5-2017

Evaluating Habitat-based Niche Requirements and Potential Recruitment Bottlenecks for Imperiled Bluehead Sucker (Catostomus discobolus)

Bryan C. Maloney
Utah State University

EVALUATING HABITAT-BASED NICHE REQUIREMENTS AND POTENTIAL

RECRUITMENT BOTTLENECKS FOR IMPERILED BLUEHEAD SUCKER

(*CATOSTOMUS DISCOBOLUS*)

by

Bryan C. Maloney

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Phaedra Budy, Ph.D. Major Professor	Jereme Gaeta, Ph.D. Co-Advisor
Joseph Wheaton, Ph.D. Committee Member	Mark R. McLellan, Ph.D. Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2017

ABSTRACT

Evaluating Habitat-based Niche Requirements and Potential Recruitment Bottlenecks for Imperiled Bluehead Sucker (*Catostomus discobolus*)

by

Bryan C. Maloney, Master of Science

Utah State University, 2017

Major Professors: Dr. Phaedra Budy and Dr. Jereme Gaeta
Department: Watershed Sciences

Changes to riverine ecosystems that alter physical and thermal habitat may cause fish recruitment bottlenecks. The Weber River has become highly degraded with many dams and diversions altering fish habitat, flow and thermal regimes, and limiting movement between reaches. Bluehead suckers (*Catostomus discobolus*) occupy only 47% of their historical range and the genetically-distinct Weber River (northern UT) population exhibits characteristics associated with a recruitment bottleneck. My objectives were to determine whether spawning and rearing habitat (thermal and physical) available in the Weber River may be limiting bluehead sucker recruitment. I used reach-based surveys to locate and quantify spawning habitat in the Weber River and Ferron Creek (central Utah), a relatively unaltered reference river. I sampled backwaters near (< 1 km) spawning reaches for juvenile sucker and surveyed habitat characteristics. I conducted laboratory experiments to evaluate juvenile bluehead sucker growth response to different temperature and velocity treatments (12-19°C, 0.004-0.18 m/s). In the Weber River and Ferron Creek, availability of gravel (4-64 mm), cobble (64-256 mm), and pools

(6-26 pools/km) were associated with use by spawning bluehead sucker. In Weber River backwaters, juvenile sucker abundance increased significantly with maximum depth (18-378 sucker; range: 19-87 cm). Laboratory results indicated that juvenile bluehead sucker growth was greatest in the cooler temperature and slower velocity treatments. Collectively these results suggest spawning habitat is limited by the availability of small, rocky substrate and pools and rearing habitat is limited by the availability of deep, slow backwaters at the optimal temperature. By evaluating factors that may limit bluehead sucker recruitment, this study will provide a template for future restoration efforts directed at recovering this imperiled population.

(90 pages)

PUBLIC ABSTRACT

Evaluating Habitat-based Niche Requirements and Potential Recruitment Bottlenecks for Imperiled Bluehead Sucker (*Catostomus discobolus*)

Bryan C. Maloney

Changes to rivers that alter physical and thermal habitat may cause fish population abundance to decline, due to fewer individuals maturing and entering the adult population. The Weber River has become highly degraded with many dams and diversions altering fish habitat, river volume, velocity, and temperature, and limiting movement between reaches. Bluehead suckers (*Catostomus discobolus*) occupy only 47% of their historical range and the genetically-distinct Weber River (northern UT) population is declining and contains few young, juvenile fish. My objectives were to determine whether spawning and rearing habitat available in the Weber River may be limiting bluehead sucker reproductive success and population growth. I used reach-based surveys to locate and quantify spawning habitat in the Weber River and Ferron Creek (central Utah), a relatively unaltered river for comparison. I sampled slow-water backwaters near (< 1 km) spawning reaches for juvenile sucker and surveyed habitat characteristics. I conducted laboratory experiments to evaluate the effect different temperature and velocity treatments (12-19°C, 0.004-0.18 m/s) have on juvenile bluehead sucker growth. In the Weber River and Ferron Creek, reaches with gravel (4-64 mm diameter), cobble (64-256 mm diameter), and pools (6-26 pools/km) were used by spawning bluehead sucker. In Weber River backwaters, deeper backwaters contained significantly more juvenile sucker (18-378 sucker; range: 19-87 cm max depth).

Laboratory results indicated that juvenile bluehead sucker growth was greatest in the cooler temperature and slower velocity treatments. Collectively these results suggest spawning habitat is limited by the availability of small, rocky substrate and pools and rearing habitat is limited by the availability of deep, slow backwaters at the optimal temperature. By evaluating factors that may limit bluehead sucker population growth, this study will provide a template for future restoration efforts directed at recovering this imperiled population.

ACKNOWLEDGMENTS

I would like to thank the many mentors that guided me through this process, particularly Phaedra Budy, Jereme Gaeta, and Gary Thiede. Phaedra provided fantastic guidance for becoming a scientist while being patient with my progress. Jereme spent countless hours improving my ability to think as an ecologist and critically analyze data. Gary taught me approximately one million things, ranging from keeping work effective and fun in the field to writing reports, permit applications, and multi-tiered emails.

I would like to sincerely thank the Utah Division of Wildlife Resources (UDWR) Northern Region Office and personnel, particularly Paul Thompson, Phil Tuttle, Sam McKay, and Chance Broderius, for their prodigious effort surveying large reaches of the Weber River for bluehead sucker and collecting juvenile bluehead sucker from the Raft River. I would like to express gratitude to the UDWR Southeastern Region Office and personnel, particularly Dan Keller, for assisting with difficult days surveying Ferron Creek for bluehead sucker. I would also like to thank the UDWR Fisheries Experiment Station for providing sucker food for the juvenile growth experiments.

I was assisted by many people at Utah State University (USU) during this study. I enjoyed working with dedicated, hard-working research technicians, Brandon Fair, Katelyn Jordan, Thomas Hafen, Tyler Arnold, and Hunter Lucas, in the field and lab. I would also like to thank the Fluvial Habitats Center (FHC) at USU, particularly Joe Wheaton, Wally Macfarlane, and Josh Gilbert, for assistance and guidance through this study. Before beginning field work, I worked in collaboration with the FHC to divide the Weber River into 300-m reaches and create a map book.

This study was funded by the UDWR, City of Ogden, Davis and Weber Counties Canal Company, PacifiCorp, Provo River Water Users Association, Trout Unlimited, Weber Basin Water Conservancy District, Weber River Water Users Association, US Department of the Interior – Bureau of Reclamation, US Geological Survey – Utah Cooperative Fish and Wildlife Research Unit (in kind), and the USU Ecology Center. Permitting assistance was provided by Tom Smart (UDWR) and Aaron Olsen of the Institutional Animal Care and Use Committee (IACUC) at USU. This research was conducted under State of Utah Certificate of Registration (COR) number 2COLL9563 and IACUC protocol number 2456.

My time in Logan would not have been the same without many wonderful friends, whether we spent time adventuring, shredding, or at the Owl.

Bryan C. Maloney

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Page

INTRODUCTION

Disturbances such as altered physical and thermal habitat, introductions of non-native predators and competitors, and anthropogenic resource extraction and emissions may induce a shift in community composition and function (Holling 1973; Mooney and Cleland 2001; Smol et al. 2005). Freshwater ecosystems are particularly sensitive to anthropogenic disturbances (Dudgeon et al. 2006) with 54% of accessible surface water consumed, contaminated, or diverted for human purposes (Postel et al. 1996). Indeed, extinctions of freshwater fauna may exceed the rates of terrestrial faunal extinctions fivefold over the next century (Ricciardi and Rasmussen 1999) due to concentrated and intense land use near freshwaters (Sala et al. 2000). High levels of biodiversity exist in freshwater ecosystems, as they contain 9.5% of all animal species despite comprising only 0.01% of the Earth's surface (Balian et al. 2008). Watershed disturbance, water resource development, pollution, and biotic factors threaten global riverine biodiversity, largely because rivers provide renewable water for human needs (Vorosmarty et al. 2010).

The over-allocation of water resources and subsequent degradation of riverine ecosystems alters physical and thermal habitat available to freshwater species (Ligon et al. 1995). Water retention and diversion is likely to result in a shift in the biological community by altering sediment erosion, transportation, and deposition (Vannote et al. 1980). The frequency and magnitude of fragmentation and flow regulation of riverine ecosystems negatively affects the majority of large rivers globally (Dynesius and Nilsson 1994; Nilsson et al. 2005; Vorosmarty et al. 2010). In the United States, for instance, dams have reduced the frequency and shifted the timing of low and high flow events (Magilligan and Nislow 2005). Dams straighten and stabilize river channels through flow regulation and the retention of sediment, diminishing in-channel complexity by reducing the processes of braiding and bar formation (Ligon et al. 1995; Graf 2006). Dams may also cause significant changes in the thermal regime of riverine ecosystems to the energetic detriment of native species. For example, cool, hypolimnetic releases from large dams may reduce water temperatures downstream and top-release dams may conversely lead to warmer temperatures downstream (Lessard and Hayes 2003).

Ecosystem alterations change physical and thermal habitat available to freshwater species and, therefore, may cause populations to experience recruitment bottlenecks. These bottlenecks occur when limiting factors hinder recruitment success, as determined by the number and fecundity of spawning fish and the ability of early life stages to rear to maturity (Hilborn and Walters 1992). These limiting factors may include reduced or altered physical habitat (Wahle and Steneck 1991), thermal habitat (Coleman and Fausch 2007), food availability (Hentschel 1998), or disturbance events (e.g., wildfire; Prior et al. 2010). Many fishes experience ontogenetic shifts as they grow, changing the factors that influence survival of individuals of different sizes (Brooks and Dodson 1965; Werner and Gilliam 1984). Juvenile and adult life stages may require different management or conservation strategies as a result of unique life stages responding to different limiting factors.

Catostomids (suckers) are particularly vulnerable to anthropogenic alterations to riverine ecosystems**.** Catostomids in North America commonly face threats of habitat degradation, non-native species, migration barriers, and water diversion (Cooke et al. 2005). Threats to catostomids and other native fishes are exacerbated by competition with society for water in the Intermountain West (Richter et al. 1997), where streamflow alterations, particularly diminished minimum and maximum flows due to dams, have caused the biological impairment of fish communities (Carlisle et al. 2010). Threats to catostomids may go unnoticed and be exacerbated due to their status as a non-game fish of little economic value and social stigmas (Cooke et al. 2005). In the upper Colorado River basin, a well-studied basin in the Intermountain West, reservoir construction and subsequent alteration to natural flow regimes has decreased river-channel complexity (Van Steeter and Pitlick 1998). Bluehead Sucker *Catostomus discobolus* are endemic to the Intermountain West, have experienced population range contraction in recent years (Budy et al. 2015), and are protected under a conservation agreement to avoid listing under the Endangered Species Act.

Bluehead suckers are native to the Colorado (N. Arizona, W. Colorado, E. Utah, SW. Wyoming), Snake (S. Idaho, N. Utah), Bear (N. Utah), and Weber River basins (N. Utah; Sigler and Miller 1963), but now occupy only 47% of their historical range (Budy et al. 2015). The bluehead sucker populations from the Weber and Snake River basins are genetically distinct from the Colorado River basin population, causing added concern for the conservation of these populations (Hopken et al. 2013; Unmack et al. 2014). The Weber River is a unique habitat for bluehead suckers, being a high-gradient alpine river draining portions of the Uinta and Wasatch mountain ranges, as opposed to the lower-gradient desert rivers it inhabits in the Colorado River Basin. Unfortunately, the Weber

River has become highly degraded with dams and diversions altering the hydrologic and thermal regimes, potentially leading to a bluehead sucker recruitment bottleneck. Adult bluehead sucker have been observed spawning on gravel (Maddux and Kepner 1988; Sublette et al. 1990) and are associated with riffles (Vanicek 1967; Stewart et al. 2005; Bower et al. 2008), pools, and locations with cover (Sigler and Miller 1963; Sublette et al. 1990; Bower et al. 2008). Larval and juvenile bluehead suckers, on the other hand, have been documented occupying shoreline and backwater habitats (Sigler and Miller 1963; Vanicek 1967) and with growth related to water temperatures (Robinson and Childs 2001). The variety of complementary habitats adult and rearing bluehead sucker are associated with require the in-channel complexity that is often degraded or lost in over-allocated rivers (Graf 2006). Bluehead sucker density is positively associated with spring discharge (Propst and Gido 2004), a hydrologic component generally reduced in heavily regulated rivers. Bluehead sucker need suitable spawning substrate (i.e., gravel) and habitat (e.g., pools) as well as sufficient slow-water rearing habitat to accommodate their full life cycle and allow for successful recruitment (Dunning et al. 1992).

My overall goal was to identify potential recruitment bottlenecks for the Weber River bluehead sucker population (Figure 1). My specific objectives were to determine the habitat characteristics associated with spawning and rearing bluehead sucker and evaluate whether the Weber River bluehead sucker population may be limited by insufficient spawning habitat, rearing habitat, or both. To accomplish this, I used a multifaceted approach including fish sampling, comparative habitat surveys (e.g., from a healthy and degraded system), and microhabitat growth experiments. This study will evaluate if the Weber River bluehead sucker population may be limited by availability of suitable spawning and rearing habitat and provide a template for appropriate restoration activities.

Study Watershed

The Weber River watershed is located in northcentral Utah, draining 6,413 km^2 and flowing 201 km primarily northwest from headwaters in the Uinta mountains (3,569 m above mean sea level; amsl) through the Wasatch mountains and into the Great Salt Lake (1,278 m amsl; Figure 2; Webber et al. 2012). Seven large dams (dam height exceeding 19 m) in the watershed have contributed to altering natural hydrologic conditions, reducing and shifting the timing of natural peak flow in spring and summer (Figures 3 and 4) and maintaining atypically high flow below dams and atypically low flow below diversions throughout the irrigation season (approximately May-September). Furthermore, large dams such as Echo and Wanship dams, each exceeding 47 m height, obstruct connectivity between river reaches and limit bluehead sucker movement, documented as great as 15 km downstream and 10 km upstream in the Weber River (Webber et al. 2012; this study). Additionally, channelization of the river for highways, railways, and residential areas has exacerbated effects of altered hydrologic conditions by reducing slow-velocity, backwater habitats (Webber et al. 2012).

In addition to physical habitat degradation, a large population of exotic, naturalized Brown Trout *Salmo trutta* is found in the Weber River with densities in some areas reaching up to 37 adult fish/km^2 (Webber et al. 2012). Brown trout are piscivorous, well adapted to a wide range of global habitats (MacCrimmon and Marshall 1968; Budy et al. 2015), able to outcompete native species occurring sympatrically (McHugh and Budy 2005), and are known to prey on naïve native fishes (Garman and Nielsen 1982; Marrin and Erman 1982). This dense population of potential predators and competitors poses new challenges for bluehead suckers in the Weber River.

Historically, bluehead sucker were one of the most abundant fishes in the Weber River (Sigler and Sigler 1966); however, current estimates suggest the population consists of less than 500 adults spread across 84 river km, split into sub-populations by impassable dams (UDWR 2015). The sub-population in the highest-elevation reach, between Echo and Wanship Dams, had experienced a recruitment bottleneck for many years and would have likely gone locally extinct due to a lack of natural recruitment if the Utah Division of Wildlife Resources (UDWR) had not translocated it (Figure 5). In contrast, sub-populations in the lower-elevation reaches, appear to have experienced occasional successful, albeit diminished, reproduction (UDWR 2012; this study).

