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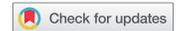
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ARTICLE

Response of Fish Population Dynamics to Mitigation Activities in a Large Regulated River

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Abstract

Extensive water development in large rivers has precipitated many negative ecological effects on native fish populations. Mitigation for such development often focuses on restoring biological integrity through remediation of the physical and chemical properties of regulated rivers. However, evaluating and defining the success of those programs can be difficult. We modeled the influence of mitigation-related environmental factors on growth and recruitment of two ecologically important native fish species (Largescale Sucker *Catostomus macrocheilus* and Mountain Whitefish *Prosopium williamsoni*) in the Kootenai River, Idaho. Artificial nutrient (phosphorus) addition best predicted the variability in annual growth of both species. Nutrient addition was positively related to Largescale Sucker growth but negatively related to Mountain Whitefish growth. The best model explained 82% of the annual variability in incremental growth for Largescale Suckers and 61% of the annual variability for Mountain Whitefish. Year-class strength of Largescale Suckers was not closely related to any of the environmental variables evaluated; however, year-class strength of Mountain Whitefish was closely associated with nutrient addition, discharge, and temperature. Most research has focused on biotic assemblages to evaluate the effects of mitigation activities on fishes, but there is an increased need to identify the influence of rehabilitation activities on fish population dynamics within those assemblages. Here, we demonstrate how fish growth can serve as an indicator of rehabilitation success in a highly regulated large river. Future fish restoration projects can likely benefit from a change in scope and from consideration of an evaluation framework involving the response of population rate functions to mitigation.

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Large rivers are nonwadeable lotic systems characterized by high habitat complexity and biodiversity and rank among the most unique and diverse ecosystems worldwide. Throughout the world, large rivers have been modified by water development activities to serve human needs (e.g., transportation, irrigation, and power generation), thereby resulting in degradation and loss of habitat used by riverine fishes (Dynesius and Nilsson 1994). Anthropogenic influences on large rivers have resulted in extinctions of many fluvial fish species (Ricciardi and Rasmussen 1999) and changes in assemblages of aquatic biota through alteration of the physical, chemical, and biological properties of riverine habitat (Bain et al. 1988; Waite and Carpenter 2000; Quist et al. 2005; Rinne et al. 2005). Water control structures (e.g., dams) and other forms of instream development (e.g., levees) have had deleterious effects on aquatic habitat in large rivers. Cumulatively, water development activities have been described as the greatest threat to aquatic biodiversity (Dynesius and Nilsson 1994; Rosenberg et al. 2000; Nilsson et al. 2005).

Changes in the overall integrity of aquatic ecosystems have prompted programs to mitigate for the adverse effects of water development. Large rivers in particular have undergone substantial water use management reform and habitat rehabilitation to offset the effects of dams and other instream development (Gore and Shields 1995; Lake et al. 2007; Romanov et al. 2012; Watkins et al. 2015a). Previous work has demonstrated that structural habitat modification (Schloesser et al. 2011; Whiteman et al. 2011) and flow management (Raymond 1988; Budy et al. 2002) can successfully mitigate for the effects of water development on native riverine fishes. Recent programs have focused on mitigating for changes in the chemical properties of aquatic systems resulting from water development (Ashley et al. 1999; Wilson et al. 2013; Ross et al. 2015). Artificial nutrient supplementation is one chemical rehabilitation tool that has been used to enhance productivity in fluvial systems with depressed nutrient loads by eliciting primary production responses (Deegan and Peterson 1992; Peterson et al. 1993; Snyder and Minshall 1996). Most previous evaluations of mitigation activities' effects on fishes have focused on the assemblage level. Although such studies are insightful, there is an increased need to identify the effect of mitigation activities on fish population dynamics within assemblages.

The Kootenai River, Idaho, is a large river where substantial water development activities have altered aquatic habitat and water chemistry (Duke et al. 1999; Fossness and Williams 2009; Ross et al. 2015). Libby Dam, a large hydropower facility on the Kootenai River, has reduced discharge variability, moderated thermal regimes, and altered downstream sediment and nutrient transport (Knudson 1993). Levees have also modified the Kootenai River through channelization and reduction of lateral flow connectivity. Nutrient dynamics have been further influenced by the impoundment created by Libby Dam, which retains approximately 63% of total phosphorus and 25% of total nitrogen, thereby limiting productivity downstream (Woods 1982).

The cumulative effects of water development activities in the Kootenai River have been shown to alter fish assemblage structure (Paragamian 2002) and have been directly linked to the collapse of fisheries for Burbot *Lota lota* (Partridge 1983; Apperson 1990; Paragamian et al. 2000; Paragamian 2012) and White Sturgeon *Acipenser transmontanus* (Paragamian et al. 2001; Paragamian and Hansen 2009). In the Kootenai River system, mitigation programs have been used for over 25 years to bolster native fish populations. These programs include increased spring releases from Libby Dam and artificial nutrient addition (Ross et al. 2015). Mitigated flows are associated with spawning of endangered White Sturgeon; however, water flows that closely match historical discharge and temperature regimes are thought to be beneficial to all native fishes in the system. In 2006, a nutrient (phosphorus) addition project was instituted to mitigate for the diminished production induced by water development on the lower portion of the Kootenai River. Based on prior studies, the Idaho portion of the Kootenai River was classified as ultra-oligotrophic and phosphorus-limited (Snyder and Minshall 1996) due to nutrients being retained in the "sink" behind Libby Dam. Therefore, it has been hypothesized that bioenergetic development in high trophic levels (i.e., fish) has been severely inhibited. A critical knowledge gap is an understanding of how the bottom-up effects of nutrient addition and discharge augmentation are manifested in Kootenai River fish populations.

