones and periods for each observation $y_{tj(i)}$. It is important to note that a site-level random effect was not estimated because there was only a single site within the control zone. Thus, a general site-level random effect would have been confounded with the control zone fixed effect.

Biomass model.— We used a similar structure to evaluate the biomass data but with the inclusion of a hurdle component to account for surveys where no fish were captured. The hurdle approach allowed us to account for any zero data (e.g., no fish sampled) while still modeling biomass with the appropriate error structure given that it is a non-zero, continuous variable. The use of this model was deemed necessary since the frequencies of samples without fish were relatively substantial for some species (e.g., 32% of data for Rainbow Trout across sample sites). The hurdle component of the model was

$$logit[p_{tj(i)}] = \boldsymbol{\beta^{hu}} \boldsymbol{X_{tj(i)}} + \alpha_{j(i)}^{hu} + \gamma_t^{hu} + \beta_{Effort}^{hu} E_{tj(i)},$$

$$\alpha_{j(i)}^{hu} \sim N(0, \sigma_\alpha^{2\ hu}),$$

$$\gamma_t^{hu} \sim N(0, \sigma_\gamma^{2\ hu}),$$

$$I[C_{tj(i)} = 0] \sim Bernoulli[p_{tj(i)}],$$

where $p_{tj(i)}$ is the probability of encountering at least one fish during a survey at subsection i in site j during year t; $C_{tj(i)}$ is the total amount of biomass observed; $\boldsymbol{\beta}^{hu}$ is a vector of estimated parameters; $\boldsymbol{X_{tj(i)}}$ is a vector of BACI predictor variables; $\alpha_{j(i)}^{hu}$ is a nested random effect from subsection i within site j on baseline p; γ_{t}^{hu} is the year-specific random effect on the baseline p; $E_{tj(i)}$ is the observed amount of effort (i.e., minutes of electrofishing) during a specific survey; β_{Effort}^{hu} is the estimated effect of effort; $y_{tj(i)}$ is the observed total number of fish captured; $\sigma_{\alpha}^{2\ hu}$ is the estimated variance parameter for the subsection-level random effect nested within each site; and $\sigma_{\gamma}^{2\ hu}$ is the estimated variance for the year-based random effect. For observations where $C_{tj(i)}$ was greater than 0, the biomass component of the model assumed that BPUE had a gamma error distribution:

$$\log\left[\mu_{tj(i)}\right] = \boldsymbol{\beta}^{BPUE}\boldsymbol{X_{tj(i)}} + \alpha_{j(i)}^{BPUE} + \gamma_{t}^{BPUE} + \log\left[E_{tj(i)}\right],$$

$$C_{tj(i)} \sim Gamma\left(\mu_{ijt}, \phi^{BPUE}\right),$$

$$\alpha_{j(i)}^{BPUE} \sim N\left(0, \sigma_{\alpha}^{2\ BPUE}\right),$$

$$\gamma_{t}^{BPUE} \sim N\left(0, \sigma_{\gamma}^{2\ BPUE}\right),$$

where $\mu_{tj(i)}$ is the estimated mean biomass from subsection i at site j during year t; $\boldsymbol{\beta}$ is a vector of estimated parameters; $\boldsymbol{X_{tj(i)}}$ is a vector of BACI predictor variables; $\alpha_{j(i)}^{BPUE}$ is a nested random effect from subsection i within site j on baseline BPUE; γ_{t}^{BPUE} is the year-specific random effect on the baseline BPUE; $E_{tj(i)}$ is the observed amount of effort (i.e., minutes of electrofishing) during a specific survey; ϕ^{BPUE} is the estimated shape parameter for the gamma distribution; $\sigma_{\alpha}^{2\ BPUE}$ is the estimated variance parameter for the subsection-level random effect; and $\sigma_{\gamma}^{2\ BPUE}$ is the estimated variance for the year-based random effect. The hurdle portion of the model was not run for the total biomass analysis because there were no observations with $C_{tj(i)}$ equal to 0 at the aggregate level. Results were provided as odds (odds = $p/[1 - p]$) in the place of probabilities. Since the hurdle model is estimated using a logit link, which is $\log[p/(1 - p)]$ = B0 + B1 + B2, odds are a typical way to report effect sizes.

Both the abundance and biomass models were fit in a Bayesian framework using STAN and the brms package in R (Bürkner 2017; R Core Team 2021). We used improper uniform priors on $(-\infty, \infty)$ for all fixed effects, a gamma distribution with both shape and scale parameters set equal to 0.01 for all shape parameters estimated as part of a gamma or negative binomial distribution, and a weakly informative generalized student's t

distribution with 3 degrees of freedom, a location parameter equal to 0, and a scale parameter equal to 10 as priors for all random effect variance parameters. The gamma distribution was chosen for its support for non-zero, continuous variables (i.e., biomass data in this study). The negative binomial distribution was chosen because it allowed us to model overdispersed (large variance) discrete data. The posterior distribution was sampled using four Markov chain–Monte Carlo chains, and each chain sampled the posterior distribution a total of 2,000 times. Within each chain, half of the samples were used in the "burn-in" process and the other half were reported as posterior samples (i.e., 4,000 samples per posterior distribution). Convergence and mixing were assessed by evaluating posterior traceplots and Gelman–Rubin statistics (Gelman and Rubin 1992). We used posterior medians as point estimates of parameters and the 90% highest probability density (HPD) credible intervals (CIs) for characterizing uncertainty of each marginal posterior distribution (Chen and Shao 1999). We also estimated posterior conditional medians and their associated 90% HPD CIs for each zone–period combination to assess model fit and to evaluate the cumulative effects of the fixed effects.

Population estimates.— Mark–recapture population estimates were regularly conducted at Hemlock Bar (Figure 1), a 3-km (9.9-ha) section of the Kootenai River within the treatment zone, from 1980 until 2016 using boat electrofishing as described by Downs (2000). Although the population surveys were not originally designed to evaluate the effect of nutrient additions on fish populations, the data were useful for monitoring trends in abundance concomitant with nutrient additions, as the estimates were generated well before nutrient addition began (i.e., 1980) and were ongoing years after the onset of nutrient addition (i.e., through 2016). During each population survey, Mountain Whitefish, Largescale Suckers, and Rainbow Trout were fin-clipped during the second week in August and recaptured the following week to allow adequate mixing in the sample reach. Population estimates were calculated using Chapman's modification of the Petersen method (Ricker 1975; Krebs 1999):

$$N = \left[(M + 1) \times \frac{C + 1}{R + 1}\right] - 1,$$

where N represents the population estimate, M represents the number of marked fish, C represents the number of fish captured during the recapture sample, and R represents the number of recapture marks in the recapture sample. The 95% confidence limits for the population estimates were calculated based on the Poisson distribution (Ricker 1975; Seber 1982).