METHODS

My research goal was to identify potential habitat-based recruitment bottlenecks for bluehead sucker in the Weber River, focusing on spawning and rearing life stages. I located and quantified associated spawning habitat by electroshocking and conducting reach-based habitat surveys in both the Weber River and Ferron Creek, a relatively unaltered surrogate river. I compared spawning reaches to non-spawning reaches in each river, using ANOVA and random forest classification to determine whether habitat associated with spawning bluehead sucker differed significantly from available habitat. I sampled backwaters within and immediately downstream of known spawning reaches in the Weber River, and evaluated the relationship between juvenile sucker abundance and size of backwaters using linear mixed-effects regression. To add a mechanistic understanding, I conducted laboratory experiments to determine the juvenile bluehead sucker growth response to different water temperature and velocity treatments and analyzed these data using linear mixed-effects regression.

Field and Laboratory Studies

Spatial extent of spawning and non-spawning locations.—I determined the spatial extent of spawning locations by surveying large reaches (approximately 20 km) of the Weber River across the contemporary bluehead sucker range. I conducted raft electrofishing surveys during 2015 and 2016 with UDWR biologists in order to locate bluehead sucker in spawning condition. I conducted a two-pass survey of the Weber River from the mouth of Weber Canyon to the Ogden River inlet (Figure 2) for bluehead sucker in spawning condition in May and June 2015. I conducted a three-pass survey of the Weber River from the Lost Creek confluence to the town of Morgan, UT for bluehead sucker in spawning condition in May 2016. I assessed spawning condition of all bluehead sucker during surveys in each year, as indicated by presence of tubercles, eggs, or milt. I measured each fish (total length and weight), scanned each fish for Passive Integrated Transponder (PIT) tags (569 bluehead sucker were previously tagged by UDWR in contemporary bluehead sucker range; UDWR, *unpublished data*), and PIT tagged all previously unmarked fish. I recorded the locations at which bluehead suckers were collected with handheld GPS units. I used UTM locations of fish collected during UDWR surveys conducted from 2006-2014 to identify additional bluehead sucker spawning locations (UDWR, *unpublished data*).

I used geographic information system (GIS; ArcMap) spatial analysis to document the locations of bluehead sucker in spawning condition following the completion of each spring (May - June) spawning survey. Sites with two or more adult (> 330 mm total length) bluehead suckers, with at least two of those adults sampled in spawning condition, constituted the center of an associated spawning reach, hereafter referred to simply as a "spawning reach". Spawning reaches extended 150 m both up and downstream from the center point, for a total reach length of 300 m. I merged spawning reaches if one spawning location occurred within 300 m of another spawning location.

In addition to spawning reaches, I randomly selected ten "non-spawning" reaches throughout the bluehead sucker historic range in which neither I nor the UDWR collected any bluehead sucker in spawning condition. I divided the Weber River sequentially, from Wanship Dam to the Ogden River inlet (Figure 2), into 300-m reaches. Using Google Earth imagery, I preliminarily marked the number of geomorphic units associated with bluehead sucker in previous studies, i.e., riffles, pools, and backwaters (Vanicek 1967; Stewart et al. 2005; Bower et al. 2008), in addition to gravel bars (an important source of substrate in riffles), large woody debris (an important source of scour for pools), and side channels (an additional measure of complexity), hereafter referred to as habitat units, occurring between Wanship Dam and the Ogden River inlet. The abundance of these habitat units marked in each reach (number per 300-m reach) was the level of complexity. Spawning reaches from my 2015 spawning survey contained an average of nine habitat units, as seen on Google Earth imagery. Therefore, I defined nine or more habitat units per 300-m reach as a complex reach. I arbitrarily defined five or less habitat units per 300-m reach as a simple reach. I randomly selected five complex and five simple reaches to capture the full range of complexity on the Weber River.

Habitat characteristics associated with spawning and non-spawning reaches.—I quantified habitat characteristics in spawning and non-spawning reaches using reach-based surveys, in order to determine whether habitat differed significantly between the two reach types. I divided each reach into five transects, equidistantly spaced (e.g., 75 m apart for 300-m reaches). I measured wetted and bankfull channel widths as well as at least twenty depths and substrate sizes using a gravelometer across each transect (Wolman 1954). I measured discharge (Marsh-McBirney Flo-Mate™ 2000) and water quality (temperature, dissolved oxygen, specific conductivity; YSI 556 MPS) at whichever transect appeared to lead to the most accurate discharge measurement (i.e., simplest channel bed). Within each reach, I classified geomorphic units by stage height and shape (concave, convex, or planar) following Wheaton et al. (2015) and measured length, width, maximum depth, and twenty depth measurements (evenly dispersed to cover the entire feature) for every riffle, pool, backwater, gravel bar, and chute/side channel. Additionally, I estimated large woody debris (LWD) and log jams at different size classes (small LWD: 10 - 15 cm diameter, 1 - 3 m length; medium LWD: > 15 - 30 cm diameter, > 3 - 6 m length; large LWD: > 30 cm diameter, > 6 m length; small log jam: ≤ 20 LWD pieces; medium log jam: 21 - 50 LWD pieces; large log jam: > 50 LWD pieces; Bouwes et al. 2011).

Comparing the Weber River to a less-degraded river system.—In order to compare habitat use of the Weber River bluehead sucker population to a population experiencing more natural and sustainable levels of recruitment, I evaluated associated spawning habitat for the bluehead sucker population in Ferron Creek, UT above Millsite Reservoir (Figure 6). Ferron Creek is located in central Utah, draining 626 km^2 of the Wasatch Plateau (highest elevation = 3400 m amsl), flowing primarily east 25.7 km into Millsite Reservoir (1893 m amsl) and an additional 42.7 km into the San Rafael River (1629 m amsl). A population of approximately 7000 bluehead sucker inhabits Ferron Creek and Millsite Reservoir (UDWR 2015). The robust population in Millsite Reservoir and Ferron Creek may allow for selection of optimal habitat, as bluehead sucker have been negatively associated with near-stream anthropogenic land use (Dauwalter et al. 2011). Ferron Creek retains a natural flow regime above Millsite Reservoir and only has small dams at higher elevations that spill over annually. In addition to the natural flow regime, Ferron Creek has few non-native fish above Millsite Reservoir (e.g., Rainbow Trout *Oncorhynchus mykiss* and Cutthroat Trout x rainbow trout hybrids *O. clarkii pleuriticus x O. mykiss)*. Instream habitat in Ferron Creek is similar to the Weber River, with similarly high gradient and rocky substrates, although Ferron Creek is narrower and shallower. Ferron Creek provides a good opportunity to evaluate bluehead sucker habitat use in a fairly-pristine river system with a robust bluehead sucker population, natural flow regime, and relative lack of non-native fishes.

In July 2016, I collaborated with the UDWR to survey 7.52 km of Ferron Creek extending upstream of Millsite Reservoir. I used a backpack electrofishing unit and otherwise followed the same protocol as in the Weber River for processing fish, mapping associated spawning locations, defining spawning and non-spawning reaches, and measuring habitat characteristics. I surveyed habitat characteristics in all eleven spawning and ten non-spawning reaches.

Quantifying physical characteristics and rearing suckers in backwaters.—I sampled backwaters near spawning reaches to quantify rearing sucker abundance and backwater habitat characteristics. I sampled all backwaters within and immediately downstream (< 1 km from downstream end of spawning reach) of all known bluehead sucker spawning reaches located in the Weber River. I sampled twenty-three backwaters in July and August 2015. I primarily used small-mesh beach seine nets due to their perceived efficacy at catching young-of-the-year (age-0) larger than approximately 15 mm total length (TL). I seined each backwater with at least three passes when possible. However, I used an electrofishing backpack unit to sample three backwaters due to their large width and depth. I sampled twelve backwaters in July and August 2016 (eleven resampled from 2015 and one previously unsampled backwater). I used a backpack electrofishing unit for at least two passes, followed by at least three passes with a seine net, for less size bias compared to sampling in 2015. I sampled to depletion during all sampling occasions in both years when possible (i.e., the backwater was not too deep, wide, or filled with vegetation/LWD to effectively sample) and removed all ineffective sampling occasions from further analyses.

After sampling each backwater, I enumerated all larval and juvenile sucker, considering all juvenile sucker ecologically synonymous due to their likely-similar niche requirements at small sizes. I measured TL of the first fifty randomly-selected individuals and identified all larval and juvenile suckers to species (bluehead sucker, Utah Sucker *C. ardens*, and Mountain Sucker *C. platyrynchus*) when possible. Additionally, I enumerated and measured TL of all non-native brown trout sampled in each backwater. I measured the area, depth (maximum depth and twenty depths spaced evenly through the full spatial extent of the backwater), and water quality (temperature, dissolved oxygen, specific conductivity; YSI 556 MPS) at the center of each backwater. In 2016, I also estimated LWD and substrate composition of each backwater sampled, using the same protocol as the spawning habitat portion of this study described above for LWD but surveying at least twenty-five substrate sizes along transects in a zig-zag pattern to cover the full width and length of each backwater.

Bluehead sucker growth experiment.—I conducted laboratory experiments to complement my field studies by determining the juvenile bluehead sucker growth response to different water temperatures and velocities (Table 1). I tested the hypotheses that juvenile growth is optimized in warmer temperature, slower velocity water relative to cooler, faster water. Working cooperatively with the UDWR, I collected 140 juvenile (90 - 200 mm TL) bluehead sucker from the Raft River (Box Elder County, UT) in spring and summer 2016. The Raft River bluehead sucker population is healthy, dense, and is part of the same evolutionarily significant unit as the Weber River population (Hopken et al. 2013). I conducted experiments in the Millville Aquatic Research Facility (MARF), Millville, UT. The experiment was performed in three oval, steel, stream-flow tanks at MARF with each slow, medium, or fast-velocity treatment consisting of water velocities within the range encountered by juvenile bluehead sucker in the Weber River. Velocity treatments were created with a single 2-horsepower (hp) water pump (medium and fast velocity) or three 1/4-hp water pumps (slow velocity) per tank and water dispersal/deflector structures (e.g., cinder blocks). Experimental treatments consisted of three water velocities and three water temperatures, cool, tepid, and warm, for a total of nine treatments (three velocity x three temperature treatments; Table 1). I used gates to close off experimental chambers (water depth approximately 50 cm, length approximately 2 m, width approximately 60 cm) on either end within the oval tanks. I used small substrate (< 90 mm diameter, the size found in the Weber River that would not disrupt water flow substantially or become suspended in fast water) to fill the floor of each experimental chamber and approximate a more natural environment. I hung semi-transparent, black screens around all experimental tanks to minimize stress to fish.

To acclimatize experimental fish prior to experimentation, I held all juvenile bluehead sucker in round, flow-through holding tanks fed by a steady inflow of aerated well water (approximately 10°C). I layered the bottom of each holding tank with large substrate (90 - 128 mm diameter) and surrounded the holding-tank area with semi-transparent, black screens to reduce stress of all fish prior to experimental trials. I PIT tagged all fish within 1-5 days of arrival at MARF. I fed all juvenile bluehead sucker ad libitum initially with frozen bloodworms (for one week to acclimate to laboratory conditions) and later with Skretting© pellet feed formulated for June Sucker *Chamistes liorus*.

I randomly selected fish for each treatment, measured each fish before and after each trial to determine growth, and quantified tank discharge and water temperature. I randomly selected juvenile bluehead sucker for each treatment at the start of each experimental trial, five for each treatment in the first round of trials, seven for each treatment in the second round of trials, and acclimated fish for at least one day (Table 2). I scanned, measured (TL), and weighed (mass, closest 0.01 g) each fish prior to experimentation. I measured discharge at the center of each experimental chamber prior to experimental trials and I used tank discharge as a metric of water velocity. I monitored hourly water temperatures during experimental trials with HOBO® temperature loggers and fed fish to excess twice daily (approximately 2 tablespoons per feeding) with automatic feeders. Following the experimental trial period (7 – 25 days), I scanned, measured, and weighed all fish within one hour of experimental trial start time. I cleaned all experimental tanks after each trial and returned juvenile bluehead suckers back to the holding tanks, keeping approximately the same number of fish in each holding tank.

Statistical Analyses

Associated spawning habitat.—I used analysis of variance (ANOVA) to compare habitat characteristics measured in spawning and non-spawning reaches and identify significant differences in substrate, depth, LWD, bankfull and wetted channel widths, geomorphic complexity, and occurrence (both abundance and relative area) of geomorphic units. To prepare data for analysis, I calculated the area and abundance of distinct geomorphic units (i.e., riffles, pools, backwaters, gravel bars, and chutes/side channels) in each reach and I categorized substrate as fines (< 4 mm diameter), gravel (4 - < 64 mm diameter), cobble (64 - < 256 mm diameter), or boulders (≥ 256 mm diameter; Wentworth 1922). I defined geomorphic complexity as the proportion of each reach composed of non-planar geomorphic units, i.e., sum of pool, riffle, and chute/side channel area divided by the wetted reach area (similar to longitudinal roughness from Gooseff et al. 2007). I standardized geomorphic and LWD habitat metrics by reach length (e.g., number of riffles per river km) to account for the greater length of the few merged spawning reaches. I standardized substrate as a proportion of each size class by total substrate measurements per reach. After evaluating the normality and variance of the data, I tested normally-distributed data with a t-test (Student 1908) and non-normally-distributed data with a Mann-Whitney U-test (Mann and Whitney 1947). I compared Weber River spawning and non-spawning reaches, and I separately compared Ferron Creek spawning and non-spawning reaches.

In addition to an ANOVA, I performed a random forest classification (Breiman 2001) to evaluate whether select habitat characteristics are significant predictors of spawning classification (i.e., spawning or non-spawning reach). Random forest models are non-parametric and are, therefore, not restricted to normally distributed variables. Random forest models also require no assumptions of relationships between response and predictor variables and are able to handle complex, highly-dimensional data, where predictor variables may outnumber observations, all characteristics of these data. I initially included all physical habitat characteristics measured in the field as variables in the random forest classification. I performed a backward stepwise variable selection procedure to create the most parsimonious model and assess variable importance relative to the full suite of variables included in the model (Guyon and Elisseeff 2003). Starting with all possible predictor variables, I calculated the area under the receiver operating characteristic curve (AUC) at each step. I calculated the mean decrease accuracy (i.e., the decrease in classification accuracy from permuting each variable) for each variable at each step and removed the variable with the lowest mean decrease accuracy. I completed the backward stepwise variable selection procedure until only one variable remained and chose the classification model with the highest AUC as my final model. To investigate robustness of my final model, I performed a sensitivity analysis by completing ten iterations at each step and calculating mean AUC for the model and mean decrease accuracy for each variable. I used partial dependence plots to visualize the trends in relationships between spawning classification and significant habitat variables. Partial dependence plots indicate the probability the model will classify a reach as a spawning or non-spawning reach across the full range of values of a habitat variable, while using the average values for all other variables included in the model. Interpretation of partial dependence plots must be made with caution, as they incorporate complex, nonparametric ecological data and should not be used for prediction or prescription. I performed all statistical analyses in the R-Cran statistical package (R Development Core Team 2017), using the 'randomForest' package (Liaw and Wiener 2002; version 4.6-12) for random forest classification and the 'verification' package to calculate AUC (NCAR 2015; version 1.42).

Rearing habitat.—I used a random forest regression to evaluate whether physical and biological characteristics are significant predictors of rearing sucker abundance. Using rearing habitat data collected in the field in 2016, I performed a backward stepwise variable selection procedure starting with all possible predictor variables (backwater area, maximum depth, mean depth, total LWD, brown trout abundance, non-native fish abundance, and proportion of total substrate composed of fines, gravel, cobble, and boulders) to create the most parsimonious model. I calculated the increase in node purity (the decrease in residual sum of squares for splitting on a variable) for each variable at each step and removed the variable with the lowest increase in node purity. I completed the backward stepwise variable selection procedure until the out-of-bag mean square error began to increase. To evaluate the robustness of my final model, I performed a sensitivity analysis by completing ten iterations at each step and calculating mean square error for the model and increase in node purity for each variable.