We sought to investigate populations of Largescale Sucker *Catostomus macrocheilus* and Mountain Whitefish *Prosopium williamsoni* to better understand the influence of mitigation activities and environmental characteristics on fish population ecology in the Kootenai River. Both species are ecologically important throughout large rivers in western North America and play an important functional role in native fish assemblages. Largescale Suckers and Mountain Whitefish are native to Idaho and can be found in both lentic and lotic systems throughout the state (Wallace and Zaroban 2012). The native distribution of Largescale Suckers is restricted to tributaries of the Columbia River, USA, and to coastal tributaries of western British Columbia, Canada (Scott and Crossman 1973; Dauble 1986). Mountain Whitefish are found as far north as the McKenzie River, British Columbia, and as far south as the Colorado River, USA (Behnke 2002). Both species are particularly ubiquitous in the Kootenai River and make up the majority of vertebrate biomass in the Idaho portion of the river (Ross et al. 2015; Smith et al. 2016). In fact, research conducted by Smith et al. (2016) and Watkins et al. (2015a) revealed that Largescale Suckers and Mountain Whitefish cumulatively composed approximately 50–65% of the catch during fish assemblage sampling. Both species are hypothesized to have positively responded to the ongoing nutrient addition project in the Kootenai River downstream of Libby Dam. Therefore, the objectives of our study were to (1) describe population characteristics (i.e., age structure, growth, recruitment, and mortality) of Largescale Suckers and Mountain Whitefish in the lower

Kootenai River; and (2) evaluate the effect of mitigation activities (i.e., nutrient addition) and water management characteristics (i.e., discharge and temperature) on growth and recruitment of both species.

METHODS

Largescale Sucker data collection.—Largescale Suckers were sampled during August 8–12, 2012, at eight long-term monitoring sites in the lower Kootenai River (Figure 1). Largescale Suckers were collected using boat-mounted, pulsed-DC electrofishing and an Infinity model control box (Midwest Lake Management, Inc., Polo, Missouri). The TL of each Largescale Sucker was measured to the nearest millimeter, and the left marginal pectoral fin ray was removed from 10 fish per 1-cm length-group (Koch et al. 2008; Quist et al. 2012). Pectoral fin rays were mounted in epoxy (Koch and Quist 2007) and sectioned with a low-speed saw (Buehler Isomet; Buehler, Inc., Lake Bluff, Illinois) as close to the proximal end of the fin ray as possible. Resulting cross-sections were viewed with a dissecting microscope using transmitted light. A single experienced reader estimated the age of each cross-section and measured distances between annuli with the Image-Pro Plus image analysis system (Media Cybernetics, Inc., Bethesda, Maryland). The reader did not have knowledge of individual fish lengths during the age estimation process.

Mountain Whitefish data collection.—Mountain Whitefish were sampled during September 2007, 2009, and 2012 at three reaches in the lower Kootenai River (Figure 1). Sampling was conducted using boat-mounted, pulsed-DC electrofishing and a VVP-15 model control box (Smith-Root, Inc., Vancouver, Washington). All Mountain Whitefish were measured for TL to the nearest millimeter, and scales were collected posterior to the insertion of the left pectoral fin from 10 fish per 1-cm length-group during each year (Watkins et al. 2015b). After drying, scales were pressed onto acetate slides, and the resulting impressions were viewed with a microfiche reader via the methods of Dauble and Gray (1977). Ages were estimated for each fish, and distances between annuli were measured. All scale impressions were viewed by two experienced readers during a mutual session without knowledge of fish length.

Environmental data collection.—We focused on nutrient addition, discharge, and temperature as covariates explaining growth and recruitment variability of Largescale Suckers and Mountain Whitefish. Phosphorus is added to the Kootenai River near the Idaho–Montana border, and additions occur from approximately mid-June through September of each year; nutrient addition has occurred annually since 2006. Artificial nutrient addition was adjusted to 3 $\mu\text{g/L}$ based on daily river discharge (Ross et al. 2015). Therefore, nutrient addition was quantified as the total number of days during the growing season (April 1–September 30) when nutrients were

added during 2006–2012. Discharge (m^3/s) data from 1989 to 2012 were obtained from the U.S. Geological Survey gauging station near the Moyie River; this station was selected due to its proximity to fish collection sites. We calculated mean discharge over the growing season for each year. Daily water temperature ($^{\circ}\text{C}$) data for the lower Kootenai River were obtained from the U.S. Army Corps of Engineers gauging station at Bonners Ferry, Idaho. Mean water temperature during the growing season was estimated for 1993–2012, the only years from which water temperature data were available (Figure 2).

Data analyses.—An age–length key was used to estimate the age structure of Largescale Sucker and Mountain Whitefish populations (Ricker 1975; Quist et al. 2012). Total annual mortality (A) was estimated using a weighted catch curve (Miranda and Bettoli 2007) for age-11 and older Largescale Suckers and for age-4 and older Mountain Whitefish, which appeared to be fully recruited to the sampling gear (Ricker 1975). Recruitment for both species was described using two age-based techniques. First, recruitment was indexed using residuals from the catch curve, where positive residuals represented strong year-classes and negative residuals represented weak year-classes (Maceina 1997). Variability in year-class strength was assessed by obtaining estimates of studentized residuals from the weighted catch curve. The recruitment coefficient of determination (RCD; Isermann et al. 2002) was also used to explain stability in recruitment. The RCD is simply the coefficient of determination (R^2) value that results from a catch-curve regression. Indices of recruitment are often useful for comparing among water bodies and provide a general idea of recruitment stability over multiple years (Isermann et al. 2002; Quist 2007).

Mean back-calculated lengths at age were estimated using the Dahl–Lea direct proportion method (Ricker 1975, 1992),

$$L_i = L_c \times (S_i/S_c),$$

where L_i is the length at annulus i ; L_c is the length at capture; S_i is the fin ray or scale radius at annulus i ; and S_c is the radius at capture. The Dahl–Lea method was used for both Largescale Sucker fin rays and Mountain Whitefish scales because the intercept parameter (a) of the body length–scale radius regression was zero (Ricker 1992). Growth was further summarized by fitting a von Bertalanffy growth model (von Bertalanffy 1938),

$$L_t = L_{\infty} [1 - e^{-K(t-t_0)}],$$

where L_t is mean length at age at the time of capture; L_{∞} is the average maximum length of fish in the population; K is the growth coefficient; and t_0 is the theoretical age when length equals 0 mm. Models were fitted via nonlinear regression techniques in R (nlstools package; Seber and Wild 2006; R Development Core Team 2012).