RESULTS

A total of 25,375 fish from 21 different species was sampled from five sites in the Kootenai River from 2002 to 2017. Approximately 97% of the fish sampled were either Mountain Whitefish, Northern Pikeminnow *Ptychocheilus oregonensis*, Largescale Suckers, Redside Shiner, Peamouth *Mylocheilus caurinus*, or Rainbow Trout (Table 1). The remaining 3% of the catch represented 16 less-abundant native and nonnative fish species. The proportion of each species in the catch remained relatively consistent across sampling years and within river zones. Mountain Whitefish, Largescale Suckers, Rainbow Trout, Peamouth, Northern Pikeminnow, and Redside Shiner dominated catch and biomass in the control and nutrient addition zones. The same species dominated catch and biomass in the downstream zone, with the exception of Mountain Whitefish and Rainbow Trout, both of which were infrequently encountered in that zone.

Fish Assemblage

The NMDS ordinations indicated that variability in fish assemblage was most closely associated with river zones and treatment period. The NMDS ordination fitted to the CPUE data indicated that sampling sites in the control and treatment zones were more closely associated with

one another than with sampling sites in the downstream zone (Figure 2). Sites in the treatment and control zones were most closely associated with Mountain Whitefish, Rainbow Trout, Westslope Cutthroat Trout, Brown Trout, and Brook Trout, whereas sites in the downstream zone were most closely associated with Northern Pikeminnow, Redside Shiner, Smallmouth Bass, and Pumpkinseed (Figure 2). Perhaps most noteworthy, standard error ellipses for the pretreatment and treatment periods in the nutrient addition zone did not overlap, suggesting that the fish assemblage (i.e., as gauged by CPUE) shifted from the pretreatment and treatment periods in that zone. Conversely, standard error ellipses for the pretreatment and treatment periods in both the control and downstream zones displayed distinct overlap (Figure 2). The PERMANOVA for CPUE corroborated the NMDS ordination plot, indicating that CPUE differed by zone ($F = 89.5$, $P = 0.001$), period ($F = 7.0$, $P = 0.002$), and the interaction between zone and period ($F = 3.2$, $P = 0.01$). The NMDS ordination that was fit to the BPUE data displayed a pattern similar to but generally less supported than those observed in the CPUE ordination. Species associations by river zone were similar to those observed in the CPUE ordination, except that Largescale Suckers were closely associated with sites in the treatment zone during the

TABLE 1. Percentage of fish species captured in total and by river zone during fall electrofishing surveys on the Kootenai River from 2002 to 2017. Species are listed in order of relative abundance. Catch represents an average over sites and years for each species.