I evaluated the relationship between the size of backwaters in the field (area and depth) and sucker abundance using a linear mixed-effects regression framework. My data were hierarchically structured with repeated measures of backwaters (repeated in eleven backwaters in 2015 and 2016) nested within site (backwater) and sites nested within year. I included two biological variables, juvenile sucker and all brown trout sampled, and two physical variables, backwater area and maximum depth, at each sampling event. I calculated average depth of each backwater as the mean of the twenty evenly-spaced depth measurements. I calculated volume as average depth multiplied by area. I first evaluated the degree to which each predictor variable was correlated, in order to remove highly-correlated variables (i.e., Pearson correlation coefficient > 0.5). As such, I removed backwater volume and average depth due to high correlations to area and maximum depth. I used the Shapiro-Wilk test (Shapiro and Wilk 1965) to evaluate the normality of the distribution of each remaining variable (total sucker juveniles sampled, maximum depth, area, brown trout sampled). I $\log_e$ transformed total number of sucker sampled and backwater area, because these two variables differed significantly from a population with a normal distribution**.** I was unable to transform total brown trout sampled to a normally-distributed population using any transformation.

I took an information theoretics approach to rank models as a function of predicting the total number of juvenile suckers in a backwater, the response variable. I performed a forward bidirectional stepwise variable selection procedure (Gelman and Hill 2008) starting with the following null (i.e., intercept-only) model:

(1) $y_i = \beta_0 + \beta_{1j[i]k[i]} + \varepsilon_{j[i]k[i]}$, for $i = 1, \ldots, n$ observations

$\beta_{1j} \sim N(\mu_{B1}, \sigma^2_{B1j})$, for j = 1, …, J.

$\beta_{1k} \sim N(\mu_{B1}, \sigma^2_{B1k})$, for k = 1, …, K.

$\varepsilon_{j[i]k[i]} \sim N(0, \sigma^2_{\varepsilon})$

where, y_i is the $\log_e$ sucker sampled for an observation *i*, β_0 is the intercept and $\beta_{1j[i]k[i]}$ is the random effect of year *j* and site *k* across backwater maximum depth, ε is the residual error. β_1 for year *j* and site *k* follows a normal distribution around the mean of μ_{B1} and a variance of σ^2_{B1}. Model residual error (ε) for year *j* and site *k* follows a normal distribution around a mean of zero with a variance of σ^2_{ε}. I used a model selection criterion of delta 4 Bayesian information criterion (BIC; Burnham and Anderson 1998). At each step, the addition or removal of variables occurred if model BIC decreased by at least 4 BIC from the previous step. I selected random effect structure by maximizing restricted maximum likelihood and fixed effect structure by maximizing log-likelihood at each step. Backwater maximum depth, $\log_e$–transformed area, brown trout sampled, and all potential interactions were the full suite of possible predictor variables (i.e., fixed effects). Interactions were only considered for inclusion if both main effects were already included separately in the model.

The full model, with all possible covariates included, was as follows:

(2) $y_i = \beta_0 + \beta X_i + \varepsilon_{j[i]k[i]}$, for $i = 1, \ldots, n$ observations

$\varepsilon_{j[i]k[i]} \sim N(0, \sigma^2_{\varepsilon})$

where, βX_i is a matrix of all possible covariates and coefficients (Table 3).

I evaluated the relationship between juvenile growth and water temperature and velocity in laboratory experiments using a linear mixed-effects regression framework. Experimental data were hierarchically structured with multiple tanks nested within each trial time. I used a hypothesis-driven approach (Gelman and Hill 2008) to test whether water temperature, velocity (measured as tank discharge), and their interaction are significant predictors of juvenile bluehead sucker growth. I calculated growth as grams per gram per day (g/g/day), i.e., change in mass (g) divided by mean mass (g) divided by duration (days) for each fish in each treatment trial**.** I used the Shapiro-Wilk test (Shapiro and Wilk 1965) to evaluate the normality of the distribution of the response variable, g/g/day. I square root transformed g/g/day (after adding 0.01) because it differed significantly from a population with a normal distribution. I removed one individual from analysis, as it exhibited a strong, negative physiological response to experimentation, losing 7.9 g when all other individuals gained 1.0-6.5 g through the same trial period. I included a random effects structure of tank nested within trial period. I evaluated significance of predictor variables based on standard error of predicted juvenile growth and analyzed full model fit based on residual error (Gelman and Hill 2008).

The full juvenile growth model, was as follows:

(3) $y_i = \beta_{7g[i]g[h[i]]} + \beta_8 x_{4i} + \beta_9 x_{5i} + \beta_{10} x_{4i} * x_{5i} + \varepsilon_{g[i]g[h[i]]}$, for $i = 1,\ldots, n$ observations

$$\beta_{7g} \sim N(\mu_{B7,} \sigma^2_{B7g}), \text{ for } g = 1, \ldots, G.$$

$$\beta_{7g[h]} \sim N(\mu_{B7,} \sigma^2_{B7g[h]}), \text{ for } g = 1, \ldots, G, \text{ and } h = 1, \ldots, H.$$

$$\varepsilon_{g[i]g[h[i]]} \sim N(0, \sigma^2 \varepsilon)$$

where, y_i is the square root transformed g/g/day for an observation *i*, $\beta_{7g[i]g[h[i]]}$ is the intercept of tank *h* nested within trial time *g*, β_8 is the slope across water temperature (x_4), β_9 is the slope across water velocity (x_5), β_{10} is the slope across water temperature and velocity ($x_4 * x_5$), ε is the residual error. β_7 for trial time *g* follows a normal distribution around the mean of μ_{B7} and a variance of σ^2_{B7g}. β_7 for tank *h* nested within trial time *g* follows a normal distribution around the mean of μ_{B7} and a variance of $\sigma^2_{B7g[h]}$. Model residual error (ε) for trial time *g* and tank *h* follows a normal distribution around a mean of zero with a variance of σ^2_{ε}.

I performed all statistical analyses in the R-Cran statistical package (R Development Core Team 2017), using the ‘randomForest’ package (Liaw and Wiener 2002; version 4.6-12) for random forest regression, the ‘lme4’ package (Bates et al. 2015; version 1.1-12) for linear regression, and the ‘effects’ package (Fox 2003; version 3.1-2) for visualizing standard error around linear mixed model predictions.

RESULTS

Spawning habitat in the Weber River

In order to evaluate potential bluehead sucker recruitment bottlenecks in the Weber River, I located and surveyed fishes in five spawning reaches in 2014 (using historical UDWR survey data; *unpublished data*), ten in 2015, and four in 2016. I surveyed habitat characteristics in eighteen of the nineteen spawning reaches but was unable to survey the nineteenth due to land-access issues. In all, I surveyed 8.93 river km and these nineteen spawning reaches represented a total of 5.93 river km or 5.7% of the Weber River from Wanship Dam downstream to the Ogden River inlet (Tables 8-11). In total, the UDWR and I collected 122 bluehead sucker in spawning condition from 2014-2016.

Spawning habitat was not significantly different from non-spawning habitat in the Weber River, aside from abundance of LWD, based on my analysis using ANOVA. No significant differences were observed between spawning and non-spawning reaches when comparing the number and proportional area of geomorphic units (pools, riffles, backwaters) found in each reach nor the proportion of substrate at any size class (e.g., gravel, cobble). Spawning reaches were not significantly more or less complex than non-spawning reaches. However, LWD was significantly more abundant in non-spawning reaches, relative to spawning reaches. Number of LWD jams ranged from 0-3 in non-spawning reaches and 0-2 in spawning reaches. Area of LWD jams ranged from 0-275 m^2 in non-spawning reaches and from 0-215 m^2 in spawning reaches. The amount of LWD (large size class; > 30 cm diameter, > 6 m length) as well as the number and area of

LWD jams occurred in greater abundance in non-spawning reaches than in spawning reaches (Wilcoxon rank sum test, $p < 0.05$**;** Figure 7).

Random forest classification supplemented ANOVA results, identifying that the availability of cobble, gravel, and riffles were significant predictors of spawning classification (final model mean AUC = 0.85; Table 4). The proportion of cobble and gravel demonstrated a positive relationship with spawning reach classification at intermediate values; as proportion cobble and gravel increase to approximately 0.3-0.45 and 0.35-0.5 of the total substrate in the reach respectively, the model was more likely to predict classification as a spawning reach (Figures 8 and 15). The number of riffles per reach, however, exhibited a negative relationship with spawning reach classification (i.e., as riffle abundance increases, the model was more likely to predict a non-spawning reach).

Spawning habitat in Ferron Creek

In order to evaluate bluehead sucker spawning habitat in a relatively unaltered stream, I located and surveyed eleven spawning reaches in 7.52 km of Ferron Creek during July 2016 spawning surveys. In all, I surveyed 7.15 river km and these eleven spawning reaches represented a total of 4.13 river km or 54.9% of Ferron Creek directly upstream from Millsite Reservoir (Tables 12-13). In total, we collected 136 bluehead sucker in 2016, 66 of which were in spawning condition.

Geomorphic composition and substrate in spawning reaches differed from non-spawning reaches, as indicated by ANOVA. Spawning reaches were composed of greater geomorphic complexity, more pools, and wider wetted channel widths. For example, the abundance of pools ranged from 2-11 pools in spawning reaches and 0-5 pools in non-spawning reaches. Geomorphic complexity, pool abundance, and mean wetted channel width were all greater in spawning reaches than in non-spawning reaches (t-test, $p < 0.05$; Figure 9).

Random forest classification complemented ANOVA for Ferron Creek, identifying that channel width and the availability of fines and gravel were significant predictors of spawning classification in the random forest classification (final model mean AUC = 0.80; Table 4). The proportion of fines in a reach demonstrated a negative relationship with spawning reach classification (i.e., as fines decrease below approximately 0.15 as a proportion of total substrate in the reach, the model was more likely to predict classification as a spawning reach; Figures 10 and 16). The proportion of gravel and mean wetted channel width, however, were positively related with spawning reach classification (i.e., as these variables increase, the model was more likely to predict classification as a spawning reach).

Physical characteristics and rearing suckers in backwaters

Backwater size and substrate observed in backwaters were significantly related to use by rearing suckers. Backwater area and availability of cobble and fines were predictors of rearing sucker abundance in the random forest regression (Table 4). Backwater area and proportion of cobble increased with rearing sucker abundance (Figure 11). However, rearing sucker abundance was inversely related to the proportion of fines. In backwaters sampled in 2016 ($n = 10$), backwater area was correlated with maximum depth (Pearson correlation coefficient = 0.58; p-value < 0.10) and average depth (Pearson correlation coefficient = 0.57; p-value < 0.10). Proportion of fines was significantly correlated with proportion of gravel (Pearson correlation coefficient = -0.83; p-value < 0.01).

In order to evaluate the relationship between backwater size and abundance of juvenile sucker, I sampled 29 backwaters to depletion through the study period (eighteen backwaters in 2015, eleven in 2016). Total juvenile sucker spp. (bluehead sucker, Utah sucker, and mountain sucker) collected ranged from 7-302 per backwater. Backwaters ranged from 19-87 cm maximum depth. The forward bidirectional variable selection procedure identified backwater maximum depth as a significant positive predictor of total sucker juvenile abundance ($\log_e$; Table 5). Indeed, models including backwater area ($\log_e$) or total brown trout sampled performed more poorly than the model containing maximum depth as the only predictor variable based on BIC. My small sample size made a nested random effects structure infeasible and necessitated that I include year and site as separate random effects in the model. Varying random effects across backwater maximum depth resulted in the best random effect structure.

Final model predictions were consistent with observed values and residual error was homoscedastic across response and predictor variables. Predicted $\log_e$ total sucker sampled per backwater demonstrated a close relationship to observed $\log_e$ total sucker sampled (Figure 17). Final model residuals were evenly distributed across both predicted $\log_e$ total sucker sampled and backwater maximum depth. Residuals of the final model ranged from -0.93 to 1.02 and did not differ significantly from a normal distribution (Shapiro-Wilk test).

The final model was as follows:

(4) $y_i = \beta_0 + \beta_{1j[i]k[i]}x_{1i} + \varepsilon_{j[i]k[i]}$, for $i = 1,\ldots, n$ observations.

$\beta_{1j} \sim N(\mu_{\beta 1}, \sigma^2_{\beta 1j})$, for j=1, …, J.

$\beta_{1k} \sim N(\mu_{\beta 1}, \sigma^2_{\beta 1k})$, for k=1, …, K.

$\varepsilon_{j[i]k[i]} \sim N(0, \sigma^2_{\varepsilon})$

where, y_i is the $\log_e$ sucker sampled for an observation *i*, β_0 is the intercept and $\beta_{1j[i]k[i]}$ is the slope of year *j* and site *k* across backwater maximum depth (x_1), ε is the residual error. β_1 for year *j* and site *k* followed a normal distribution around the mean of μ_{B1} and a variance of σ^2_{B1}. Model residual error (ε) for year *j* and site *k* followed a normal distribution around a mean of zero with a variance of σ^2_{ε}.

Total sucker sampled ($\log_e$) was positively related to backwater maximum depth (Table 6; Figure 12). The predictions of β_1 (slope) varied from 4.2 for the grand mean model to 4.5 and 3.9 for years 2016 and 2015, respectively, likely because I conducted a more thorough sampling in 2016 by electrofishing in addition to seining.

Bluehead sucker growth experiment

Experiment treatments of water velocity and temperature were significant predictors of juvenile bluehead sucker growth, determined using a linear mixed-effects regression framework. Water velocity and temperature were both negatively related to juvenile growth (Tables 7 and 14). Growth of juvenile bluehead suckers decreased weakly with increasing temperature ($\beta_8 = -0.0033$), with an important interaction between temperature and velocity. Juveniles grew significantly more in the slow velocity treatment, relative to the fast velocity treatment, at cooler temperatures but not at warmer temperatures (Figure 13). Growth of juvenile bluehead suckers decreased with increasing velocity ($\beta_9 = -1.6$), with greater disparity between cooler and warmer temperatures. Juvenile growth differed significantly across the range of velocities tested in the laboratory in the cool temperature treatment only (Figure 14).

Residual error was homoscedastic across response and predictor variables and model predictions were consistent with observed values. Predicted square root transformed g/g/day demonstrated a close relationship to observed square root transformed g/g/day (Figure 18). Full model residuals were evenly distributed across predicted g/g/day and both response variables, i.e., water velocity and temperature experiment treatments. Residuals of the full model ranged from -0.042 to 0.037 and did not differ significantly from a normal distribution (Shapiro-Wilk test). Predicted juvenile growth was consistent with observed growth.

DISCUSSION

Native fishes throughout the Intermountain West are imperiled due to anthropogenic stressors, and having experienced a rangewide contraction in recent years, bluehead sucker are no different. Bluehead sucker are rarely the focus of research studies or management concern, as they are generally perceived as a non-charismatic, non-game species (Budy et al. 2015, Laub and Budy 2015). The bluehead sucker population in the Weber River appears to have experienced a recruitment bottleneck, and understanding why and how has important conservation implications. My findings suggest the availability of suitable spawning and rearing habitat may be a critical limiting factor for bluehead sucker recruitment in the Weber River. I determined that spawning bluehead sucker disproportionately use habitats with substrate and geomorphic characteristics that are largely depleted in the Weber River, confirmed by a comparison to the more pristine Ferron Creek. In the laboratory, I determined the relationship between juvenile growth and water temperatures and velocities. Together, the field and laboratory portions of this study established spawning and rearing habitat characteristics associated with bluehead sucker and identified pools, gravel, cobble, and deep, cool, slow-water as being important. The contemporary hydrologic regime of the Weber River has likely diminished these associated and optimal habitats identified. Restoring habitat for the critical life stages of spawning and rearing bluehead sucker could eliminate the recruitment bottleneck and lead to successful restoration and conservation of the population.