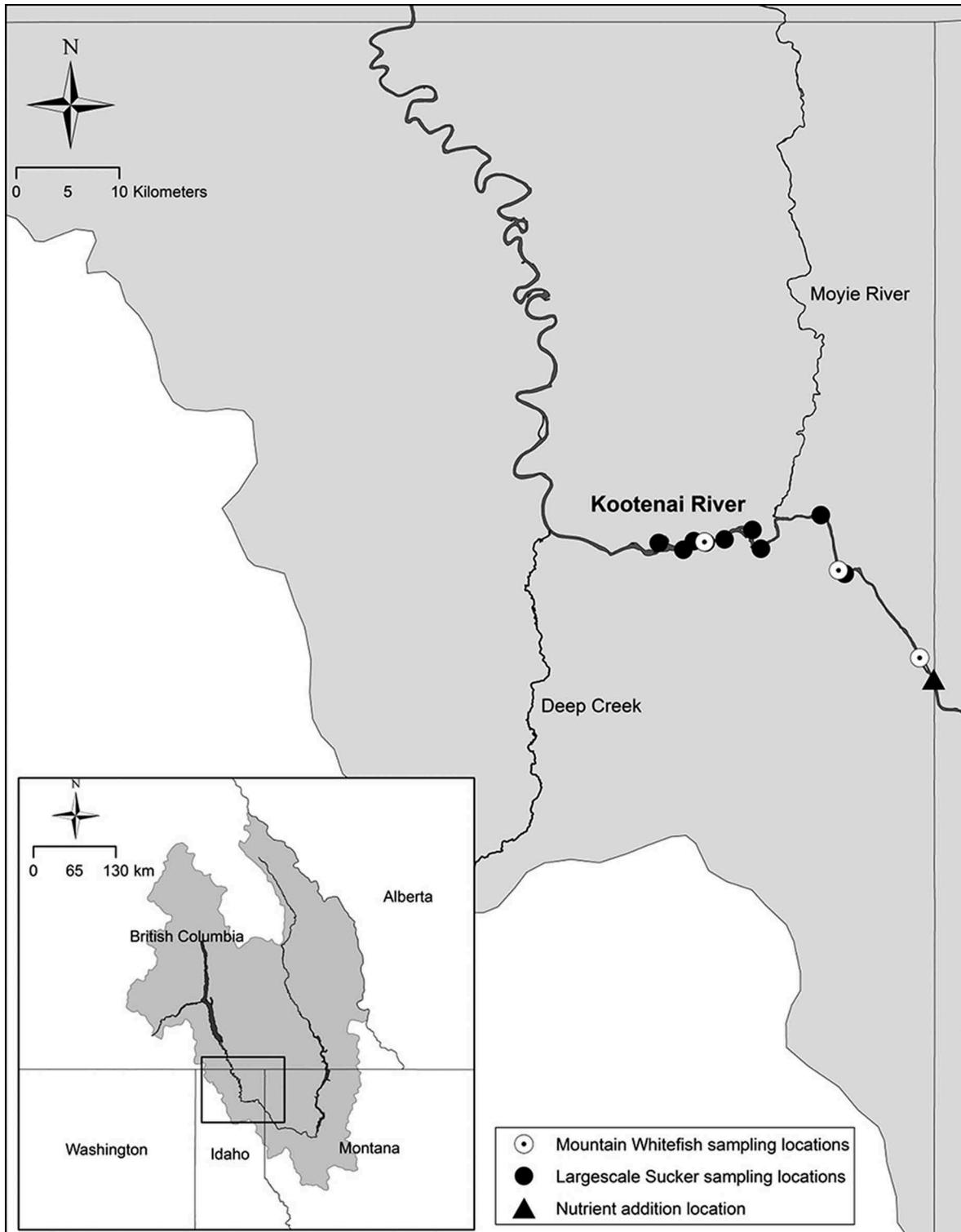


FIGURE 1. Map showing the locations of the Kootenai River, Libby Dam, fish sampling sites, and the nutrient addition site near the Idaho–Montana border. The Kootenai River watershed is indicated in gray.

Calcified structures (e.g., fin rays) contain information on multiple years spanning the entire life of the fish. Therefore, a one-time sample using calcified structures can provide

insights on fish growth over multiple years when long-term data are unavailable (Weisberg et al. 2010). Annual somatic growth of fishes can be partitioned into effects due to age (i.e.,

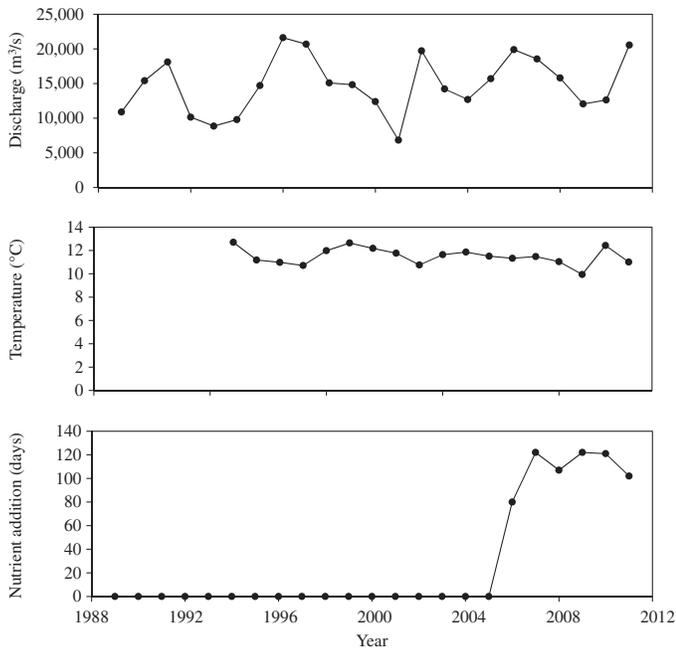


FIGURE 2. Environmental data associated with mitigation activities in the Kootenai River, Idaho, including mean discharge and water temperature during the growing season (April 1–September 30) and number of days on which nutrients were added to the system.