| Common name	Scientific name	All zones	Control	Treatment	Downstream
Mountain Whitefish	*Prosopium williamsoni*	44.44	59.88	75.91	4.31
Northern Pikeminnow	*Ptychocheilus oregonensis*	15.47	4.03	2.42	35.52
Largescale Sucker	*Catostomus macrocheilus*	12.33	10.41	10.64	12.98
Redside Shiner	*Richardsonius balteatus*	10.12	5.02	3.38	20.64
Peamouth	*Mylocheilus caurinus*	9.66	2.09	0.44	23.37
Rainbow Trout	*Oncorhynchus mykiss*	5.15	16.95	6.42	1.20
Longnose Sucker	*Catostomus catostomus*	0.94	0.36	0.22	0.74
Yellow Perch	*Perca flavescens*	0.81	0.00	0.00	0.81
Westslope Cutthroat Trout	*O. clarkii lewisi*	0.31	0.57	0.20	0.13
Slimy Sculpin	*Cottus cognatus*	0.28	0.20	0.14	0.46
Longnose Dace	*Rhinichthys cataractae*	0.20	0.02	0.35	0.01
Kokanee	*O. nerka*	0.18	0.18	<0.01	<0.01
Pumpkinseed	*Lepomis gibbosus*	0.08	0.00	0.01	0.28
Brown Trout	*Salmo trutta*	0.08	0.43	0.09	0.01
Burbot	*Lota lota*	0.06	0.00	0.03	0.02
Brook Trout	*Salvelinus fontinalis*	0.02	0.09	0.01	0.00
Brown Bullhead	*Ameiurus nebulosus*	0.01	0.00	0.00	0.01
Bull Trout	*Salvelinus confluentus*	0.01	0.01	0.00	0.00
Bluegill	*Lepomis macrochirus*	<0.01	0.00	0.00	<0.01
Smallmouth Bass	*Micropterus dolomieu*	<0.01	0.00	0.00	<0.01
Black Crappie	*Pomoxis nigromaculatus*	<0.01	0.00	0.00	<0.01
Largemouth Bass	*Micropterus salmoides*	<0.01	0.00	0.00	<0.01
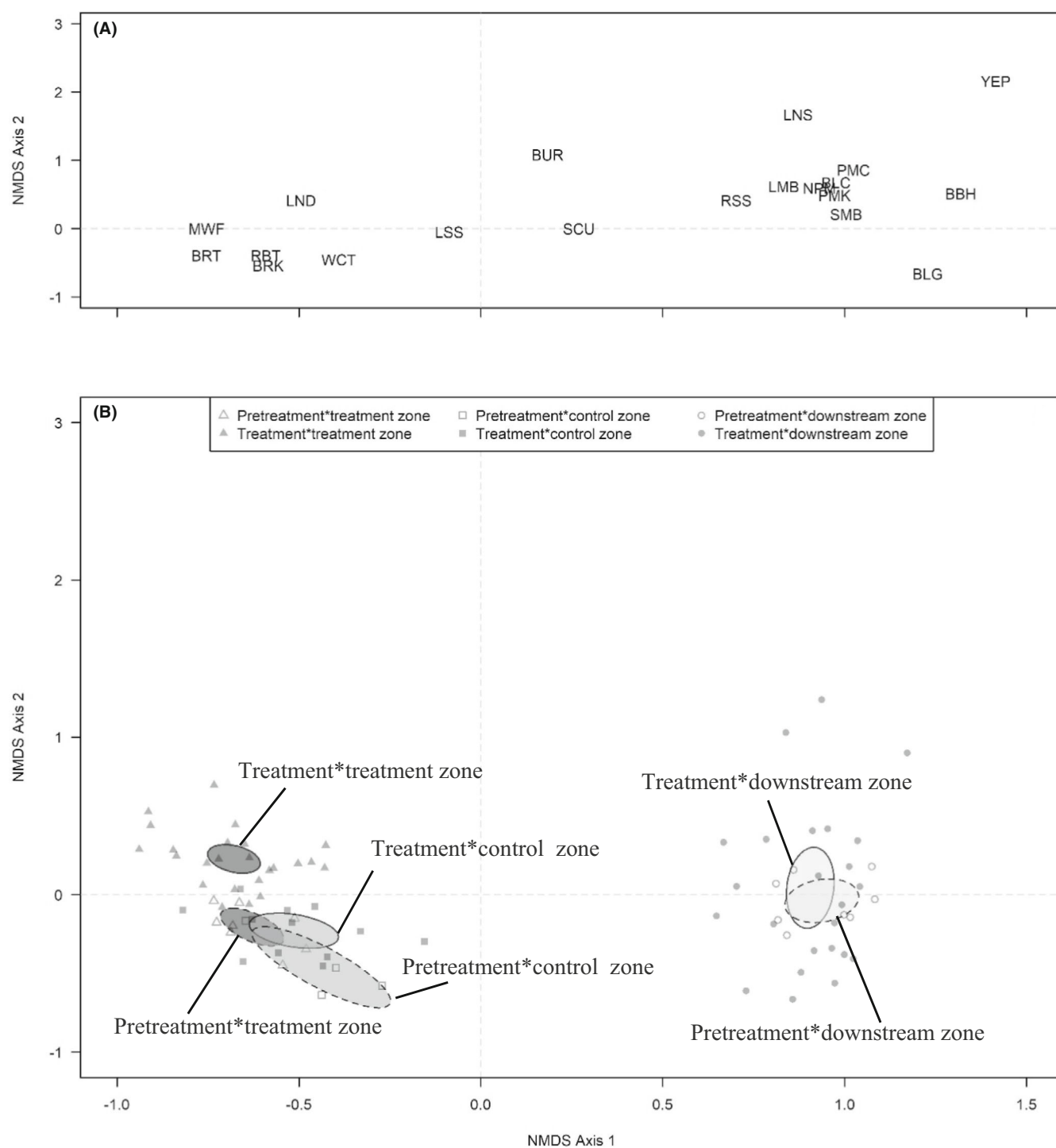
FIGURE 2. Nonmetric multidimensional scaling (NMDS) ordination (stress = 0.06) of the Kootenai River fish assemblage using the CPUE data: **(A)** species scores are displayed in the ordination space; and **(B)** site–year combinations in the treatment, control, and downstream zones are displayed in the ordination space. Taxa presented in panel A include Brown Bullhead (BBH), Bluegill (BLG), Brook Trout (BRK), Brown Trout (BRT), Burbot (BUR), Black Crappie (BLC), Largemouth Bass (LMB), Longnose Dace (LND), Longnose Sucker (LNS), Largescale Sucker (LSS), Mountain Whitefish (MWF), Northern Pikeminnow (NPM), Peamouth (PMC), Pumpkinseed (PMK), Rainbow Trout (RBT), Redside Shiner (RSS), Slimy Sculpin (SCU), Smallmouth Bass (SMB), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP). Shaded ellipses in panels A and B depict SEs in the ordination space.

treatment period (Figure 3). Similar to the CPUE ordination, pretreatment and treatment period ellipses in the nutrient addition zone did not display distinct overlap for the BPUE ordination. The PERMANOVA for BPUE generally supported the NMDS ordination plot: BPUE differed by zone ($F = 57.1$, $P = 0.001$) and period ($F = 6.2$, $P = 0.003$) but not the interaction between the two ($F = 1.4$, $P = 0.22$).

Catch–Abundance Model

Abundance modeling showed that mean CPUE increased during the treatment period relative to the pretreatment period ($\beta^{CPUE}_{TreatmentPeriod}$) across zones for Mountain Whitefish (+80%; CI: +22%, +152%), Rainbow Trout (+129%; CI: +52%, +262%), and total fish (+66%, CI: +12%, +146%; Figure 4). However, within the treatment zone, Largescale Sucker CPUE increased an estimated 82% (CI: +20%, +156%) and the total CPUE of all fish species increased an estimated 28% (CI: 0%, +60%) during the treatment period ($\beta^{CPUE}_{TreatmentZone:TreatmentPeriod}$; Figure 4). The estimated effect of the nutrient treatment on CPUE within the downstream zone was negative ($\beta^{CPUE}_{DownstreamZone:TreatmentPeriod}$) for total fish (i.e., all species combined; −30%, CI: −45%, −11%), Mountain Whitefish (−48%; CI: −66%, −20%), and Rainbow Trout (−44%; CI: −64%, −11%). The main effect of the downstream zone on catch rates ($\beta^{CPUE}_{DownstreamZone}$) was largely negative for Mountain Whitefish (−89%; CI: −96%, −75%) and Rainbow Trout (−90%; CI: −96%, −80%) relative to the control zone (Figure 4), which simply implies that the two species were not abundant in the downstream zone relative to the control zone. All other fixed effects estimated in the catch modeling provided little evidence (e.g., 90% CIs included 0) of a meaningful effect on catch. Lastly, the random effects suggested that estimated variance was higher among the subsections nested within each site compared to the random effect estimated among years for each model run (i.e., spatial variance > temporal variance).