Field surveys of reaches associated with fecund bluehead sucker revealed correlation with particular habitat features. Substrate composition in the reach was an important component of spawning habitat, with spawning bluehead sucker using reaches in which cobble and gravel comprised three quarters of total substrate. Gravel and cobble are important to spawners like bluehead sucker, because they allow for burial and aeration of fertilized eggs, leading to greater survival of embryos and emergence of larvae (e.g., Montgomery et al. 1997; Geist and Dauble 1998). These results correspond with previous studies that have observed bluehead sucker spawning on gravel (Maddux and Kepner 1988; Sublette et al. 1990; Otis 1994) and associated fecund adults with use of rocky habitats (Vanicek 1967; Stewart et al. 2005; Bower et al. 2008). In contrast, spawning bluehead sucker were associated with less LWD and riffles compared to previous studies (e.g., Vanicek 1967; Bower et al. 2008). However, bluehead sucker are likely not selecting spawning habitat for lack of LWD, as LWD can create scour pools that may be important habitat for bluehead sucker in spawning condition (Abbe and Montgomery 1996). Rather, the ostensible negative relationship of fecund bluehead sucker to LWD abundance may reflect very limited availability of LWD overall due to degraded riparian vegetation over large reaches of the Weber River. Riparian communities are often degraded downstream of large dams, due to reductions in flood peaks and groundwater levels (Nilsson and Berggren 2000).

In addition, comparison of bluehead sucker spawning habitat in the Weber River and Ferron Creek, a stream in relatively pristine condition and with fewer confounding factors, also identified potential limiting habitat characteristics. Attempting to draw conclusions regarding habitat use versus preference is a major challenge with many habitat use studies, as identifying true habitat preference requires the removal or control of extraneous factors (e.g., competition, predation; Rosenfeld 2003). Therefore, I compared spawning habitat in both rivers, because bluehead sucker may have the opportunity to select more optimal habitat in Ferron Creek, relative to the Weber River. The hydrologic and thermal regime and in-stream habitat remain largely unaltered, and there are few other non-native and potentially competing or predatory fishes (Holden and Stalnaker 1975; Martinez et al. 1994; Stewart et al. 2005). Spawning bluehead sucker in Ferron Creek were associated with reaches containing more pools, larger wetted channel widths, more gravel, and less fine substrate. Use of habitats with more pools and larger wetted channel widths by fecund bluehead suckers corroborates the results from other studies, where bluehead sucker likely used pools for refuge and feeding (Bower et al. 2008; Banks 2009). These habitat characteristics are stream features commonly lost in regulated streams due to altered hydrologic conditions and channelization (Gaeuman et al. 2005).

Somewhat unsurprisingly, spawning habitat use in Ferron Creek did not completely concur with spawning habitat survey results from the more-degraded Weber River. One similarity was that substrate (gravel, cobble, lack of fines) comprising the reach was identified by my models as important in both rivers, with prevalence of small, rocky substrates predicting use by fecund bluehead sucker as spawning habitat. However, bluehead sucker in Ferron Creek were associated with more complex habitats composed of more pools and wider wetted channel widths, as opposed to bluehead sucker in the Weber River**.** One important caveat when interpreting these results, however, is that partial dependence plots must be read with caution, especially when comparing the results from the two rivers. In addition, partial dependence plots should not be used for prediction or direct prescription of restoration actions (i.e., based on finite values on the x axis). Notwithstanding, the collective results from the two rivers suggest that spawning habitat, and therefore spawning success (e.g., Soulsby et al. 2001; Grabowski and Isely 2007), is limited by the availability of pools, gravel, and cobble. The occurrence of pools, gravel, and cobble is likely limited in the Weber River. Furthermore, the fact that spawning bluehead sucker in the Weber River used less complex habitat than in Ferron Creek suggests their habitat-based realized niche may be confined due to other biotic factors (e.g., Douglas et al. 1991; Shelton et al. 2008). Bluehead sucker may not use optimal in-stream habitat in the highly-altered Weber River, due to the presence of non-native fishes which represent likely competitors and predators (Martinez et al. 1994; Walser et al. 1999). For instance, sub adult or small adult bluehead sucker may be preyed on or harassed by brown trout (Garman and Nielsen 1982; Marrin and Erman 1982); in this system, brown trout consume fishes up to 300 mm TL (this study; *unpublished data*).

The results of the rearing habitat component of my study suggest the availability of suitable rearing habitat may also be a limiting factor for bluehead sucker recruitment in the Weber River. Loss of slow-water rearing habitat is common in regulated rivers of the Intermountain West (e.g., Schmidt et al. 2001; Grams and Schmidt 2002). In the field, deeper backwaters were associated with use by more rearing sucker juveniles, concurring with previous research (Haines and Tyus 1990). These results indicate that size of rearing habitats (i.e., depth, this study) is important to rearing sucker, in addition to the availability of these complementary habitats (Sigler and Miller 1963; Vanicek 1967). Furthermore, backwaters must contain water at the optimal temperatures in order to facilitate growth and survival of juvenile sucker (Robinson and Childs 2001). Although not the focus of this study, I did not detect any association between brown trout and rearing sucker habitat use. Elsewhere, bluehead sucker larvae are common prey items for non-native predators (Ruppert et al. 1993; Marsh and Douglas 1997), found in lower densities where non-native predators are abundant (Gido and Propst 2012), and possible competitors for food resources with non-native fish (Seegert et al. 2014). However, brown trout use of backwater habitats may be too sporadic to detect with sampling events conducted once per summer, as herein (e.g., Heggenes 2002). Interestingly, backwater area was highly correlated with maximum depth but not average depth. This pattern indicates that backwaters with high surface area have at least one deep area but may be shallower on average than smaller backwaters.

In the laboratory, juvenile bluehead sucker performed consistently better in slow-velocity treatments and, somewhat surprisingly, performed well in cool-temperature treatments. My laboratory experiments complemented the field study by evaluating the optimal water temperature and velocity for juvenile growth in a controlled setting (Kitchell et al. 1977). Coleman and Fausch (2007) used a similar experimental approach to determine larval growth, and later survival, across temperature treatments. Relative to historical conditions, the dams and diversions throughout the main-stem Weber River may diminish slow-water habitat and lead to altered water temperatures downstream due to hypolimnetic dam releases, impoundments, and de-watering. The result that growth was greatest in slower velocity treatments is consistent with many studies that associate juvenile bluehead sucker with slow-velocity near-shore habitats (e.g., Haines and Tyus 1990; Robinson et al. 1998). However, previous research also suggests water temperatures of approximately 17.5°C are positively related to juvenile bluehead sucker growth (Robinson and Childs 2001). In contrast, I found a slight negative relationship between juvenile growth and water temperature, with an interaction between temperature and velocity. These results are in agreement with the energetic expectation that temperature and velocity will have an interactive effect on fish growth (e.g., Hill and Grossman 1993). In addition, juvenile bluehead sucker from the Snake/Bonneville evolutionarily significant unit (Hopken et al. 2013), which are genetically distinct enough to potentially warrant listing as a unique species (Unmack et al. 2014) or sub species (Bangs et al. 2017), may be locally adapted to the cooler water temperatures in the extremely alpine Weber and Raft Rivers, as opposed to juveniles from the warmer, more desert Colorado River Basin. The lack of slow-velocity habitat and altered temperature regime likely have significant impacts on rearing bluehead sucker growth and therefore, survival (Anderson 1988). This pattern has been documented elsewhere in regulated rivers in the Intermountain West (e.g., Marsh 1985; Clarkson and Childs 2000).

Due to the low densities of bluehead sucker juveniles in the Weber River, I had to make some assumptions regarding the ecological equivalence of juveniles of all native sucker species in this study. I counted Utah sucker and mountain sucker juveniles synonymously with bluehead sucker juveniles, due to the lack of bluehead sucker juveniles available to sample. Although they likely have a large degree of niche overlap at this small size, this overlap has not been tested empirically. Utah sucker are much more abundant relative to bluehead sucker in the Weber River; their success may be due to faster growth rates, subsequent competitive edge, and large adult size. For instance, Utah sucker juveniles could exceed the gape limitation of predatory fishes (e.g., brown trout) in a shorter time if they grow more quickly than bluehead sucker (e.g., Jensen et al. 2008). Furthermore, larger Utah sucker adults may be able to outcompete bluehead sucker for optimal spawning habitat, considering the two fish use similar spawning habitat and often hybridize (UDWR 2015; Bangs et al. 2017). Alternatively, Utah sucker may be a more generalist species that is less affected by certain aspects of habitat degradation and, therefore, has higher survival rates and reproductive success. For example, it is possible Utah sucker have a slightly different fundamental niche (Laub and Budy 2015) and can better utilize contemporary temperatures and velocities, although this remains unknown. Nonetheless, juvenile Utah sucker and bluehead sucker are likely extremely similar in juvenile habitat preference (Ross 1986), providing a reasonable surrogate to use.

I faced some additional limitations in study design and implementation resulting from low adult densities and other confounding factors. One limitation is that I could not effectively observe spawning behavior and locate precise spawning sites, due to the low densities of bluehead sucker adults and size and turbidity of the river, and I therefore assumed that presence of bluehead sucker in spawning condition indicated spawning habitat. I expect bluehead sucker are spawning near their sampling locations (< 150 m) and, if not, they are using the habitat we sampled them in during a critical time period. Another limitation is that bluehead sucker could not occupy spawning or rearing habitats at saturated densities due to the small population size in the Weber River (Rosenfeld and Hatfield 2006). An additional limitation is the abundance and community of non-native fishes, which indicates that the Weber River provides suitable habitat for a diverse assemblage of fishes potentially confounding bluehead sucker habitat use (Werner et al. 1983). However, to address these limitations, I also located and assessed spawning habitat in a surrogate river system, Ferron Creek, where bluehead sucker have the opportunity to select optimal habitat in a similarly steep, alpine river in absence of non-native fish. The comparative results from Ferron Creek, therefore, helps further my understanding of unimpaired habitat use by adult, fecund bluehead sucker. I also identified potential recruitment bottlenecks by evaluating juvenile growth in controlled microhabitat experiments (similar to Imsland et al. 1996; Jonassen et al. 1999). Determining optimal water velocity and temperature for juvenile growth helps to elucidate why juvenile recruitment into the sub-adult and adult classes may be low in the Weber River (Coleman and Fausch 2007). My study therefore provides a multifaceted approach for studying habitat associations for small, imperiled populations existing in degraded systems.

Management Implications

The results of my study increase our understanding of bluehead sucker niche requirements and aid in identifying a population recruitment bottleneck in the Weber

River, thus providing critical information to guide future restoration and conservation efforts for this population and beyond. A watershed-scale approach to restoring habitat for the bluehead sucker population involves restoring the natural hydrologic regime, or a closer approximation (Stanford et al. 1996). Increasing spring floods will allow the river to create and dynamically maintain in-stream habitat critical for spawning and rearing life stages (Palmer et al. 2005), as well as promote riparian recruitment and thus LWD recruitment into the system (Rood et al. 2003). An important caveat for restoring natural hydrologic conditions is that floodplain connectivity will need to be increased beforehand, in order for the river to create and maintain in-stream habitat during flood events. At a more local spatial scale for healthy sucker populations, water extraction would need to be limited to quantities that will not deplete and degrade bluehead sucker habitat. Reach-based restoration efforts directed towards bluehead sucker habitat could include the addition of gravel and cobble, especially directly downstream of the two large mainstem dams (Merz and Setka 2004). However, effective reach-based restoration necessitates the availability of adequate suitable spawning and rearing habitat within close proximity, to allow different life stages to use complementary habitats (Dunning et al. 1992; Jones et al. 2003). These efforts may be challenged as salmonids are often the focus of a majority of habitat restoration projects, and those approaches may not always be successful for catostomids (McManamay et al. 2010). For instance, scientific knowledge and an adaptive management framework are being used to prescribe restoration actions directed at native fish populations that include bluehead sucker, in the San Rafael River, UT (Laub et al. 2015). For example, Laub et al. (2015) propose restoration actions such as removing non-native riparian vegetation and facilitating dam-building activity by beaver to enhance natural river processes, as opposed to the hard-engineered structures often directed at salmonid habitat restoration. Proactive conservation efforts directed at this bluehead sucker population may prevent listing under the Endangered Species Act. My study provides specific information on potential habitat-based limiting factors for the Weber River bluehead sucker population and, if translated into management and restoration goals, can help conserve this imperiled population.

REFERENCES

Abbe, T. B., and D. R. Montgomery. 1996. Large woody debris jams, channel hydraulics and habitat formation in large rivers. Regulated Rivers Research & Management, 12:201-221.

Anderson, J. T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. Journal of Northwest Atlantic Fishery Science, 8:55-66.

Balian, E. V., H. Segers, C. Lévêque, and K. Martens. 2008. The freshwater animal diversity assessment: an overview of the results. Hydrobiologia, 595:627-637.

Bangs, M. R., M. R. Douglas, P. Thompson, and M. E. Douglas. 2017. Anthropogenic Impacts Facilitate Native Fish Hybridization in the Bonneville Basin of Western North America. Transactions of the American Fisheries Society, 146:16-21.

Banks, D. T. 2009. Abundance, habitat use, and movements of bluehead suckers, flannelmouth suckers, white suckers, and hybrid catostomids in Little Sandy Creek, a tributary to the Big Sandy River in Wyoming. (Master's thesis). University of Wyoming.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67:1-48. doi:10.18637/jss.v067.i01.

Bouwes, N., J. Moberg, N. Weber, B. Bouwes, S. Bennett, C. Beasley, C.E. Jordan, P. Nelle, M. Polino, S. Rentmeester, B. Semmens, C. Volk, M.B. Ward, and J. White. 2011. Scientific protocol for salmonid habitat surveys within the Columbia Habitat Monitoring Program. Prepared by the Integrated Status and Effectiveness Monitoring Program and published by Terraqua, Inc., Wauconda, Washington. 118p.

Bower, M. R., W. A. Hubert, and F. J. Rahel. 2008. Habitat features affect bluehead sucker, flannelmouth sucker, and roundtail chub across a headwater tributary system in the Colorado River basin. Journal of Freshwater Ecology, 23:347-357.

Breiman, L. 2001. Random forests. Machine learning, 45:5-32.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science, 150:28-25.

Budy, P., M. M. Conner, N. L. Salant, and W. W. Macfarlane. 2015. An occupancy-based quantification of the highly imperiled status of desert fishes of the southwestern United States. Conservation Biology, 29:1142-1152.

Carlisle, D. M., D. M. Wolock, and M. R. Meador. 2010. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. Frontiers in Ecology and the Environment, 9:264-270.

Clarkson, R. W., and M. R. Childs. 2000. Temperature effects of hypolimnial-release dams on early life stages of Colorado River Basin big-river fishes. Copeia, 2000:402-412.

Coleman, M. A., and K. D. Fausch. 2007. Cold summer temperature regimes cause a recruitment bottleneck in age-0 Colorado River cutthroat trout reared in laboratory streams. Transactions of the American Fisheries Society, 136:639-654.

Cooke, S. J., C. M. Bunt, S. J. Hamilton, C. A. Jennings, M. P. Pearson, M. S. Cooperman, and D. F. Markle. 2005. Threats, conservation strategies, and prognosis for suckers (Catostomidae) in North America: insights from regional case studies of a diverse family of non-game fishes. Biological Conservation, 121:317-331.