size) and environmental conditions in discrete time intervals (i.e., years). Growth is highly influenced by fish length, and length dependently increases as a function of age, making it difficult to partition variability due to size and variability due to environmental conditions. Furthermore, growth tends to be highly correlated within an individual through time and between fish in the same years (Weisberg 1993). To address this issue, a repeated-measures, mixed-effects model was used to examine the effects of age and year on incremental growth of Largescale Suckers and Mountain Whitefish (Weisberg et al. 2010),

$$y_{cka} = l_a + h_{c+a-1} + f_{ck} + e_{cka},$$

where y_{cka} is the a th annular increment for the k th fish from the c th year-class; l_a is the annular increment for a fish in the a th year of life; h_{c+a-1} is the environmental effect for year $l = c + a - 1$, which is the year that a fish in year-class c was age a ; f_{ck} is the effect of fish k in the c th year-class; and e_{cka} is the model error. Age was treated as a fixed effect, and year was treated as a random effect (i.e., each year was considered a random draw from the sampling distribution) in the model, and repeated measures were taken from each fish. An autoregressive covariance structure was used, and models were fitted using R (lme4 package; R Development Core Team 2012). Incremental growth was modeled for age-1–9 Largescale Suckers and

age-1–8 Mountain Whitefish. The eldest ages (i.e., increments) were removed from the Largescale Sucker sample rather than individual fish. Variability in incremental growth for the eldest years for individual fish was very low, and growth was slow. As such, even slight imprecision in annulus measurements caused substantial error in our evaluation of incremental growth. In addition, the most critical periods of growth during the life history of a fish are those when growth is high and potentially more variable because the timing of important life history events can be affected (Post 2003).

An information-theoretic approach was used to select among competing linear multiple-regression models explaining variability in growth and recruitment (Burnham and Anderson 2002). Seven candidate models were developed for growth, including models incorporating nutrient addition only, discharge only, or temperature only, and additive models including all possible combinations of covariates. Three candidate models were developed for recruitment, including models incorporating discharge only or temperature only and an additive model with both discharge and temperature. Models for growth used random-effect intercept estimates of growth (i.e., year effect) as the dependent response variable. Models for recruitment used studentized residual estimates representing year-class strength (i.e., catch-curve residuals) as the dependent response variable. Nutrient addition was not included as a covariate in recruitment models for Largescale Sucker because ages 1–10 were excluded from the catch curve (i.e., not fully recruited to electrofishing gear). Multicollinearity among explanatory variables was assessed prior to creating candidate models. No covariates were significantly correlated ($r \leq |0.70|$, $P \geq 0.05$). Akaike's information criterion corrected for small sample size (AIC_c) was used to rank candidate models and select the best model. Information theory only ranks models, but all models may be poor indicators of growth and recruitment; therefore, R^2 was used as a measure of model fit.

After completion of growth analyses, we were interested in understanding how the relationship between abundance and growth might influence the effect of nutrient addition on Largescale Suckers and Mountain Whitefish. The CPUE (fish per minute of electrofishing) was highly correlated with days of nutrient addition, which restricted our ability to include both covariates in multiple regression models ($r = 0.93$, $P = 0.001$). Some long-term data on Mountain Whitefish abundance during pre- and post-nutrient-addition years (2000–2011) were available, but similar data for Largescale Suckers were not available. As such, we conducted a post hoc evaluation of the relationship between annual CPUE (i.e., relative abundance) and growth of Mountain Whitefish by using simple linear regression to provide insight on possible density-dependent interactions.

RESULTS

Largescale Sucker

Overall, 595 Largescale Suckers were sampled from the Kootenai River during August 2012. Of those individuals, we estimated age and incremental growth from 407 Largescale Suckers. Total length varied from 105 to 642 mm, and age varied from 1 to 23 years. Total annual mortality was relatively low (Table 1), and recruitment was highly variable among years (Table 1; Figure 3). Our estimate of A likely represents only natural mortality because the Largescale Sucker is not a game fish species. Year-class strength has been variable and recent cohorts (i.e., 1998–2002) were weak, yet all age-classes within the age range were represented (Figure 3).

Multiple-regression models explained little variability in year-class strength ($R^2 \leq 0.27$; Table 2). The best model contained only temperature, but the model containing discharge was as parsimonious as the best model (ΔAIC_c difference [ΔAIC_c] = 0.59; Table 2). The slope coefficient estimates for temperature and discharge were imprecise for each of the top-two models (Table 3). Because reliable residual estimates could not be obtained for years overlapping with nutrient addition activities (i.e., 1988–2005), we were unable to evaluate the influence of nutrient addition on the year-class strength of Largescale Suckers.

As hypothesized, growth of individuals showed a declining pattern with age. Growth increments were variable among years and increased between 2005 and 2009 (Figure 4). Unlike year-class strength, variability in growth was explained by environmental covariates related to mitigation activities. Nutrient addition was the most important covariate predicting the incremental growth of Largescale Suckers (Table 4), and the relationship was positive. The second-best model predicting incremental growth contained both nutrient addition and temperature but was not as parsimonious as the top model ($\Delta AIC_c = 3.05$). Approximately 82% of the variability in incremental growth of Largescale Suckers was explained by nutrient addition during the growing season. The slope coefficient estimate of nutrient addition in the top model was precise (i.e., the 95% confidence interval [CI] did not overlap zero), and a mean increase of 0.15 mm in growth was predicted for each 1-unit (i.e., day) increase in nutrient addition (Table 5). Discharge and temperature were not important predictors of Largescale Sucker growth.