Biomass Model

Trends in BPUE were similar to those observed for CPUE. In the hurdle portion of the model, we estimated that the odds of not observing a Mountain Whitefish or a Rainbow Trout in the downstream zone ($\beta^{hu}_{DownstreamZone}$) were 85.76 (90% HPD CI: 3.69, 2,393.48) and 309.58 (90% HPD CI: 23.0, 5,111.67) times greater, respectively, relative to the control zone. Additionally, we estimated that the odds of not observing a Rainbow Trout in the treatment zone ($\beta^{hu}_{TreatmentZone}$) were 18.16 (CI: 1.08, 296.52) times greater compared to the control zone (Figure 5). There was no evidence that the rest of the fixed effects in all of the other hurdle models influenced the probability of not observing a particular species. The gamma

regression portion of the model estimated that biomass tended to be lowest in the downstream zone relative to the control zone across periods ($\beta^{BPUE}_{DownstreamZone}$) for total fish (i.e., all species combined; −43%, CI: −66%, −1%), Mountain Whitefish (−97%; CI: −99%, −95%), and Rainbow Trout (−80%, CI: −89%, −65%; Figure 5). Biomass per unit of effort increased over the treatment period ($\beta^{BPUE}_{TreatmentPeriod}$) across all zones (combined) for Mountain Whitefish (+46%; CI: +3.1%, +114%) and Rainbow Trout (+91%; CI: +27%, +182%) relative to the pretreatment period. The model also estimated a decrease in mean biomass within the downstream zone during the treatment period ($\beta^{BPUE}_{DownstreamZone:TreatmentPeriod}$) for Mountain Whitefish (−55%, CI: −72%, −29%) and Rainbow Trout (−38%, CI: −62%, −0.1%; Figure 5). Lastly, within the treatment zone and during the treatment period ($\beta^{BPUE}_{TreatmentZone:TreatmentPeriod}$), mean biomass of total fish (+46%; CI: +11%, +92%) and Largescale Suckers (+111%; CI: +33%, +216%) increased. There was little support for all of the other estimated fixed effects. For the estimated random effects, variance was higher among the subsections nested within each site compared to the random effect estimated among years for each model run (i.e., spatial variance > temporal variance).

One thing to note is that species-specific and total BPUE and CPUE were highly variable within each zone and treatment across all years sampled. Both zero data and extremely high values (four- to sevenfold greater than median values) were common when aggregating data across zone and treatment. The extreme variability of CPUE and BPUE values was likely the result of large amounts of habitat variability present within each site. The potential outlier values resulted in highly skewed distributions of observed CPUE and BPUE. The resulting observed mean CPUE and BPUE values were sensitive to these few large observations, resulting in observed mean values that were much larger than the observed median values. That said, the model estimates fit the majority of the data well (Figures 4, 5). More specifically, the 90% CIs covered the bulk of the data in each zone/period category.