Dauwalter, D. C., S. J. Wenger, K. R. Gelwicks, and K. A. Fesenmyer. 2011. Land use associations with distributions of declining native fishes in the Upper Colorado River Basin. Transactions of the American Fisheries Society, 140:646-658.

Douglas, M. E., P. C. Marsh, and W. L. Minckley. 1994. Indigenous fishes of western North America and the hypothesis of competitive displacement: Meda fulgida (Cyprinidae) as a case study. Copeia, 9-19.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews, 81:163-182.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos, 169-175.

Dynesius, M., and C Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science, 266:753-762.

Fox, J. 2003. Effect Displays in R for Generalised Linear Models. Journal of Statistical Software, 8:1-27. URL http://www.jstatsoft.org/v08/i15/.

Gaeuman, D., J. C. Schmidt, and P. R. Wilcock. 2005. Complex channel responses to changes in stream flow and sediment supply on the lower Duchesne River, Utah. Geomorphology, 64:185-206.

Garman, G. C., and L. A. Nielsen. 1982. Piscivority by stocked brown trout (*Salmo trutta*) and its impact on the nongame fish community of Bottom Creek, Virginia. Canadian Journal of Fisheries and Aquatic Sciences, 39:862-869.

Geist, D. R., and D. D. Dauble. 1998. Redd site selection and spawning habitat use by fall chinook salmon: the importance of geomorphic features in large rivers. Environmental Management, 22:655-669.

Gido, K. B., and D. L. Propst. 2012. Long-term dynamics of native and nonnative fishes in the San Juan River, New Mexico and Utah, under a partially managed flow regime. Transactions of the American Fisheries Society, 141:645-659.

Gooseff, M. N., R. O. Hall, and J. L. Tank. 2007. Relating transient storage to channel complexity in streams of varying land use in Jackson Hole, Wyoming. Water Resources Research, 43:1.

Grabowski, T. B., and J. J. Isely. 2007. Effects of flow fluctuations on the spawning habitat of a riverine fish. Southeastern Naturalist, 6:471-478.

Graf, W. L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology, 79:336-360.

Grams, P. E., and J. C. Schmidt. 2002. Streamflow regulation and multi-level flood plain formation: channel narrowing on the aggrading Green River in the eastern Uinta Mountains, Colorado and Utah. Geomorphology, 44:337-360.

Guyon, I., and A. Elisseeff. 2003. An introduction to variable and feature selection. Journal of machine learning research, 3:1157-1182.

Heggenes, J. 2002. Flexible summer habitat selection by wild, allopatric brown trout in lotic environments. Transactions of the American Fisheries Society, 131:287-298.

Hentschel, B. T. 1998. Spectrofluorometric quantification of neutral and polar lipids suggests a food-related recruitment bottleneck for juveniles of a deposit-feeding polychaete population. Limnology and Oceanography, 43:543-549.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Reviews in Fish Biology and Fisheries, 2:177-178.

Hill, J., and G. D. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology, 74:685-698.

Holden, P. B., and C. B. Stalnaker. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River basins, 1967-1973. Transactions of the American Fisheries Society, 104:217-231.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics, 4:1-23.

Hopken, M. W., M. R. Douglas, and M. E. Douglas. 2013. Stream hierarchy defines riverscape genetics of a North American desert fish. Molecular Ecology, 22:956-971.

Imsland, A. K., L. M. Sunde, A. Folkvord, and S. O. Stefansson. 1996. The interaction of temperature and fish size on growth of juvenile turbot. Journal of fish biology, 49:926-940.

Jensen, H., K. K. Kahilainen, P. A. Amundsen, K. Ø. Gjelland, A. Tuomaala, T. Malinen, and T. Bøhn. 2008. Predation by brown trout (*Salmo trutta*) along a diversifying prey community gradient. Canadian Journal of Fisheries and Aquatic Sciences, 65:1831-1841.

Jonassen, T. M., A. K. Imsland, and S. O. Stefansson. 1999. The interaction of temperature and fish size on growth of juvenile halibut. Journal of fish biology, 54:556-572.

Jones, M. L., J. K. Netto, J. D. Stockwell, and J. B. Mion. 2003. Does the value of newly accessible spawning habitat for walleye (*Stizostedion vitreum*) depend on its location relative to nursery habitats? Canadian Journal of Fisheries and Aquatic Sciences, 60:1527-1538.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Board of Canada, 34:1922-1935.

Koch, J. D., and M. C. Quist. 2007. A technique for preparing fin rays and spines for age and growth analysis. North American Journal of Fisheries Management, 27:782-784.

Laub, B. G., & P. Budy. 2015. Assessing the likely effectiveness of multispecies management for imperiled desert fishes with niche overlap analysis. Conservation Biology, 29:1153-1163.

Laub, B. G., J. Jimenez, and P. Budy. 2015. Application of science-based restoration planning to a desert river system. Environmental management, 55:1246-1261.

Lessard, J. L., and D. B. Hayes. 2003. Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. River research and applications, 19:721-732.

Liaw, A, & M. Wiener. 2002. Classification and Regression by randomForest. R News 2:18-22.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams. BioScience, 45:183-192.

MacCrimmon, H. R., and T. L. Marshall. 1968. World distribution of brown trout, *Salmo trutta*. Journal of the Fisheries Board of Canada, 25:2527-2548.

Maddux, H. R., and W. G. Kepner. 1988. Spawning of bluehead sucker in Kanab Creek, Arizona Pisces: (Catostomidae). The Southwestern Naturalist, 33:364-365.

Magilligan, F. J., and K. H. Nislow. 2005. Changes in hydrologic regime by dams. Geomorphology, 71:61-78.

Mann, H. B., and D. R. Whitney. 1947. On a test of whether one of two random variables is stochastically larger than the other. The Annals of Mathematical Statistics, 18:50-60.

Marrin, D. L., and D. C. Erman. 1982. Evidence against competition between trout and nongame fishes in Stampede Reservoir, California. North American Journal of Fisheries Management, 2:262-269.

Marsh, P. C. 1985. Effect of incubation temperature on survival of embryos of native Colorado River fishes. The Southwestern Naturalist, 30:129-140.

Marsh, P. C., and M. E. Douglas. 1997. Predation by introduced fishes on endangered humpback chub and other native species in the Little Colorado River, Arizona. Transactions of the American Fisheries Society, 126:343-346.

Martinez, P. J., T. E. Chart, M. A. Trammell, J. G. Wullschleger, and E. P. Bergersen. 1994. Fish species composition before and after construction of a main stem reservoir on the White River, Colorado. Environmental Biology of Fishes, 40:227-239.

McHugh, P., and P. Budy. 2005. An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient. Canadian Journal of Fisheries and Aquatic Sciences, 62:2784-2795.

McManamay, R. A., D. J. Orth, C. A. Dolloff, and M. A. Cantrell. 2010. Gravel addition as a habitat restoration technique for tailwaters. North American Journal of Fisheries Management, 30:1238-1257.

Merz, J. E., and J. D. Setka. 2004. Evaluation of a spawning habitat enhancement site for chinook salmon in a regulated California river. North American Journal of Fisheries Management, 24:397-407.

Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Schuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences, 53:1061-1070.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences, 98:5446-5451.

NCAR – Research Applications Laboratory. 2015. Verification: Weather Forecast Verification Utilities. R package version 1.42. https://CRAN.R-project.org/package=verification

Nilsson, C., and K. Berggren. 2000. Alterations of Riparian Ecosystems Caused by River Regulation: Dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time. BioScience, 50:783-792.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. Science, 308:405-408.

Otis, E. O. 1994. Distribution, abundance, and composition of fishes in Bright Angel and Kanab Creeks, Grand Canyon National Park, Arizona. (Master's thesis). Retrieved from http://arizona.openrepository.com/arizona/handle/10150/278418

Palmer, M. A., E. S. Bernhardt, J. D. Allan, P. S. Lake, G. Alexander, S. Brooks, J. Carr, S. Clayton, C. N. Dahm, J. Follstad Shah, D. L. Galat, S. G. Loss, P. Goodwin, D. D. Hart, B. Hassett, R. Jenkinson, G. M. Kondolf, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, and E. Sudduth. 2005. Standards for ecologically successful river restoration. Journal of Applied Ecology, 42:208-217.

Prior, L. D., R. J. Williams, and D. M. Bowman. 2010. Experimental evidence that fire causes a tree recruitment bottleneck in an Australian tropical savanna. Journal of Tropical Ecology, 26:595-603.

Postel, S. L., G. C. Daily, and P. R. Ehrlich. 1996. Human appropriation of renewable fresh water. Science, 271:785-788.

Propst, D. L., and K. B. Gido. 2004. Responses of native and nonnative fishes to natural flow regime mimicry in the San Juan River. Transactions of the American Fisheries Society, 133:922-931.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conservation Biology, 13:1220-1222.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology, 11:1081-1093.

Robinson, A. T., and M. R. Childs. 2001. Juvenile growth of native fishes in the Little Colorado River and in a thermally modified portion of the Colorado River. North American Journal of Fisheries Management, 21:809-815.

Robinson, A. T., R. W. Clarkson, and R. E. Forrest. 1998. Dispersal of larval fishes in a regulated river tributary. Transactions of the American Fisheries Society, 127:772-786

Rood, S. B., J. H. Braatne, and F. M. Hughes. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. Tree Physiology, 23:1113-1124.

Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society, 132:953-968.

Rosenfeld, J. S., and T. Hatfield. 2006. Information needs for assessing critical habitat of freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences, 63:683-698.

Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia, 1986:352-388.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science, 287:1770-1774.

Schmidt, J. C., R. A. Parnell, P. E. Grams, J. E. Hazel, M. A. Kaplinski, L. E. Stevens, and T. L. Hoffnagle. 2001. The 1996 controlled flood in Grand Canyon: flow, sediment transport, and geomorphic change. Ecological Applications, 11:657-671.

Seegert, S. E. Z., E. J. Rosi-Marshall, C. V. Baxter, T. A. Kennedy, R. O. Hall Jr, and W. F. Cross. 2014. High diet overlap between native small-bodied fishes and nonnative fathead minnow in the Colorado River, Grand Canyon, Arizona. Transactions of the American Fisheries Society, 143:1072-1083.

Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika, 52:591-611.

Shelton, J. M., J. A. Day, and C. L. Griffiths. 2008. Influence of largemouth bass, *Micropterus salmoides*, on abundance and habitat selection of Cape galaxias,

Galaxias zebratus, in a mountain stream in the Cape Floristic Region, South Africa. African Journal of Aquatic Science, 33:201-210.

Sigler, W. F., and R. R. Miller. 1963. Fishes of Utah. Utah State Department of Fish and Game, Salt Lake City, Utah. 203p.

Sigler, W. F., and J. W. Sigler. 1996. Fishes of Utah; a natural history. University of Utah Press, Salt Lake City, Utah. 375p.

Smol, J. P., A. P. Wolfe, H. J. B. Birks, M. S. Douglas, V. J. Jones, A. Korhola, R. Pienitz, K. Ruhland, S. Sorvari, D. Antoniades, S. J. Brooks, M-A. Fallu, M. Hughes, B. E. Keatley, T. E. Laing, N. Michelutti, L. Nazarova, M. Nyman, A. M. Paterson, B. Perren, R. Quinlan, M. Rautio, E. Saulnier-Talbot, S. Siitonen, N. Solovieva, and J. Weckstrom. 2005. Climate-driven regime shifts in the biological communities of arctic lakes. Proceedings of the National Academy of Sciences of the United States of America, 102:4397-4402.

Soulsby, C., A. F. Youngson, H. J. Moir, and I. A. Malcolm. 2001. Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: a preliminary assessment. Science of the Total Environment, 265:295-307.

Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. River Research and Applications, 12:391-413.

Stewart, G., R. Anderson, and E. Wohl. 2005. Two-dimensional modelling of habitat suitability as a function of discharge on two Colorado rivers. River Research and Applications, 21:1061-1074.

Student. 1908. The probable error of a mean. Biometrika, 6:1-25.

Sublette, E. J., D. M. Hatch, and M. Sublette. 1990. The fishes of New Mexico. University of New Mexico Press, Albuquerque, New Mexico. 393p.

Unmack P. J., T. E. Dowling, N. J. Laitinen, C. L. Secor, R. L. Mayden, D. K. Shiozawa, and G. R. Smith. 2014) Influence of Introgression and Geological Processes on Phylogenetic Relationships of Western North American Mountain Suckers (*Pantosteus*, Catostomidae). PLoS ONE 9:e90061.

Utah Division of Wildlife Resources 2012. Three Species Monitoring Summary. Utah Division of Wildlife Resources, Salt Lake City, Utah. Publication Number 13-22.

Utah Division of Wildlife Resources 2015. Three Species Monitoring Summary. Utah Division of Wildlife Resources, Salt Lake City, Utah. Publication Number 16-14.

Vanicek, C. D. 1967. Ecological Studies of Native Greenriver Fishes Below Flaming Gorge Dam, 1964-1966 (Doctoral dissertation). Retrieved from http://digitalcommons.usu.edu/etd/2893/

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences, 37:130-137.

Van Steeter, M. M., and J. Pitlick. 1998. Geomorphology and endangered fish habitats of the upper Colorado River: 1. Historic changes in streamflow, sediment load, and channel morphology. Water Resources Research, 34:287-302.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. Reidy Liermann, and P. M. Davies. 2010. Global threats to human water security and river biodiversity. Nature, 467:555-561.

Wahle, R., and R. Steneck. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Marine Ecology Progress Series, 69:231-243.

Walser, C. A., M. C. Belk, and D. K. Shiozawa. 1999. Habitat use of leatherside chub (*Gila copei*) in the presence of predatory brown trout (*Salmo trutta*). The Great Basin Naturalist, 59:272-277.

Walsworth, T. E., P. Budy, and G. P. Thiede. 2013. Longer food chains and crowded niche space: effects of multiple invaders on desert stream food web structure. Ecology of Freshwater Fish, 22:439-452.

Webber, P. A., P. D. Thompson, and P. Budy. 2012. Status and Structure of Two Populations of the Bluehead Sucker (*Catostomus discobolus*) in the Weber River, Utah. The Southwestern Naturalist, 57:267-276.

Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology, 30:377-392.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics, 15:393-425.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology, 64:1540-1548.

Wheaton, J. M., K. A. Fryirs, G. Brierley, S. G. Bangen, N. Bouwes, and G. O'Brien. 2015. Geomorphic mapping and taxonomy of fluvial landforms. Geomorphology, 248:273-295.

Wolman, M. G. 1954. A method of sampling coarse river-bed material. Transactions American Geophysical Union, 35:951-956.

TABLES AND FIGURES

TABLE 1.—Experimental treatments by variable (temperature and velocity) used to test hypotheses.

Treatment and variable	Target value
Cool temperature	12 ºC
Tepid temperature	15 ºC
Warm temperature	18 ºC
Slow velocity	0.0 m/s
Medium velocity	0.1 m/s
Fast velocity	0.2 m/s

TABLE 2.—Experimental treatments by trial, number of bluehead sucker used in each treatment, and period of experimental trials conducted during June-October 2016.

		Discharge (m^3/s, range)			
Trial	Temperature (°C, range)	Slow (0.0034-0.0080)	Medium (0.021-0.027)	Fast (0.043-0.049)	Period (days)
Trial 1	Cool (11.7-12.0)	5	5	5	7
	Tepid (15.2-15.5)	5	5	5	25
	Warm (17.4-17.8)	5	5	5	13
Trial 2	Cool (12.0-12.1)	7	7	7	14
	Tepid (15.3-15.5)	7	7	7	14
	Warm (19.0-19.1)	7	7	7	14

TABLE 3.—A matrix of all possible covariates and their slope parameters for the juvenile sucker backwater use linear mixed model.