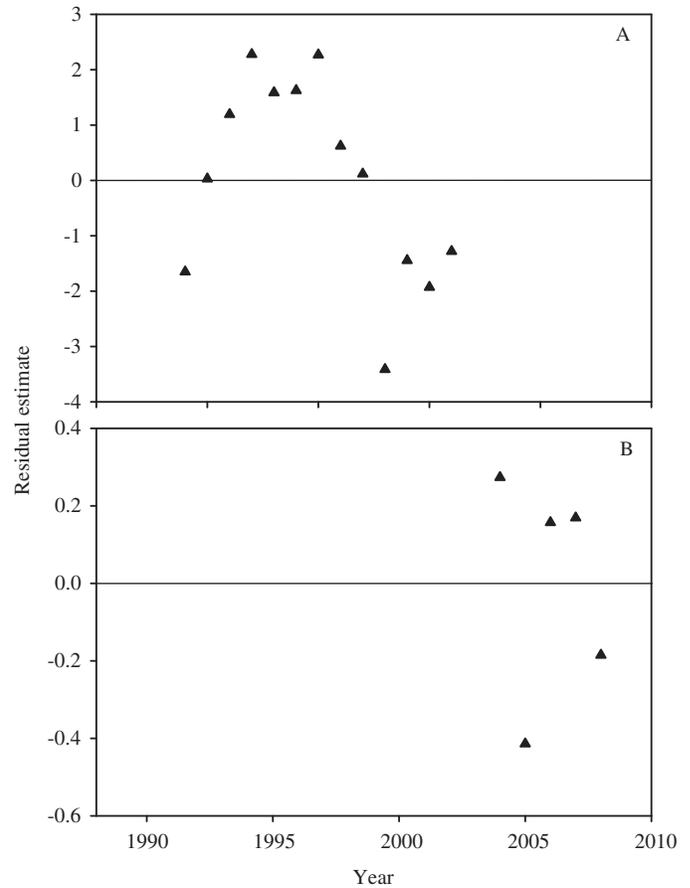


FIGURE 3. Studentized residuals from catch curves developed to predict year-class strength of (A) Largescale Suckers and (B) Mountain Whitefish sampled from the Kootenai River, Idaho, in 2012. Positive residuals represent strong year-classes, and negative residuals represent weak year-classes.

Mountain Whitefish

In total, 1,627 Mountain Whitefish were sampled from the Kootenai River during September in 2007, 2009, and 2012. Of those fish, 552 were included in the analysis of incremental growth. Given the absence of long-term recruitment data, only the 2012 sample was used in the analysis of year-class strength because it contained the most recent age data. The TL of Mountain Whitefish varied from 78 to 472 mm, and estimated age varied from 0 to 8 years. Total annual mortality was high, and recruitment was very stable (Table 1). Unlike Largescale Suckers, the A of Mountain Whitefish likely represents a combination of natural mortality and fishing mortality because the Mountain Whitefish is a game fish species in Idaho.

TABLE 1. Sample size (n), estimated von Bertalanffy growth equation, total annual mortality (A), and recruitment coefficient of determination (RCD) for Largescale Sucker and Mountain Whitefish populations sampled from the Kootenai River, Idaho.

Species	n	von Bertalanffy equation	A (%)	RCD
Largescale Sucker	595	$L_{age} = 544 \{1 - e^{[-0.139(age + 1.068)]}\}$	20.4	0.77
Mountain Whitefish	1,627	$L_{age} = 468 \{1 - e^{[-0.091(age + 2.909)]}\}$	64.6	0.97

TABLE 2. Multiple-regression models predicting year-class strength of Largescale Suckers and Mountain Whitefish from the Kootenai River, Idaho, in 2012. Explanatory variables include the number of days of nutrient (phosphorus) addition (Nutrient), mean discharge (Q ; m^3/s) during the growing season (April 1–September 30), and mean water temperature (Temp; $^{\circ}C$) during the growing season. The number of model parameters (K), Akaike’s information criterion corrected for small sample size (AIC_c), AIC_c weight (w_i), percent of the maximum w_i (%Max w_i), evidence ratio ($ER = \max w_i/w_i$), and coefficient of determination (R^2) are included. Top models are indicated by bold italic text and the direction of the relationship is indicated by a plus or minus symbol.

Model	K	AIC_c	ΔAIC_c	w_i	%Max w_i	ER	R^2
Largescale Sucker							
<i>-Temp</i>	3	43.33	0.00	0.57	100	1.00	0.06
<i>-Q</i>	3	43.92	0.59	0.42	73.68	1.36	0.14
<i>-Temp, -Q</i>	4	52.62	9.29	0.01	1.75	57.00	0.27
Mountain Whitefish							
<i>+Temp, +Nutrient, +Q</i>	5	-54.81	0.00	1.00	100	1.00	0.34
+Temp	3	29.62	84.43	0.00	0.00	0.00	0.08
+Nutrient	3	30.45	85.26	0.00	0.00	0.00	0.28
+Q	3	30.61	85.42	0.00	0.00	0.00	0.32
+Temp, +Nutrient	4	43.20	98.01	0.00	0.00	0.00	0.33
+Nutrient, +Q	4	48.44	103.25	0.00	0.00	0.00	0.32
+Temp, +Q	4	48.74	103.55	0.00	0.00	0.00	0.36

Models developed to predict the year-class strength of Mountain Whitefish had better explanatory power than similar models for Largescale Suckers (Table 2). The best model of Mountain Whitefish year-class strength was the most highly parameterized model, containing nutrient addition,

TABLE 3. Parameter estimates, SEs, and lower and upper 95% confidence limits (CLs) for parameters from the top models predicting year-class strength of Largescale Suckers and Mountain Whitefish sampled from the Kootenai River, Idaho, in 2012. Model parameters include the number of days of nutrient (phosphorus) addition (Nutrient), mean discharge (Q ; m^3/s) during the growing season (April 1–September 30), and mean water temperature (Temp; $^{\circ}C$) during the growing season.

Species	Model parameter	Estimate	SE	95% CLs	
				Lower	Upper
Largescale Sucker	Temp	-0.415	0.544	-1.747	0.916
Mountain Whitefish	Temp	0.591	0.434	-4.925	6.108
	Nutrient	0.005	0.004	-0.054	0.064
	Q	0.0005	0.0003	-0.003	0.003