Population estimates at Hemlock Bar largely corroborated CPUE data from sites in the nutrient addition zone. Specifically, mean abundance estimates for all three focal indicator species increased from the pretreatment to treatment periods (Figure 6). Furthermore, temporal trends in CPUE estimates tracked closely with temporal trends in abundance estimates for each focal indicator species (Figure 4), suggesting that CPUE was a viable surrogate for abundance. Abundance estimates were not available for the three species at locations in the control zone, precluding full evaluation of changes as a result of nutrient additions. Regardless, inferences gleaned from abundance estimates spanning the pretreatment to treatment periods support interpretations from more formal analyses.
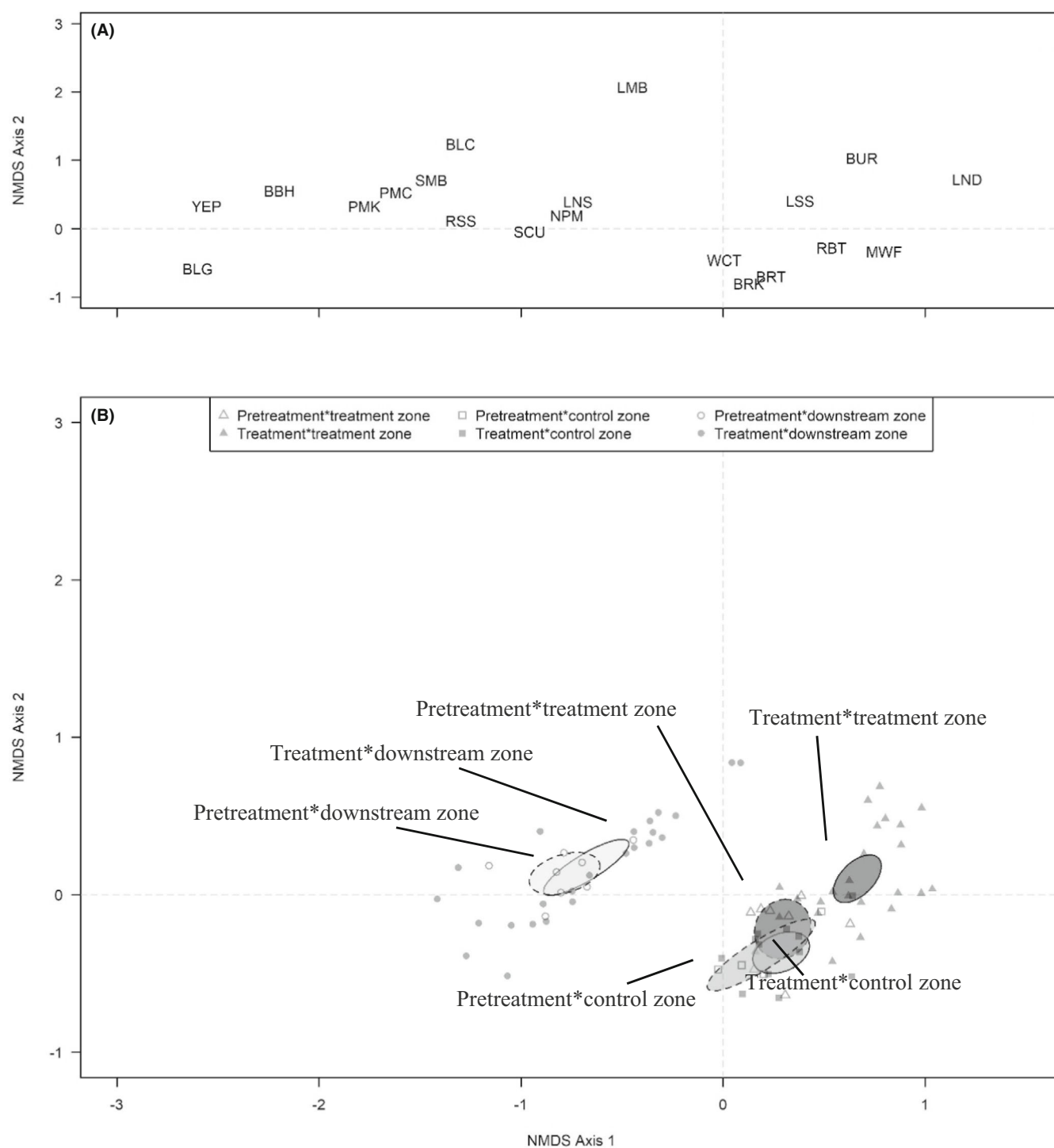
FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordination (stress = 0.09) of the Kootenai River fish assemblage using the biomass-per-unit-of-effort data: **(A)** species scores are displayed in the ordination space; and **(B)** site–year combinations in the treatment, control, and downstream zones are displayed in the ordination space. Taxa presented in panel A include Brown Bullhead (BBH), Bluegill (BLG), Brook Trout (BRK), Brown Trout (BRT), Burbot (BUR), Black Crappie (BLC), Largemouth Bass (LMB), Longnose Dace (LND), Longnose Sucker (LNS), Largescale Sucker (LSS), Mountain Whitefish (MWF), Northern Pikeminnow (NPM), Peamouth (PMC), Pumpkinseed (PMK), Rainbow Trout (RBT), Redside Shiner (RSS), Slimy Sculpin (SCU), Smallmouth Bass (SMB), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP). Shaded ellipses in panels A and B depict SEs in the ordination space.
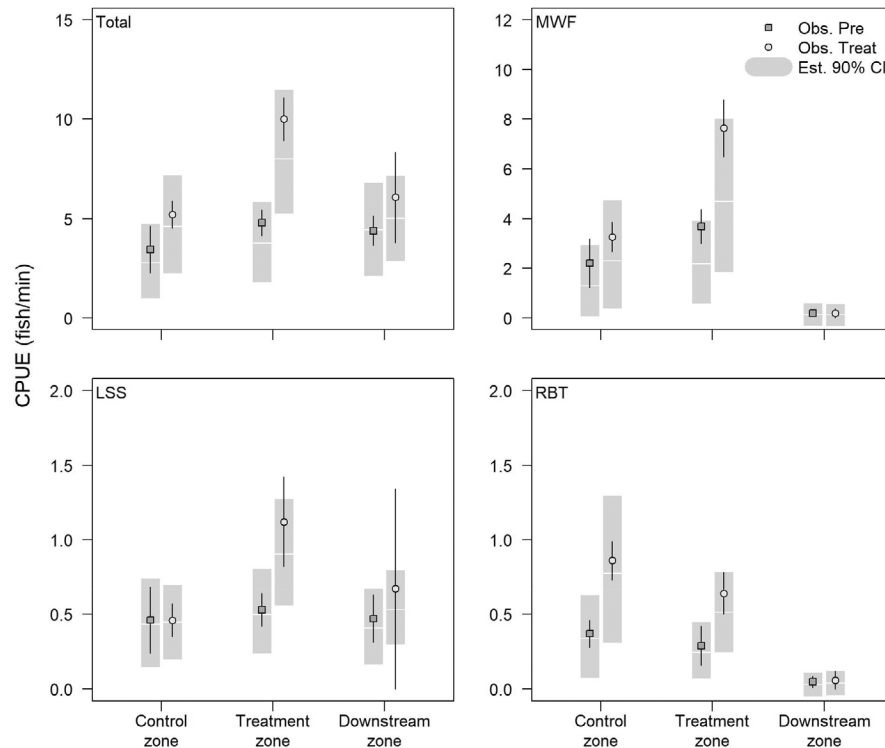
FIGURE 4. Estimated conditional posterior credible intervals (box plots) from the abundance modeling and the observed (Obs.) CPUE (number of fish/min of electrofishing) values (points) for each combination of zone (control, treatment, and downstream) and period (pretreatment [Pre] and treatment [Treat]). Error bars on observed data (points) represent ±1 SE. High values of CPUE and zero-inflated data led to highly skewed distributions across species and zones. Species abbreviations are as follows: Largescale Sucker (LSS), Mountain Whitefish (MWF), and Rainbow Trout (RBT).

DISCUSSION

The addition of nutrients to the Kootenai River increased fish abundance and biomass over a 20-km stretch of river downstream from the treatment site. Initial multivariate analyses indicated a slight shift in CPUE metrics within the treatment and control zones of the river from the pretreatment to treatment periods. Further analysis indicated that the greatest increase over the treatment period was in the Largescale Sucker population, with a 44% increase in abundance and a 55% increase in biomass in the treatment zone. Similarly, a marked increase in the same response variables was observed in Rainbow Trout and Mountain Whitefish; however, these observations were not supported in our statistical modeling. The observed increases in focal indicator species were corroborated with trend population estimates performed at the same time of year. The mechanisms responsible for the increases are likely bottom-up effects on trophic production that ultimately increased food resources for fish. Hoyle et al. (2014) reported that following the first 5 years of fertilization to the Kootenai River, there was a sixfold increase in chlorophyll accrual rates and densities of edible green algae and diatoms increased by 30%. Therefore, it is