Slope parameter	Possible covariates
$\beta 1_{j[i]k[i]}$	max depth (x_1)
$\beta_{2j[i]k[i]}$	$\log_e$ area (x_2)
$\beta 3_{j[i]k[i]}$	brown trout (x_3)
$\beta 4_{j[i]k[i]}$	max depth * $\log_e$ area ($x_1 * x_2$)
$\beta 5_{j[i]k[i]}$	max depth * brown trout ($x_1 * x_3$)
$\beta 6_{j[i]k[i]}$	$\log_e$ area * brown trout ($x_2 * x_3$)

TABLE 4.—Significant variables included in the final random forest models analyzing spawning habitat in the Weber River and Ferron Creek (classification) and rearing sucker backwater use (regression). Variable importance reported for spawning habitat in the Weber River and Ferron Creek is mean decrease accuracy, or the decrease in classification accuracy from permuting each variable. Variable importance reported for rearing sucker backwater use is percent increase mean square error, or the decrease in regression accuracy from permuting each variable. All substrate variables were standardized as a proportion of the total substrate in the reach or backwater. Riffle abundance was standardized as number of riffles per km. I surveyed spawning and non-spawning reaches in the Weber River in June-September 2015 and May-June 2016 and in Ferron Creek in July 2016. I surveyed ten backwaters in the Weber River in August 2016.

Analysis	Habitat variable	Variable importance
Spawning habitat in the Weber River	Cobble	38.0
	Gravel	27.0
	Riffle abundance	24.9
Spawning habitat in Ferron Creek	Mean wetted channel width	9.9
	Fines	8.1
	Gravel	8.1
Rearing sucker backwater use	Fines	27.9
	Backwater area	26.9
	Cobble	24.7

TABLE 5.—Variables added to the juvenile sucker backwater use linear mixed model at each step and their Bayesian information criterion (BIC) value and delta BIC relative to the best model from the previous step. Models in step 1 are compared to the BIC value of the intercept only model in step 0. Models in step 2 are compared to the BIC value of step 1a.

Step	Variable	ΔBIC	BIC
0	intercept only	0	92.9
1a	(+) max depth	-4.11	88.8
1b	(+) $\log_e$ area	1.16	94.0
1c	(+) brown trout	3.32	96.2
2a	(+) $\log_e$ area	2.00	90.8
2b	(+) brown trout	3.35	92.1
2c	(-) max depth	4.11	92.9

TABLE 6.—Backwater sucker use linear mixed model components and sample size (n), random effect parameters with standard deviation (SD), and fixed effect coefficient (coef) parameter estimates (est) and standard error (SE).

Model details		Random effects		Fixed effects		
Model component	n	Parameter	SD	Coef parameter	Coef Est	Coef SE
Sample event	28	Residual	0.59	Intercept (β_0)	2.1	0.42
Site	19	Year slope (β_{1j})	0.54	Max depth (β_1)	4.2	0.98
Year	2	Site slope (β_{1k})	1.1			

TABLE 7.—Juvenile bluehead sucker growth experiment linear mixed model components and sample size (n), random effect parameters with standard deviation (SD), and fixed effect coefficient (coef) parameter estimates (est) and standard error (SE).

Model details		Random effects		Fixed effects		
Model component	n	Parameter	SD	Coef parameter	Coef Est	Coef SE
Individual	102	Residual	0.016	Intercept (β_7)	0.16	0.041
Trial period	6	Trial (β_{7g})	0.014	Temp (β_8)	-0.0033	0.0027
Tank	3	Tank/trial ($\beta_{7g[h]}$)	0.0067	Velocity (β_9)	-1.6	0.78
				Temp * Velocity (β_{10})	0.082	0.050

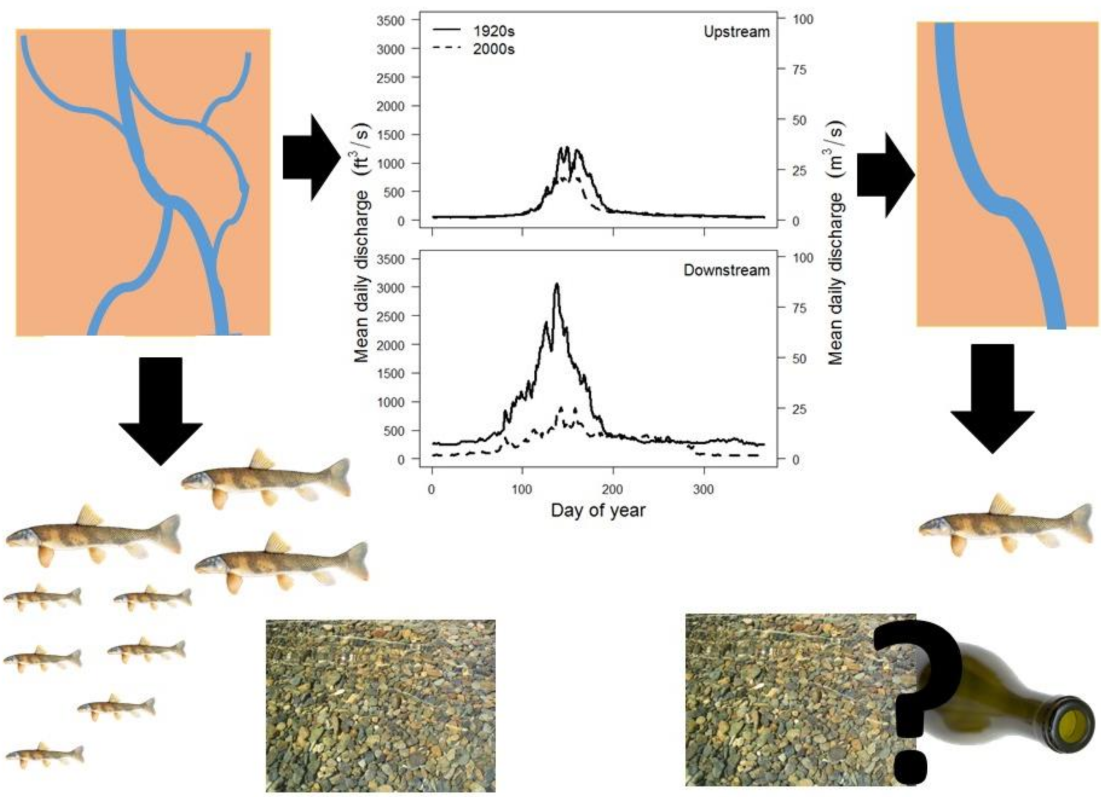

FIGURE 1.—A conceptual model displaying how the Weber River, UT has been altered from historic conditions, when a robust bluehead sucker population existed, indicating the existence of adequate complementary spawning and rearing habitats (left). However, over-allocation of water and dams have altered natural hydrologic conditions, displayed as mean daily discharge across day of year (DOY) for an upstream, “reference” site (USGS gage 10128500 near Oakley, UT; above all major dams and diversions) and a downstream, “impacted” site (USGS gage 10136500 at Gateway, UT; downstream of most major dams and diversions). Data are displayed as the 50th percentile for the 1920s (1921-1930) and 2000s (2006-2015) and DOY of 1 represents January 1 (top center). Currently, the Weber River is a more simplified geomorphic channel, in which the bluehead sucker population is repressed and at risk of local extinction, possibly due to a lack of suitable spawning and rearing habitat (right). My objective for this study was to identify potential habitat-based recruitment bottlenecks.

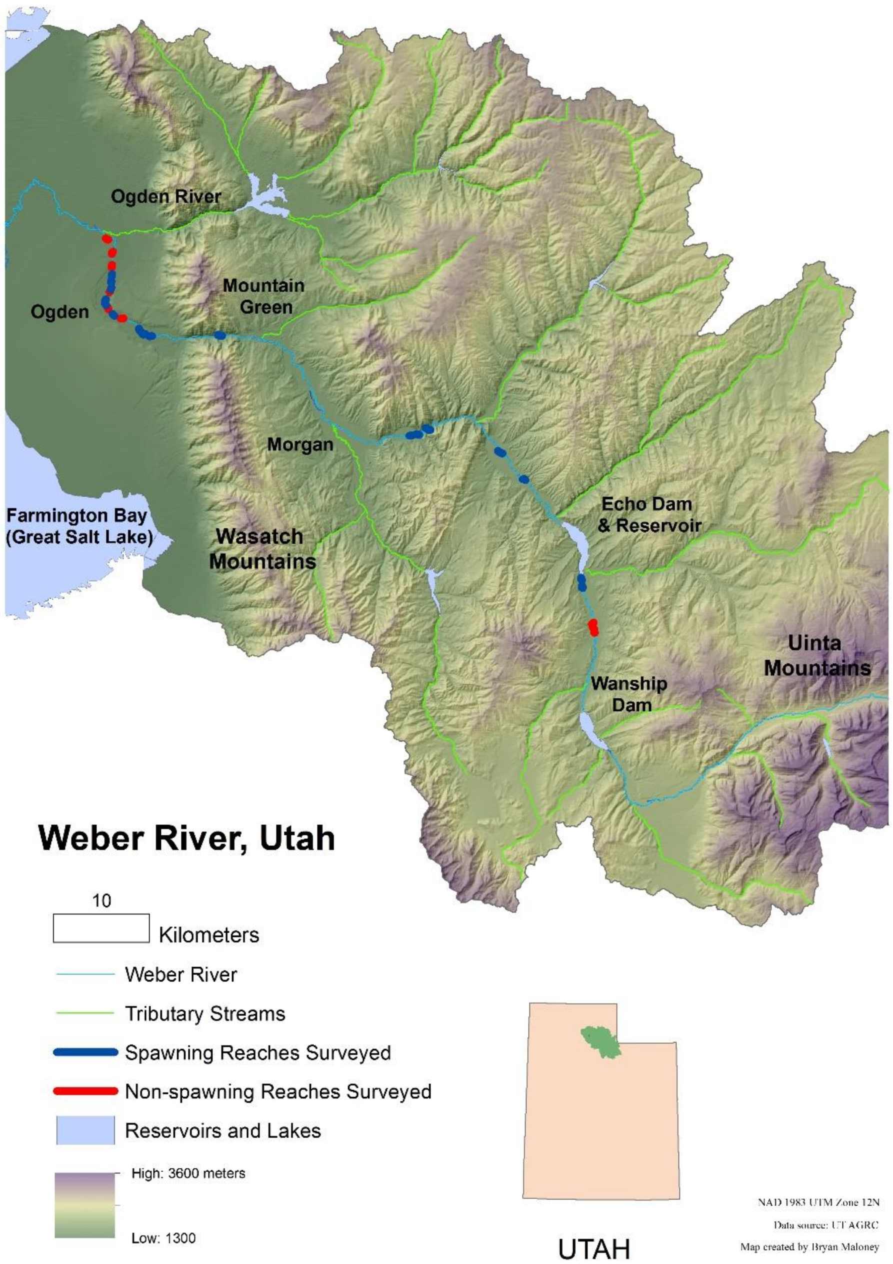

FIGURE 2.—Map of the Weber River watershed located in northern Utah. The Weber River drains the Uinta and Wasatch Mountains and flows primarily northwest into the Great Salt Lake. The contemporary bluehead sucker range extends approximately 104 river km from Wanship Dam downstream to the Ogden River inlet.

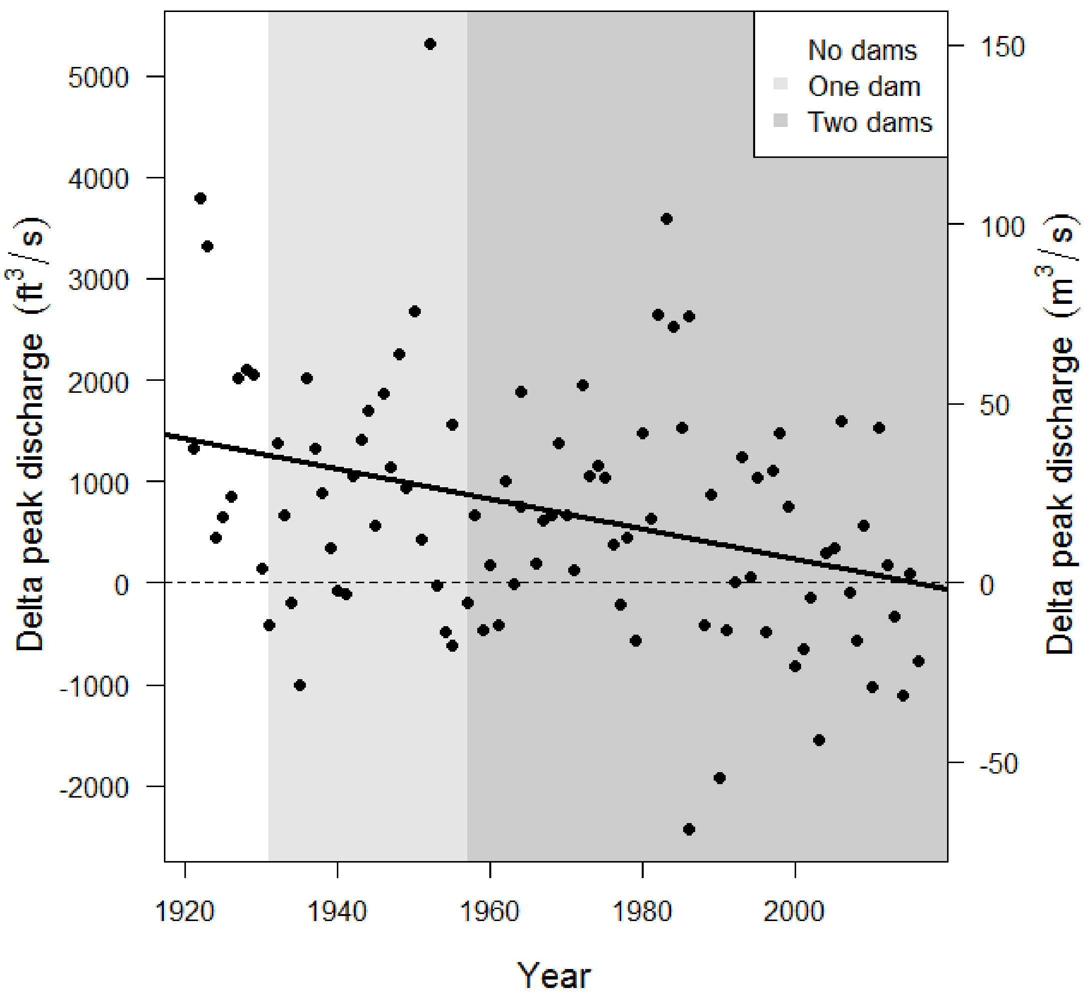

FIGURE 3.—Delta peak annual discharge for two Weber River, UT USGS gages plotted across year. Delta peak annual discharge represents peak annual discharge of a downstream site (USGS gage 10136500 at Gateway, UT; downstream of most major dams and diversions) minus peak annual discharge of an upstream, "reference" site (USGS gage 10128500 near Oakley, UT; above all major dams and diversions). Polygons represent periods on the main stem Weber River with no very large dams (> 47 m height; white), one very large dam (Echo Dam; light gray), and two very large dams (Echo and Wanship Dams; dark gray). The solid black line represents linear regression of delta peak annual discharge across time (adjusted $r^2 = 0.10$; $p < 0.01$). The dashed black line represents delta peak annual discharge of zero, at which the peak annual discharge is equal at the upstream and downstream sites.