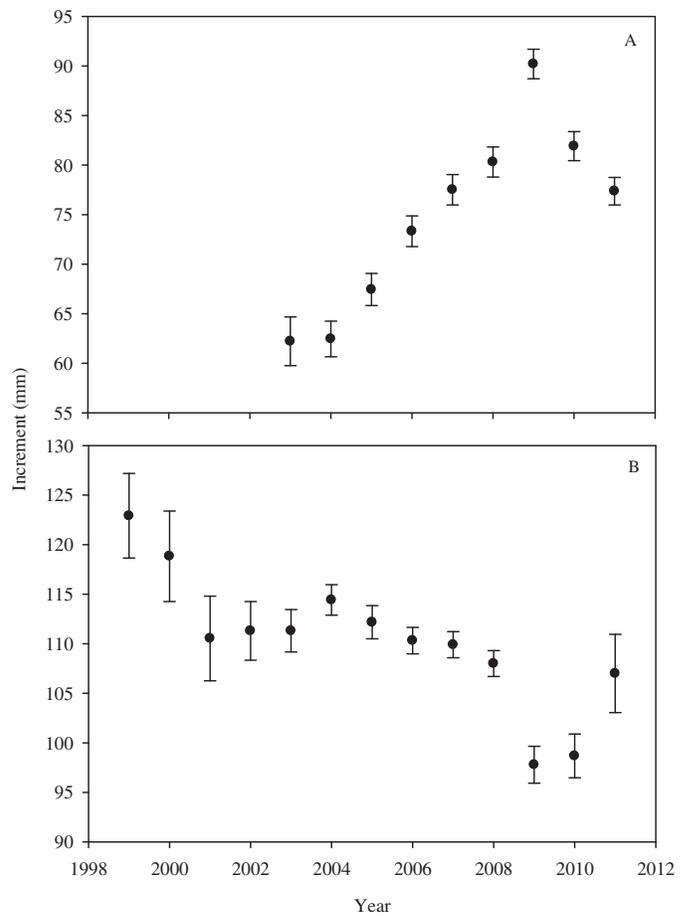


FIGURE 4. Growth increment estimates by year for (A) Largescale Suckers (sampled in 2012) and (B) Mountain Whitefish (sampled in 2007, 2009, and 2012) from the Kootenai River, Idaho.

discharge, and temperature. Covariates in the best model explained 34% of the variability in year-class strength, but the slope estimates were imprecise (Table 3). Multiple regression models developed for Mountain Whitefish growth were similar to those for Largescale Suckers in that nutrient addition was the most important covariate (Table 4). The model incorporating only nutrient addition had good explanatory power and provided a precise estimate (Table 5). Over half (61%) of the variation in annual growth of Mountain Whitefish was explained by nutrient addition. Although the model incorporating both nutrient addition and temperature was as parsimonious as the top model, temperature was an imprecise covariate predicting Mountain Whitefish growth. Unlike the results for Largescale Suckers, the relationship between growth of Mountain Whitefish and nutrient addition was negative. An expected mean decrease of 0.089 mm was predicted for every 1-d increase in the duration of nutrient addition (Table 5). Similar to Largescale Suckers, temperature and

TABLE 4. Multiple-regression models predicting growth of Largescale Suckers (sampled in 2012) and Mountain Whitefish (sampled in 2007, 2009, and 2012) from the Kootenai River, Idaho. Explanatory variables include the number of days of nutrient addition (Nutrient), mean discharge (Q ; m^3/s) during the growing season (April 1–September 30), and mean water temperature (Temp; $^{\circ}C$) during the growing season. The number of model parameters (K), Akaike’s information criterion corrected for small sample size (AIC_c), AIC_c weight (w_i), percent of the maximum w_i (%Max w_i), evidence ratio ($ER = \max w_i/w_i$), and coefficient of determination (R^2) are included. Top models are indicated by bold italic text and the direction of the relationship is indicated by a plus or minus symbol.

Model	K	AIC_c	ΔAIC_c	w_i	%Max w_i	ER	R^2
Largescale Sucker							
+Nutrient	3	59.15	0.00	0.70	100	1.00	0.82
+Nutrient, +Temp	4	62.20	3.05	0.15	21.43	4.67	0.86
+Nutrient, $-Q$	4	62.53	3.38	0.13	18.57	5.38	0.85
+Nutrient, +Temp, $-Q$	5	66.56	7.41	0.02	2.86	35.00	0.93
+Temp	3	72.46	13.32	0.00	0.00	0.00	0.19
$-Q$	3	75.50	16.35	0.00	0.00	0.00	0.14
+Temp, $-Q$	4	89.58	20.43	0.00	0.00	0.00	0.06
Mountain Whitefish							
$-Nutrient$	3	83.98	0.00	0.54	100	1.00	0.61
$-Nutrient$, +Temp	4	85.89	1.92	0.21	38.88	2.57	0.55
$-Nutrient$, + Q	4	86.04	2.06	0.19	35.19	2.84	0.55
+Temp	3	89.89	5.92	0.03	5.55	18.00	0.24
$-Nutrient$, +Temp, + Q	5	90.07	6.09	0.03	5.55	18.00	0.56
+Temp, + Q	4	93.35	9.38	0.00	0.00	0.00	0.21
+ Q	3	94.51	10.53	0.00	0.00	0.00	0.09

discharge were not important covariates explaining the growth of Mountain Whitefish.

The post hoc evaluation of Mountain Whitefish growth demonstrated that incremental growth was negatively related to CPUE (Figure 5). We estimated an expected mean decrease of 1.79 mm in annual Mountain Whitefish growth for every 1-fish/min increase in CPUE. Around half (54%) of the annual variation in incremental growth of Mountain Whitefish was explained by CPUE.

DISCUSSION

Our study provides a general framework for evaluating the response of population dynamic rate functions to mitigation actions in a large river, and this approach can be widely applied to other systems and a variety of management actions. Here, we evaluated the population dynamics of two important yet poorly understood species in the Kootenai River. This study demonstrated that artificial nutrient

TABLE 5. Parameter estimates, SEs, and lower and upper 95% confidence limits (CLs) for parameters from the top models predicting the incremental growth of Largescale Suckers and Mountain Whitefish sampled from the Kootenai River, Idaho. Model parameters include the number of days of nutrient (phosphorus) addition (Nutrient).

Species	Model parameter	Estimate	SE	95% CLs	
				Lower	Upper
Largescale Sucker	Nutrient	0.153	0.025	0.093	0.213
Mountain Whitefish	Nutrient	-0.089	0.024	-0.141	-0.036

addition was the most important mitigation action influencing growth of both Largescale Suckers and Mountain Whitefish. Environmental characteristics associated with mitigation actions explained less variability in recruitment, especially for Largescale Suckers. Discharge and temperature associated with flow management were neither important nor plausible predictors of population rate functions for either species.