not surprising that Largescale Suckers—a species known to have diets comprised of nearly 90% periphyton (Dauble 1986)—exhibited the most notable responses to nutrient additions. Likewise, Minshall et al. (2014) reported a 69% increase in the total abundance of benthic macroinvertebrates and a 49% increase in their biomass after the addition of nutrients to the Kootenai River. As such, it is logical that Rainbow Trout and Mountain Whitefish, two species known to feed primarily on macroinvertebrates and their larvae, also exhibited notable increases in the treatment zone. However, the biomass and catch modeling was not directly able to attribute the increases in these species to the addition of nutrients. Similar studies of other western rivers have documented positive effects of fertilization to fish populations through the increase in trophic production. Peterson et al. (1993) reported an increase in the abundance of young-of-the-year Arctic Grayling *Thymallus arcticus* in the Kuparuk River, Alaska, following 4 years of fertilization and attributed it to increases in epilithic algae and insects. A comparable study by Wilson et al. (2003) in south coastal British Columbia reported a fourfold increase in Rainbow Trout abundance following four seasons of inorganic nutrient
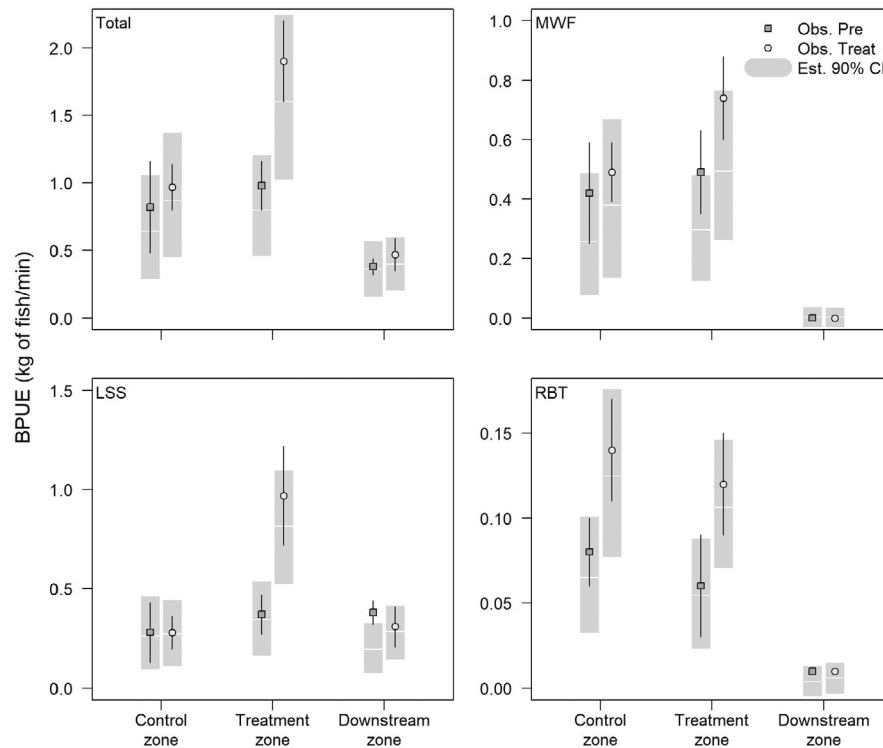
FIGURE 5. Estimated conditional posterior credible intervals (box plots) from the biomass modeling and the observed (Obs.) biomass-per-unit-of-effort (BPUE; kg of fish/min of electrofishing) values (points) for each combination of zone (control, treatment, and downstream) and period (pretreatment [Pre] and treatment [Treat]). Error bars on the observed data (points) represent ±1 SE. High values of BPUE and zero-inflated data led to highly skewed distributions across species and zones. Species abbreviations are as follows: Largescale Sucker (LSS), Mountain Whitefish (MWF), and Rainbow Trout (RBT).

additions. Our results were largely consistent with those reported in the literature.

Although abundance of three focal indicator fish species increased during nutrient addition, the magnitude of their respective increases was not equal. Largescale Suckers most notably responded to nutrient addition efforts, followed by Mountain Whitefish and then Rainbow Trout. Watkins et al. (2017) evaluated the influence of nutrient addition and other mitigation efforts in the Kootenai River on the growth, survival, and recruitment of Largescale Suckers and Mountain Whitefish and found that incremental growth of Largescale Suckers was positively correlated with the addition of nutrients. We documented marked increases in biomass of Largescale Suckers in response to nutrient addition, corroborating the findings of Watkins et al. (2017). Conversely, Watkins et al. (2017) found that although the abundance of Mountain Whitefish nearly doubled after nutrient additions began, incremental growth declined, suggesting a possible density-dependent response in growth beginning around 2010. Similarly, we documented a decline in biomass of Mountain Whitefish in later treatment years, which corroborated their findings.