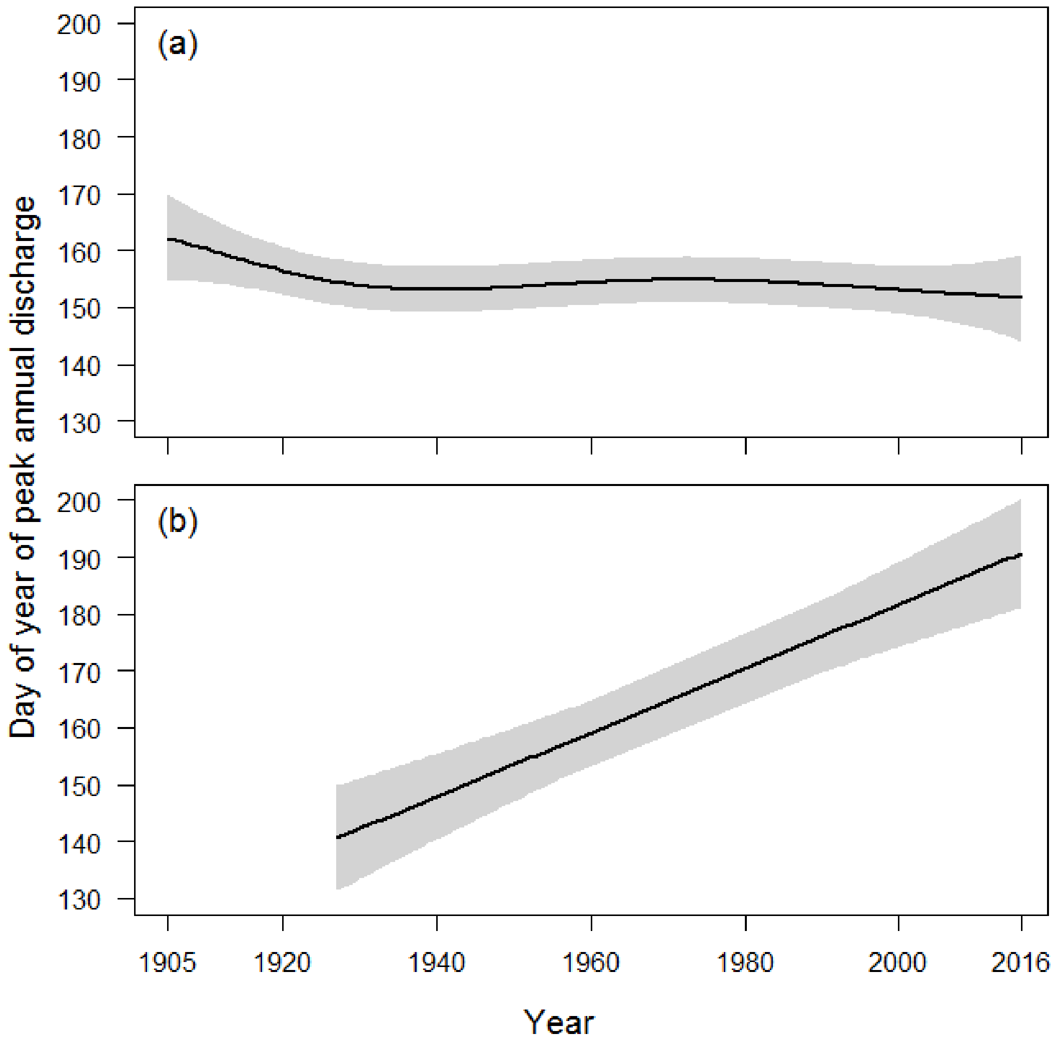

FIGURE 4.—Day of year (DOY) of peak annual discharge for two Weber River, UT USGS gages plotted across year. The DOY 130 represents May 10 and the DOY 200 represents July 19. (a) USGS gage 10128500 near Oakley, UT, above all major dams and diversions; record exists from 1905-2016. (b) USGS gage 1013200 at Echo, UT, downstream of Echo Dam; record exists from 1927-1958 and 1989-2016. Black lines represent generalized additive model (GAM) predictions and gray polygons represent ± 1.96 standard error around GAM predictions.

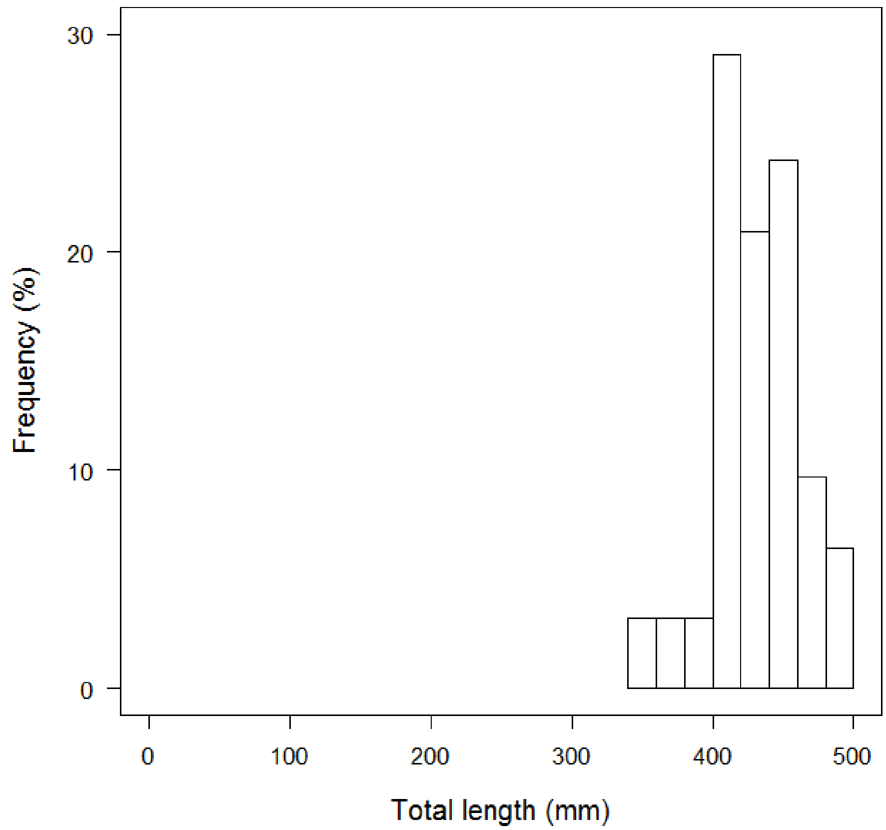

FIGURE 5.—Length-frequency histogram of the bluehead sucker sub-population inhabiting the Weber River, UT reach between Echo and Wanship Dams (Figure 2). These data represent all bluehead sucker sampled in this reach in July 2014 (n = 62). Only the first encounter was included if fish were sampled multiple times during July 2014.

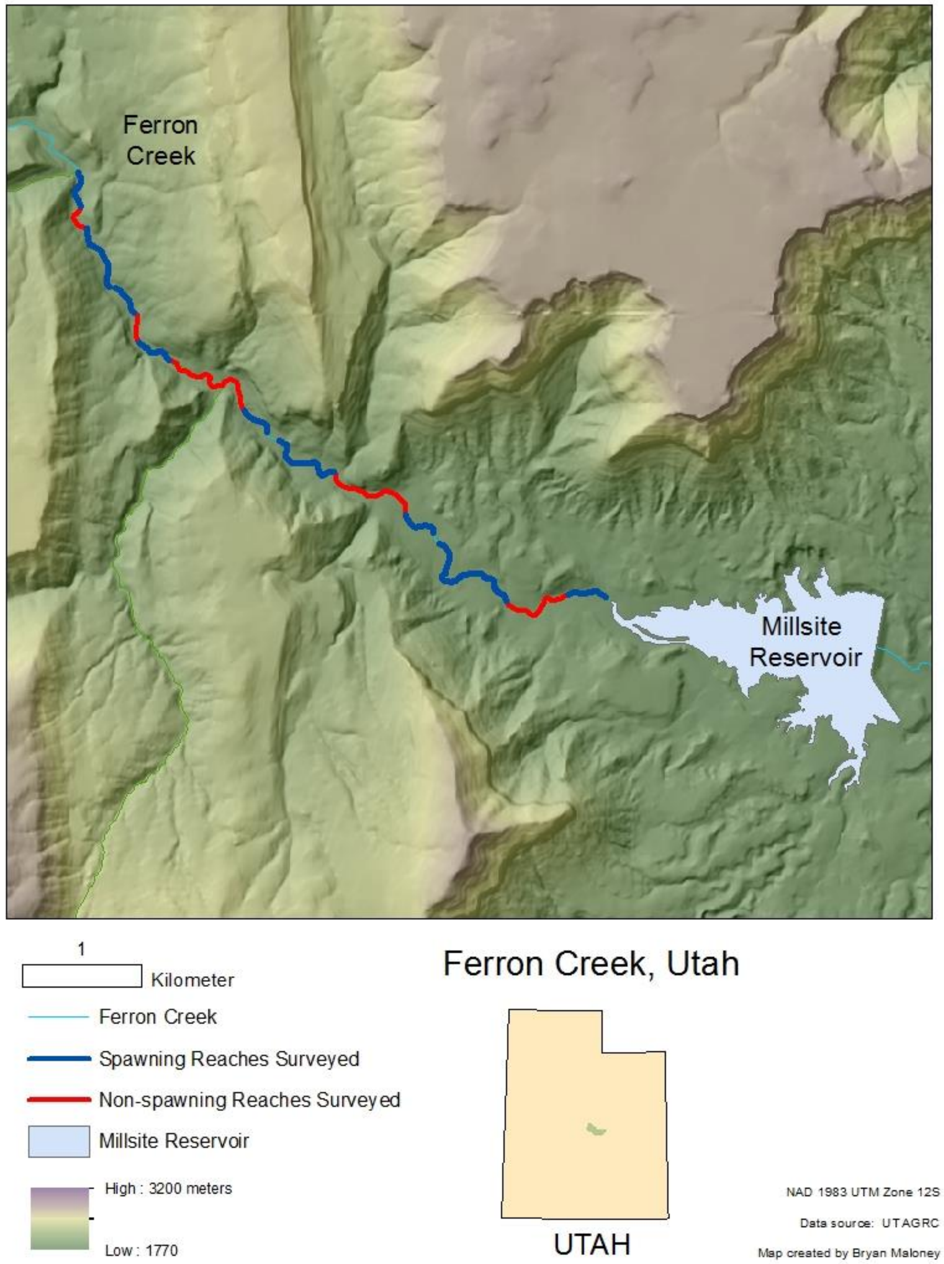

FIGURE 6.—Map of Ferron Creek, UT extending upstream from Millsite Reservoir. In cooperation with UDWR biologists, I surveyed 7.52 km of Ferron Creek (through range of blue and red colored reaches down to reservoir) for bluehead sucker in spawning condition in July 2016. I sampled 137 unique bluehead sucker and located 11 spawning reaches (blue lines on map). In addition to surveying habitat characteristics in spawning reaches, I additionally surveyed 10 non-spawning reaches for comparison.

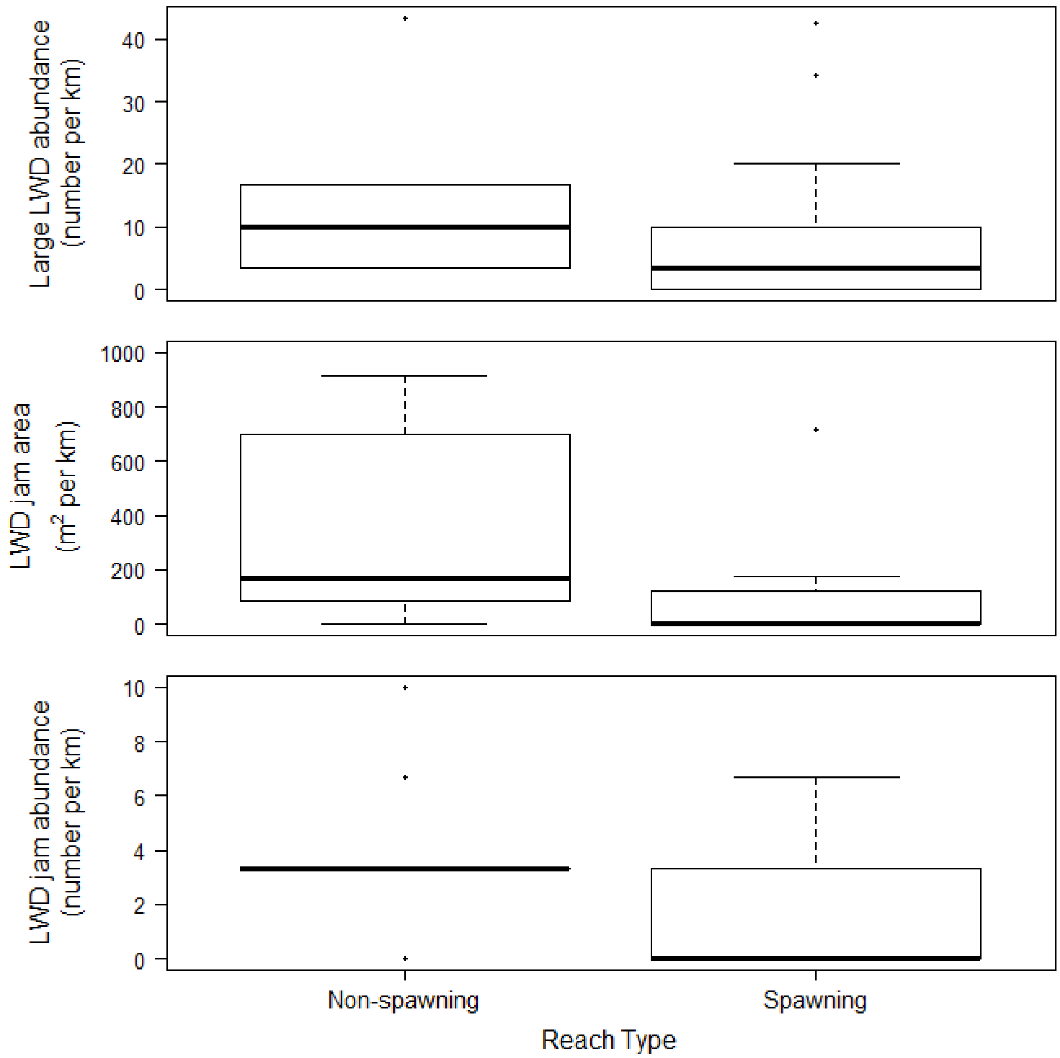

FIGURE 7.—Habitat variables that differed significantly between spawning and non-spawning reaches in the Weber River, UT, based on ANOVA (Wilcoxon rank sum test; $p < 0.05$). Surveyed in June - September 2015 and May - June 2016. All values are reported per river km. Dark line indicates median value of data. Upper and lower edge of boxes indicate first and third quartiles of data. Edge of whiskers indicate smallest and largest values of data. Points outside of boxplots indicate outlier data.