Previous work associated with understanding how mitigation actions influence fish has more broadly focused on community assembly (Fischer et al. 2010; Watkins et al. 2015a; Smith et al. 2016), but future evaluations can likely benefit from a change in scope. Assemblage-level effects are often subtle and difficult to detect, especially in regulated western river systems with depauperate fish assemblages (Hughes and Gammon 1987; Quist et al. 2004; Ross et al. 2015; Smith et al. 2016), where measurable effects can take long periods of time to manifest or may be confounded by sampling constraints (e.g., detection of species with low detection rates; Smith et al. 2015). Although the change in assemblage structure may be a desired level of

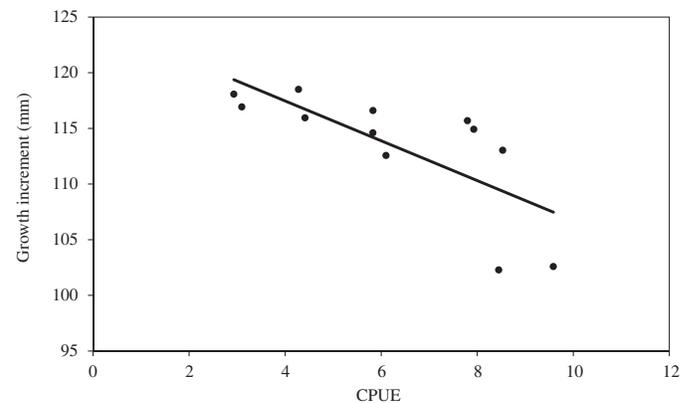


FIGURE 5. Relationship between the CPUE (fish per minute of electrofishing) and growth increment of Mountain Whitefish captured from the Kootenai River, Idaho, during 2000–2011.

inference, changes in biotic assemblages are directly influenced by processes occurring at the population level. Ultimately, population rate functions determine the abundance and size structure of each species in an assemblage. In addition, many specialist fish species are sensitive to environmental alterations, and changes in population rate functions can reflect relevant changes in habitat or water quality (Buktenica et al. 2007; Rowell et al. 2008). Understanding population responses can be accumulated with limited sampling and retrospective analyses, whereas assemblage-level responses generally require intensive, long-term monitoring (Gido et al. 2002). Therefore, rate functions may provide a useful assessment of management activities and offer some ability to forecast assemblage shifts (Nener et al. 1995; McPhail and Troffe 1998; Cash et al. 2000; Meyer et al. 2009).

Recruitment is an important regulatory mechanism acting on fish populations, but it is challenging to accurately characterize without long-term data (Maceina and Pereira 2007). Recruitment dynamics are influenced by a variety of environmental conditions. Lotic systems are characterized by high physical variability among processes that operate concomitantly to govern recruitment dynamics among years (Poff et al. 1997; Gutreuter et al. 1999; Giannico and Hinch 2003; Poff and Zimmerman 2010). Long-term data are typically lacking for fish species that are not of imminent conservation concern or do not have high recreational value; the Largescale Sucker and Mountain Whitefish are no exception. As such, we relied on retrospective analyses using age-based data to evaluate recruitment patterns. Quist and Spiegel (2010) evaluated recruitment variability of eight catostomids in several large rivers in Iowa and found that recruitment was generally not stable. Those authors reported RCD values varying from 0.49 for Silver Redhorses *Moxostoma anisurum* in the Shell Rock River to 0.96 for Shorthead Redhorses *M. macrolepidotum* in the Wapsipinicon River. Within species, RCD was most variable (0.56–0.95) for Northern Hog Suckers *Hypentelium nigricans* among four study rivers (Quist and Spiegel 2010). Although Quist and Spiegel (2010) reported variable recruitment, they demonstrated that catostomid recruitment was more consistent than recruitment reported for other species. Furthermore, no evidence of year-class failure was observed, which is consistent with our study (RCD = 0.77) and others (Reid 2009). Similar to our study results, Mountain Whitefish recruitment was reported to be very stable in large rivers in Idaho, including the Kootenai River (Meyer et al. 2009). Meyer et al. (2009) used catch curves to estimate population-specific rates of mortality in 20 Mountain Whitefish populations within Idaho. Values of A (mean A = 18.0%; range = 9.0–37.0%) were lower than that observed in our study (A = 64.6%). The estimated mean RCD among all Idaho Mountain Whitefish populations was 0.61 (range = 0.39–0.86; Meyer et al. 2009), suggesting that recruitment of Mountain Whitefish in the Kootenai River is remarkably stable in comparison to neighboring populations.

The residual technique is typically used to evaluate recruitment patterns of short-lived species (e.g., crappies *Pomoxis* spp., maximum age ~ 10 years; Maceina 1997; Isermann et al. 2002). We surmise that catch-curve analysis is a reasonable method for characterizing general recruitment stability but may not be entirely useful for accurately quantifying year-class strength of longer-lived species, such as the Largescale Sucker. Use of catch-curve residuals to index year-class strength of long-lived species may be problematic because long-lived species experience mortality over a longer time period in which high variation in environmental and assemblage characteristics can occur (Mauk and Boxrucker 2004; Kwak et al. 2006). Conversely, Mountain Whitefish in the Kootenai River are short-lived, similar to species for which catch curves were originally developed, and therefore serve as an excellent candidate species for using the catch-curve-based technique to retrospectively evaluate year-class strength. Although our reported recruitment indices for Mountain Whitefish were derived from data collected in 2012, which did not span the time frame before nutrient addition began in the Kootenai River, we previously performed analyses with 2007 data showing that recruitment was equally stable prior to nutrient addition. Although the year-class strength of Largescale Suckers was highly variable and not closely related to temperature and discharge, the year-class strength of Mountain Whitefish was stable across various levels of temperature, discharge, and nutrient addition. Collectively, the covariates explained around one-third of the variability in Mountain Whitefish recruitment. Similar relationships have been described for salmonids, including Mountain Whitefish, in other riverine systems (e.g., Thompson and Davies 1976; Alexander et al. 2006). Our results are not surprising given the recent consistency in Mountain Whitefish recruitment and the increased production that was likely elicited from discharge management and nutrient addition.

The most interesting pattern among both of our study species concerned incremental growth. We hypothesized that the growth of each species would be positively related to the environmental covariates based on the premise that bottom-up effects on primary production were likely increasing food resources. However, the positive relationship between growth of Largescale Suckers and nutrient addition was in stark contrast to the negative relationship for Mountain Whitefish. Largescale Suckers have been reported to feed primarily on periphyton (e.g., diatoms), chironomid larvae, and trichopteran larvae, with the most common food item by volume being periphyton (i.e., up to 90%; Dauble 1986). Nutrient addition in the Kootenai River has significantly increased the density and total biomass of periphyton (Hoyle et al. 2014), a response that has also been observed in other nutrient enhancement studies (Kohler et al. 2008; Kohler and Taki 2010). Particularly in floodplain-driven ecosystems, the availability of nutrients (primarily phosphorus) is governed by water-

derived exchanges between the adjacent terrestrial area and downstream transport from headwater erosion (Spink et al. 1998). As such, growth of fishes in regulated rivers is thought to be a critical indicator of ecosystem productivity. Artificial enhancement of limiting nutrients can mitigate for production loss and can elicit functional response changes. It is probable that increases in primary and tertiary production in the lower Kootenai River improved the abundance of prey types that were used by Largescale Suckers, thus promoting positive changes in somatic growth.