It is important to note that biomass of Mountain Whitefish in the treatment zone has been consistently increasing since its lowest point in 2012; however, it is unknown whether growth of individual fish has changed since 2012. The observed response of Mountain Whitefish is not entirely understood; however, such unanticipated results are not unique to the Kootenai River. For example, reduced growth caused by intraspecific competition, indirectly caused by nutrient additions, was reported for Arctic Grayling in the Kuparuk River, Alaska (Deegan et al. 1997). It is also plausible that our trend monitoring years (2002–2017) simply captured the cyclical behavior of Mountain Whitefish population dynamics in the Kootenai River. Population cycles in various freshwater and anadromous fish species are well documented (Townsend 1989; Levy and Wood 1992). Such cyclical behavior is often attributed to the effects of density dependence on fecundity or survival of eggs or larvae subject to interaction with predators. Similar studies on the growth, survival, and recruitment of Rainbow Trout have not been completed but would likely enhance the body of knowledge on salmonid responses to nutrient additions in the Kootenai River and elsewhere.
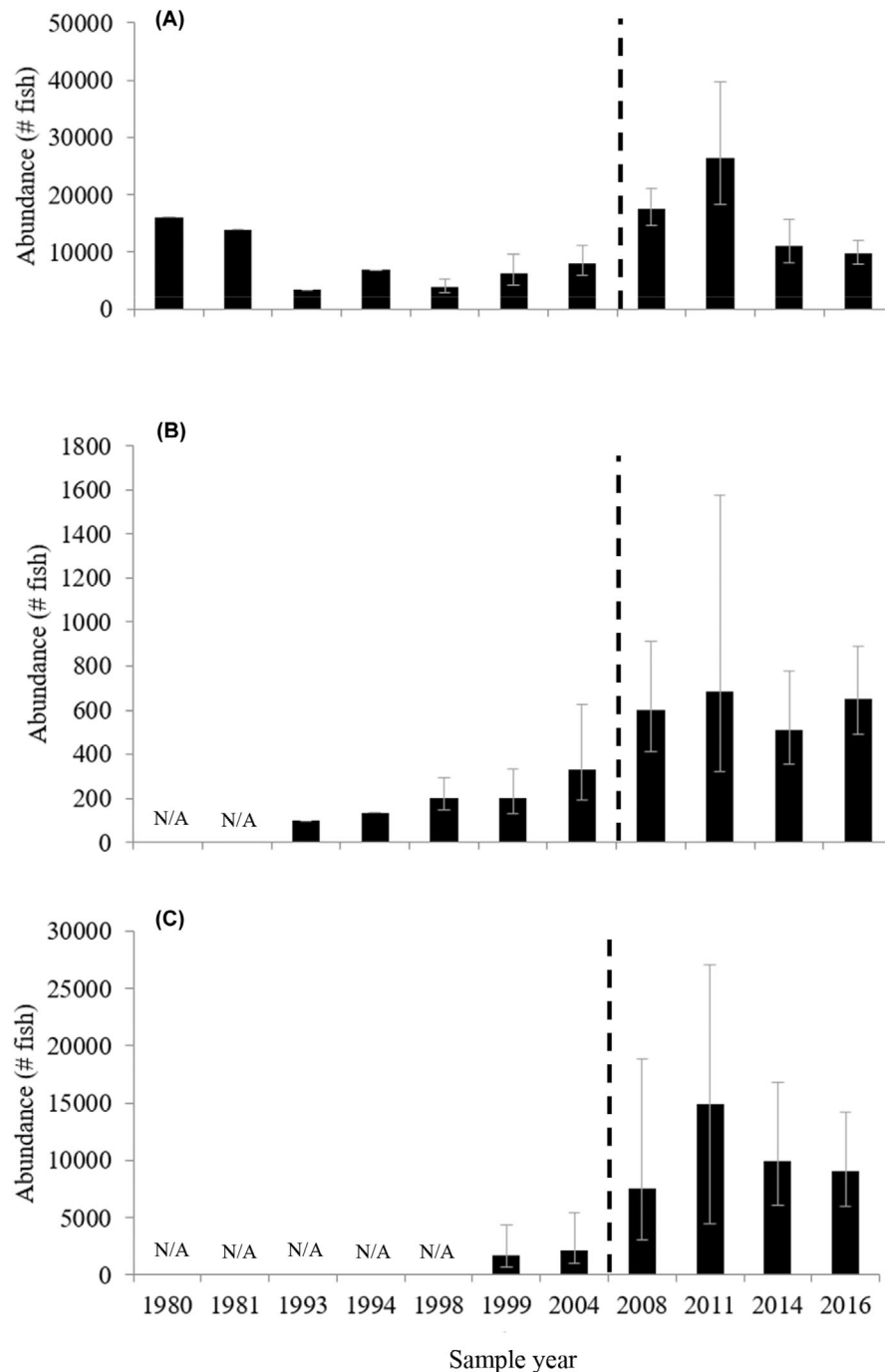
FIGURE 6. Abundance estimates for **(A)** Mountain Whitefish, **(B)** Rainbow Trout, and **(C)** Largescale Suckers in a 3-km (9.9-ha) reach located in the treatment zone of the Kootenai River. Estimates represent the number of fish of each species within the river reach, and error bars represent upper and lower 95% confidence limits. The dashed black line denotes the year (2006) when nutrient additions began in the river.

All multivariate and univariate analyses indicated that abundance and biomass of Rainbow Trout increased to the same or greater degree from the pretreatment to treatment periods in the control zone compared to the treatment zone. The result was initially surprising, but upon further investigation of spatiotemporal movements and behaviors of Rainbow Trout in the Kootenai River, the finding was logical. The control zone, located approximately 10 rkm above the treatment zone, was assumed to be independent from other sampling locations yet close enough to be comparable in habitat complexity and ambient productivity at lower trophic levels. For most species

sampled at each trophic level, the distance from the control zone to the nutrient addition zone was sufficient to maintain independence (Holderman et al. 2009; Hoyle 2012; Minshall et al. 2014); however, results from our study indicate that nutrient treatments may have affected Rainbow Trout in both the control and treatment zones. Although the mechanisms driving the observed response are not entirely understood, they are likely linked to adult spawning activity. Results from a previous telemetry study indicated that the majority of adult Rainbow Trout residing in the treatment zone migrate upstream (i.e., past the control zone) and enter tributaries in Montana to spawn (Walters et al. 2005). Spawning migrations of Rainbow Trout occur in the spring, which does not temporally coincide with fall sampling efforts for our study. Therefore, it is unlikely that movement of adult Rainbow Trout directly influenced abundance and biomass in the control zone. In fact, when evaluating size data, the majority of the observed increases in Rainbow Trout in both the control and treatment zones were attributable to juvenile Rainbow Trout, indicative of an increase in recruitment. Johnston et al. (1999) found that after 5 years of adding inorganic nutrients to a montane lake in British Columbia, Rainbow Trout reproductive output, growth, and yield significantly increased. Although not quantified, it is possible that Rainbow Trout within the treatment zone of the Kootenai River experienced greater reproductive potential during the treatment period, resulting in increased production from both Idaho and Montana tributaries. Bradford and Taylor (1997) found that stream-type Chinook Salmon O. tshawytscha exhibited post-emergence dispersal patterns reaching up to 100 km downstream. It is possible that Rainbow Trout that were spawned in Montana tributaries exhibited dispersal patterns that increased abundances in both the control and treatment zones of the Kootenai River. A long-term population monitoring survey of Rainbow Trout conducted by Montana Fish, Wildlife, and Parks showed that the majority of dispersal occurs during the early juvenile years, followed by establishing a well-defined, localized home range as adults (James Dunnigan, Montana Fish Wildlife, and Parks, personal communication). Such results highlight the need to fully understand recruitment trends of Rainbow Trout in the Kootenai River as well as the extent of migration behavior when designing a study to evaluate treatment effects on a particular fish species.

Although observing results of large-scale mitigation activities within a relatively short period of time (i.e., within 3–5 years) may be a reasonable expectation, fish life histories and longevities complicate the timeframe during which effects might be detected. Researchers and managers should carefully consider program objectives and hypotheses and subsequent timeframes for sampling and data analysis to ensure a more thorough and comprehensive interpretation of mitigation effects. For example, Watkins et al. (2017) found that Largescale Suckers in our study area were not fully recruited to boat electrofishing gear until approximately age 11. Regardless of the mechanism(s), it is clear that the benefits of performing a long-term evaluation allowed us to capture the effects of nutrient addition on this particular species that otherwise might have been missed if sampling had been discontinued after 3–5 years. Similarly, the long-term sampling design of our study allowed us to capture the initial increases in numbers and subsequent declines in growth (i.e., density-dependent response; Watkins et al. 2017) of Mountain Whitefish that likely would have been missed if sampling duration had been shorter. Other stream fertilization studies suggested that short-term studies (even up to 8 years) were poor predictors of the full ecological effects that nutrient addition efforts might eventually provide to a system (Slavik et al. 2004). It is also likely that other considerations (e.g., inferential scope) beyond spatiotemporal should be considered when designing a large-scale nutrient addition program such as the one on the Kootenai River.