Mountain Whitefish feed primarily on chironomid and trichopteran larvae, but in contrast to Largescale Suckers, they do not consume periphyton (unless incidentally; Pontius and Parker 1973). Although the density of chironomid larvae increased by nearly 50% after nutrient addition began in the Kootenai River (Minshall et al. 2014), a positive growth response in Mountain Whitefish was not observed. One likely explanation for this lack of positive response is the potential effect of density dependence on growth of Mountain Whitefish. Estimates of Mountain Whitefish abundance in the Kootenai River have nearly doubled since nutrient addition efforts began, but condition (i.e., relative weight [W_r]) and mean length have declined during the same period (Ross et al. 2015; Hardy et al. 2016). Similar responses have been observed for salmonids in other nutrient addition studies. For instance, Deegan et al. (1997) reported that groups of Arctic Grayling *Thymallus arcticus* that were exposed to artificially elevated nutrient levels and fish densities in the Kuparuk River, Alaska, had significantly lower growth rates and poorer body condition than groups that were exposed to elevated nutrients and lower fish densities. Blackwell et al. (2000) identified several studies in which W_r and growth were negatively correlated with fish density, further supporting the contention that density-dependent interactions may be limiting the growth of Mountain Whitefish in the Kootenai River. In contrast to the aforementioned studies, Meyer et al. (2009) found that among nearly 2,000 study sites surveyed in Idaho, including the Kootenai River, there were no instances in which Mountain Whitefish abundance was correlated with growth. However, Meyer et al. (2009) conducted their study during 2005 and 2006, years that did not span the extent of nutrient addition in the Kootenai River. The peculiar relationship between Mountain Whitefish growth and nutrient addition raises questions about the interaction of these variables with abundance, particularly with regard to the expression of density dependence in the population. The post hoc analysis provides support for the notion that nutrient addition may be indirectly precipitating a negative somatic growth response in the Mountain Whitefish population—one that is likely driven by intraspecific resource competition. Although we were not able to include abundance measures in our initial models of incremental growth, the pattern that later emerged was striking. Given the stable recruitment expressed by Mountain Whitefish in the Kootenai River, elevated production from

artificial nutrient addition has likely increased the number of adult recruits to the population. However, while production benefits have increased the Mountain Whitefish standing stock, those benefits are not sufficient to promote increased somatic growth.

Ongoing monitoring and evaluation efforts in the Kootenai River have indicated that the Mountain Whitefish population has been increasing in abundance since nutrient addition began in 2006 (Ross et al. 2015). Given the negative growth response shown here, those prior findings may indicate that the standing stock of Mountain Whitefish is nearing its carrying capacity relative to artificially elevated productivity (i.e., reaching an alternative stable state). Other studies have also found that the standing stock of fish is highly correlated with the concentration of dissolved nutrients. For example, McFadden and Cooper (1962) observed that the standing stock of Brown Trout *Salmo trutta* was greatest in streams with high concentrations of dissolved solids and was lowest in streams that were less fertile. Carrying capacity of any ecosystem is difficult to accurately quantify; however, it is widely accepted that carrying capacities exist for all ecosystems and that population sizes of organisms vary around the total number an ecosystem can support (i.e., density dependence; Fowler 1981; Bayley 1988). Carrying capacities in biological populations are largely based on ecological theory, but the concept is important for gauging the influence of mitigation activities on fishes.

Largescale Suckers and Mountain Whitefish are important components of the Kootenai River fish assemblage. Both species can provide important prey for piscivorous species, such as the Bull Trout *Salvelinus confluentus*, Redband Trout *O. mykiss gairdneri*, and White Sturgeon (Dauble 1986). Given this understanding, it is likely that Largescale Sucker recruitment supports bioenergetic development in many recreationally and ecologically important fish populations at higher trophic levels. Despite nutrient addition being the single most important predictor of incremental growth in both Largescale Suckers and Mountain Whitefish, we observed a starkly different relationship for these species. This differential growth response is likely an artifact of life history differences between the two species. Largescale Suckers are longer lived and later maturing than Mountain Whitefish, and the effects of nutrient addition on population abundance may manifest more quickly in populations of shorter-lived species. For instance, Mountain Whitefish growth may have been positively influenced during the early stages of nutrient addition, but perhaps the resulting effects on fecundity and recruitment (given the recruitment stability observed) have caused incremental growth to decline.

The matter of scope in ecology is one that has long vexed scientists (Fausch et al. 2002; Fischer et al. 2010). Fishery scientists are often tasked with identifying the most useful and meaningful level of inference for evaluations of fishery management actions. Since rate functions (e.g., growth) are typically manifested prior to changes in fish assemblage structure, it may be important in many studies to quantify metrics at both levels (i.e., population and assemblage) to holistically evaluate management actions. Traditional fishery

monitoring can benefit from some incorporation of population dynamic measures to more fully understand the complex relationship between mitigation actions and fish assemblage structure. In addition, a better understanding of how fish population dynamics respond to mitigation actions can allow resource managers to forecast potential assemblage shifts and undesirable population responses. Most mitigation measures in regulated rivers focus on a limited number of species that are often of imminent conservation concern; however, there is a need to holistically consider the full suite of externalities that can manifest across populations. Of utmost importance is the consideration of changes to rate functions of nontarget species that can precipitate transitions in population and therefore assemblage structure. Mitigation for water development occurs in a number of large rivers that support fishes with various life history strategies (Schloesser et al. 2011; Watkins et al. 2015a). As such, comprehensive evaluations of nontarget species along with consideration of the life history variability among target species will lead to more effective execution of mitigation measures. Ultimately, careful consideration of project scope and mitigation trade-offs will help fishery scientists to better measure restoration success in large river ecosystems and the associated benefits to fluvial fishes.

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