The matter of inferential scope in fisheries research and management is paramount and carries significant implications (e.g., time and budget). Fisheries scientists must balance the need for adequate inference with financial and logistical realities. Failure to adequately do so may result in improperly managed fisheries and ill-informed decision making (Fausch et al. 2002; Fischer et al. 2010). Fish populations often respond to mitigation actions in predictable ways (Watkins et al. 2017). Prior to responding at the assemblage level, populations often manifest a response in rate functions (i.e., growth, survival, or recruitment; Watkins et al. 2017). We first evaluated the effects of nutrient additions at the assemblage level using descriptive multivariate analyses (i.e., NMDS). While the NMDS indicated some slight shifts in fish assemblage, it was clear that further information was needed to more explicitly understand how nutrient additions were affecting populations. Catch and biomass modeling provided further clarity than the NMDS models by revealing which species responded the most to the treatment. Population abundance estimates corroborated the results of the catch and biomass models. However, further clarity was needed to understand some of the unexpected trends in catch and biomass that were observed. Watkins et al. (2017) evaluated the effects of nutrient additions on rate functions (growth, survival, and recruitment) of Mountain Whitefish and Largescale Suckers, and our results, coupled with theirs, nearly completed our understanding of fish response to the nutrient addition program on the Kootenai River. Our study has allowed researchers and managers to adaptively manage the program and consider possibly expanding the program to other portions of the Kootenai River. It would be beneficial for fishery scientists to carefully consider project scope

and financial and logistical realities to ensure that success of restoration projects can be adequately measured.

Abundance, biomass, and structure of the fish assemblage exhibited longitudinal decay by 20–45 rkm downstream from the treatment site. Smith et al. (2016) reported similar longitudinal shifts in the Kootenai River fish assemblage and attributed those shifts largely to differences in habitat among the three study reaches. In addition, since the Kootenai River is a dam-regulated river, dam operations influence the temperature, sediment, discharge, and nutrient regimes in the river, all of which directly influence the fish assemblage. Little evidence of nutrients affecting fish communities was found in the downstream zone at sampling sites KR4 and KR2, which were located approximately 45 and 100 rkm, respectively, downstream of the treatment site. Although Mountain Whitefish and Rainbow Trout biomass decreased in the downstream zone from the pretreatment to treatment periods, the decrease was not biologically meaningful. Smith et al. (2016) reported that Rainbow Trout and Mountain Whitefish were not closely associated with the downstream zone and its habitat, and our NMDS results corroborated their finding. Mountain Whitefish and Rainbow Trout biomass in the downstream zone from 2002 to 2017 represented only 0.74% and 1.72%, respectively, of the total biomass in that zone. Similar to our observation of rapid longitudinal decay in fish abundance, biomass, and structure by 20–45 rkm downstream from the treatment site, similar but more pronounced and rapid longitudinal decay was reported for water quality (e.g., soluble reactive phosphorus and dissolved inorganic nitrogen), chlorophyll *a*, and benthic macroinvertebrates (Holderman et al. 2009; Hoyle 2012; Minshall et al. 2014; i.e., 10–15 rkm). The uptake distance of nutrients is directly related to water velocity and the ability of the trophic communities to "spiral" nutrients and release them back into the water column (Mulholland 1996; Ashley and Stockner 2003). Nutrient dosing sites are often strategically located at maximum uptake distances to remain consistent with a river's more natural food web processes. For example, the Keough River in British Columbia flows 30 km from the source to the ocean and possessed a spiraling distance of approximately 6 km (Ashley and Stockner 2003). A slow-release fertilizer was applied at five equidistant locations to facilitate sustained nutrient effects throughout the system (Ashley and Stockner 2003). Although additional research is required to fully understand nutrient spiraling processes in the Kootenai River, our results, along with the documented effects on other trophic levels, suggest a potential need for additional dosing sites to extend the benefits of nutrients to fish communities and lower trophic levels in the lower parts of the basin.

Like many large rivers in the northwestern United States, the Kootenai River basin is a highly altered system, adjusting to the effects of impoundment and subsequent spatiotemporal alterations in flow, water temperature, hydrologic regime, and nutrient regime (Snyder and Minshall 2005). As such, the Kootenai River has been the target of extensive mitigation efforts and supporting research, monitoring, and evaluation. Because of this, there is the potential for unaccounted factors to confound the results of our evaluation. For example, Smith et al. (2016) found that the fish assemblage in the Kootenai River shifted longitudinally in ways that confounded nutrient-defined river zones with geomorphic habitat types. However, for the purpose of the study reported herein, treatment comparisons of interest were within each river zone, not among river zones, which lessened the concerns over confounding the results of this study. Likewise, factors such as angler harvest could potentially influence or confound these types of evaluations. Although a potential influence, fishing regulations in the Idaho and Montana sections of the Kootenai River remained unchanged during the entirety of the study. Furthermore, the conservative regulations in the Idaho section (2 trout·d^{-1}·angler^{-1}, with no harvest allowed on trout under 406 mm [16 in]) essentially functioned as a catch-and-release fishery (Hardy et al. 2013). The study results reported herein could not account for the many anthropogenic perturbations and subsequent mitigation and restoration activities, so it is possible that some of the reported results are confounded by factors beyond the scope of this study.

Although the benefits of nutrient addition and its positive influence on multiple trophic levels are well understood (Perrin et al. 1987; Slaney and Ward 1993; Bowden et al. 1994; Tank et al. 2008), the Kootenai River is approximately 30 times larger in discharge than other rivers that have been experimentally fertilized (Minshall et al. 2014), making it the largest river fertilization program in the world to date. For this reason alone, our study is a defining milestone and provides compelling evidence that the mitigation of nutrient declines in rivers of sizes similar to the Kootenai River can result in positive influences on the fish community where food is limiting growth, survival, and recruitment.

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