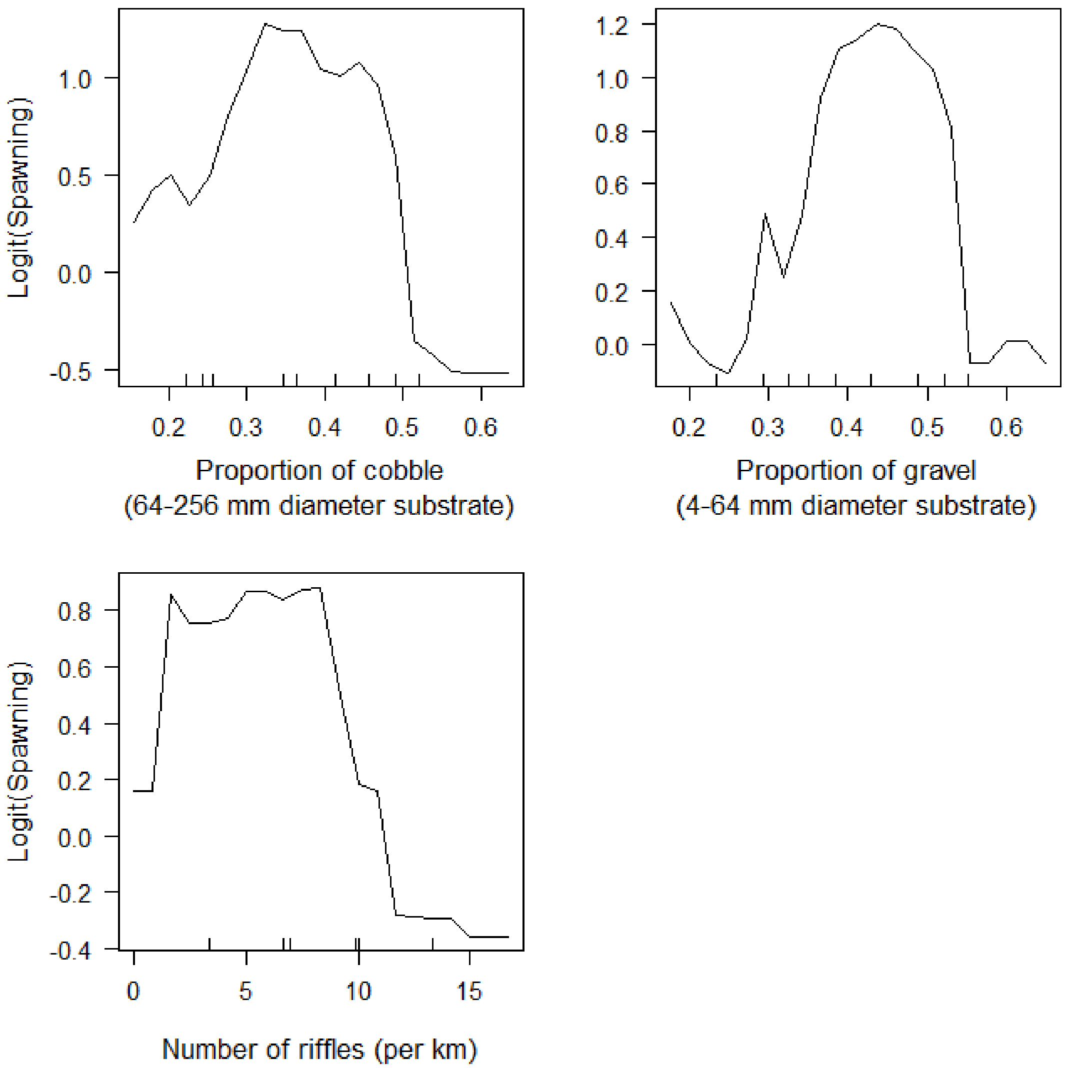

FIGURE 8.—Partial dependence plots for random forest classification of significant habitat characteristics (Table 4) in the Weber River, UT. The y-axis displays the predicted probability of classifying a reach as a spawning reach with average values for all other significant predictor variables. Greater logit(spawning) values have a more positive influence for classification in the model (i.e., when y-axis values are greater, the model is more likely to classify a reach as a spawning reach). Variables displayed per km are per river km.

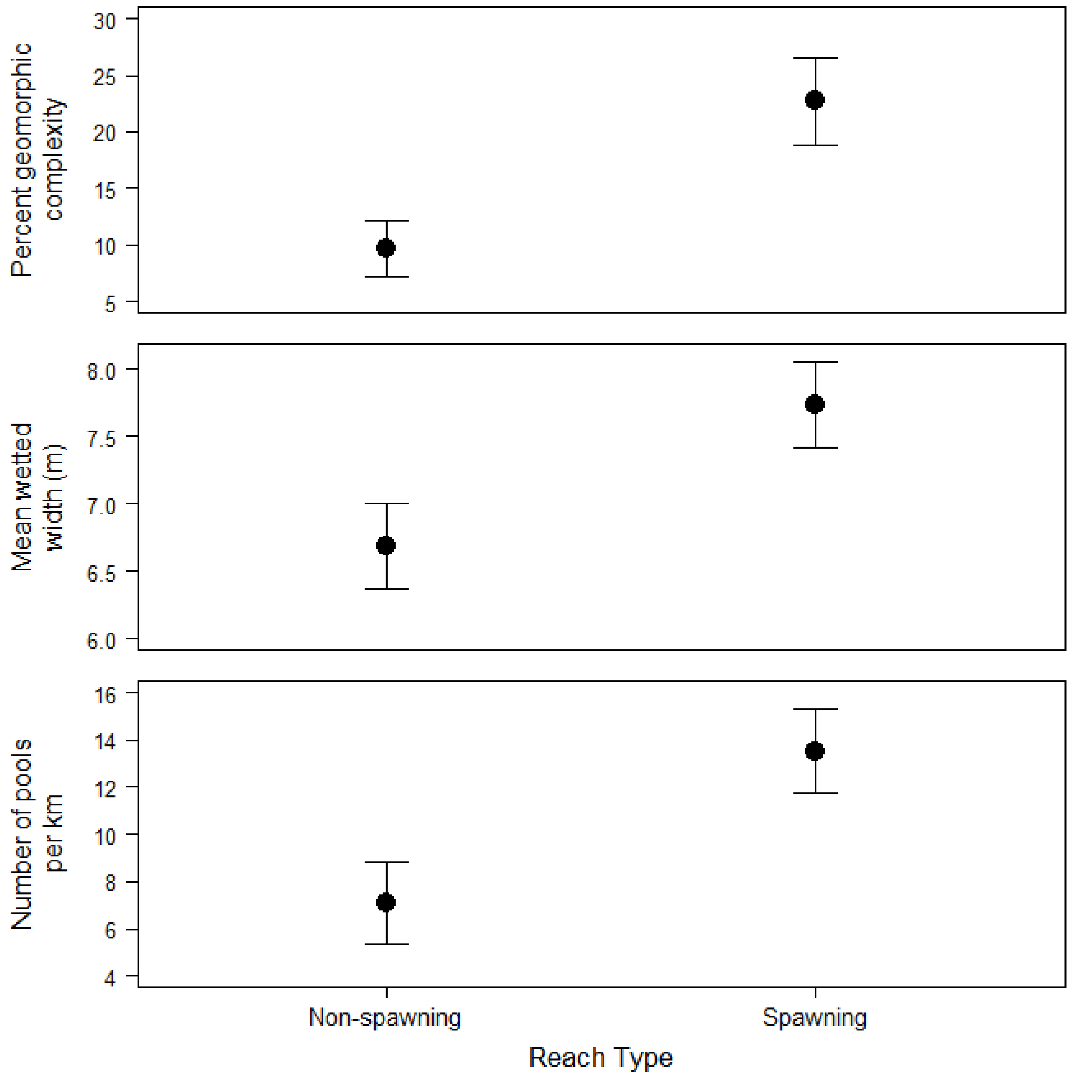

FIGURE 9.—Habitat variables that differed significantly between spawning and non-spawning reaches in Ferron Creek, UT, based on ANOVA (t-test; $p < 0.05$). I surveyed eleven spawning reaches and ten non-spawning reaches in July 2016. Percent geomorphic complexity represents proportion of each reach composed of non-planar geomorphic units (riffles and pools). Data are displayed as mean values (points) with standard error around the mean.

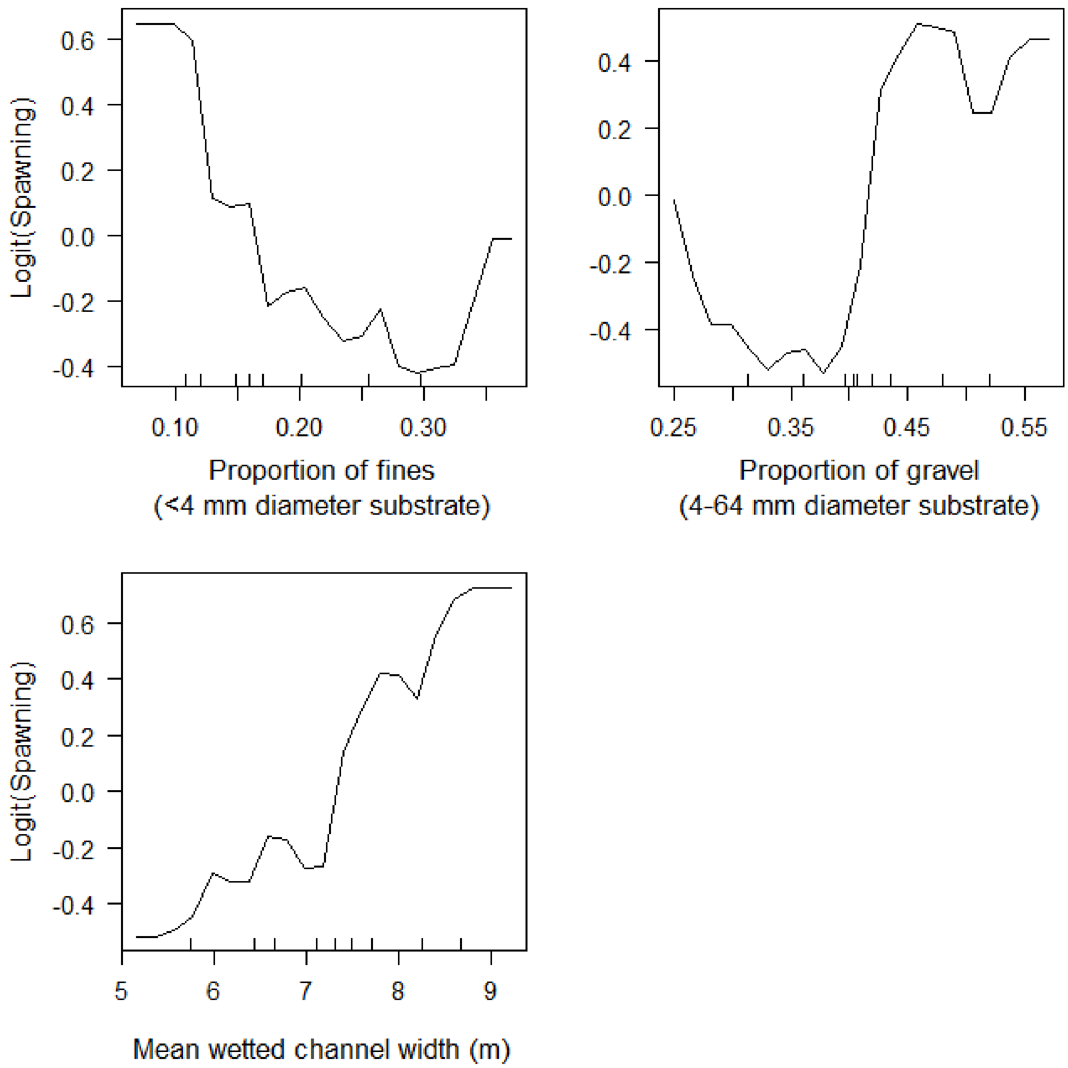

FIGURE 10.—Partial dependence plots for random forest classification of significant habitat characteristics (Table 4) in Ferron Creek, UT. The y-axis displays the predicted probability of classifying a reach as a spawning reach with average values for all other significant predictor variables. Greater logit(spawning) values have a more positive influence for classification in the model (i.e., when y-axis values are greater, the model is more likely to classify a reach as a spawning reach).

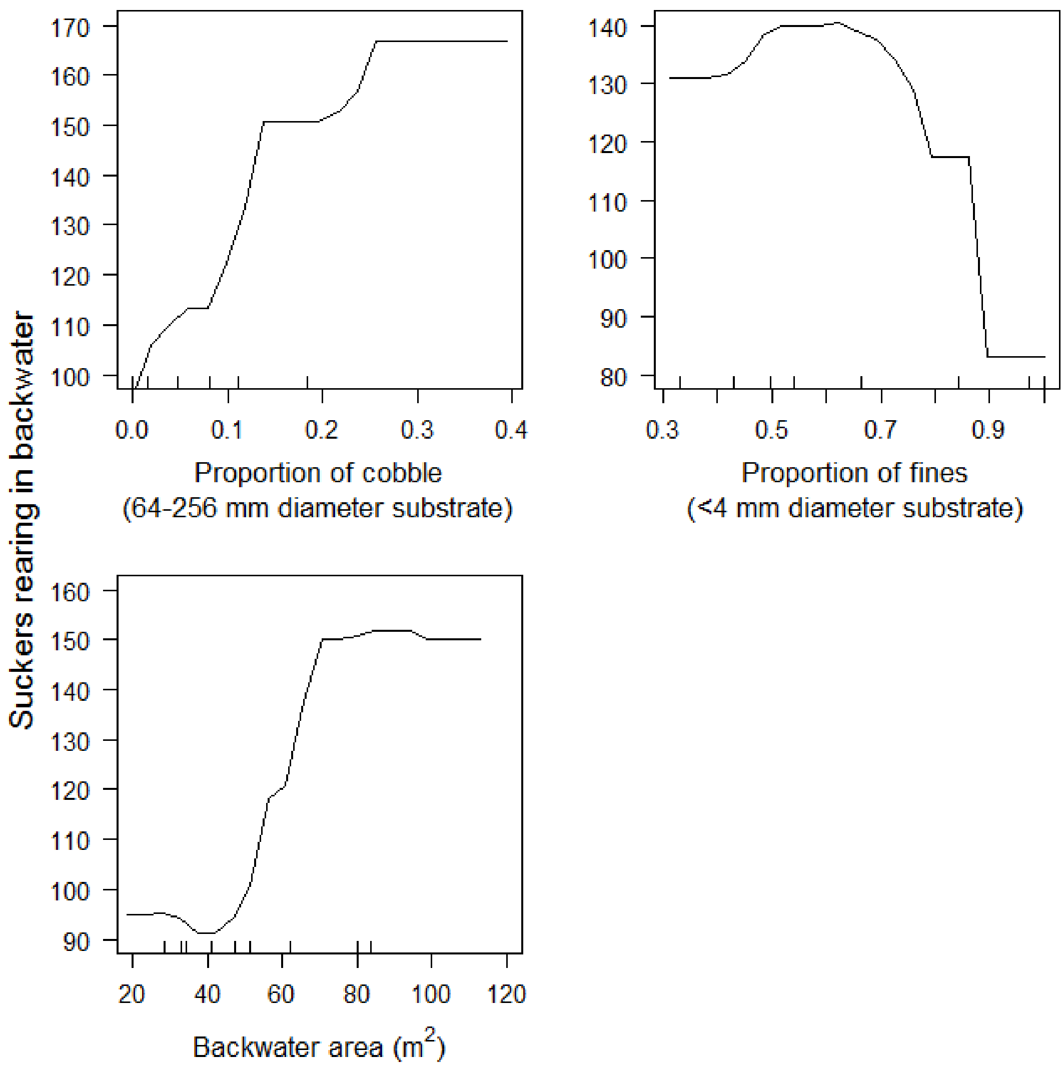

FIGURE 11.—Partial dependence plots for random forest regression of significant backwater characteristics (Table 4) in the Weber River, UT. The y-axis displays the predicted abundance or rearing suckers in a backwater with average values for all other significant predictor variables.

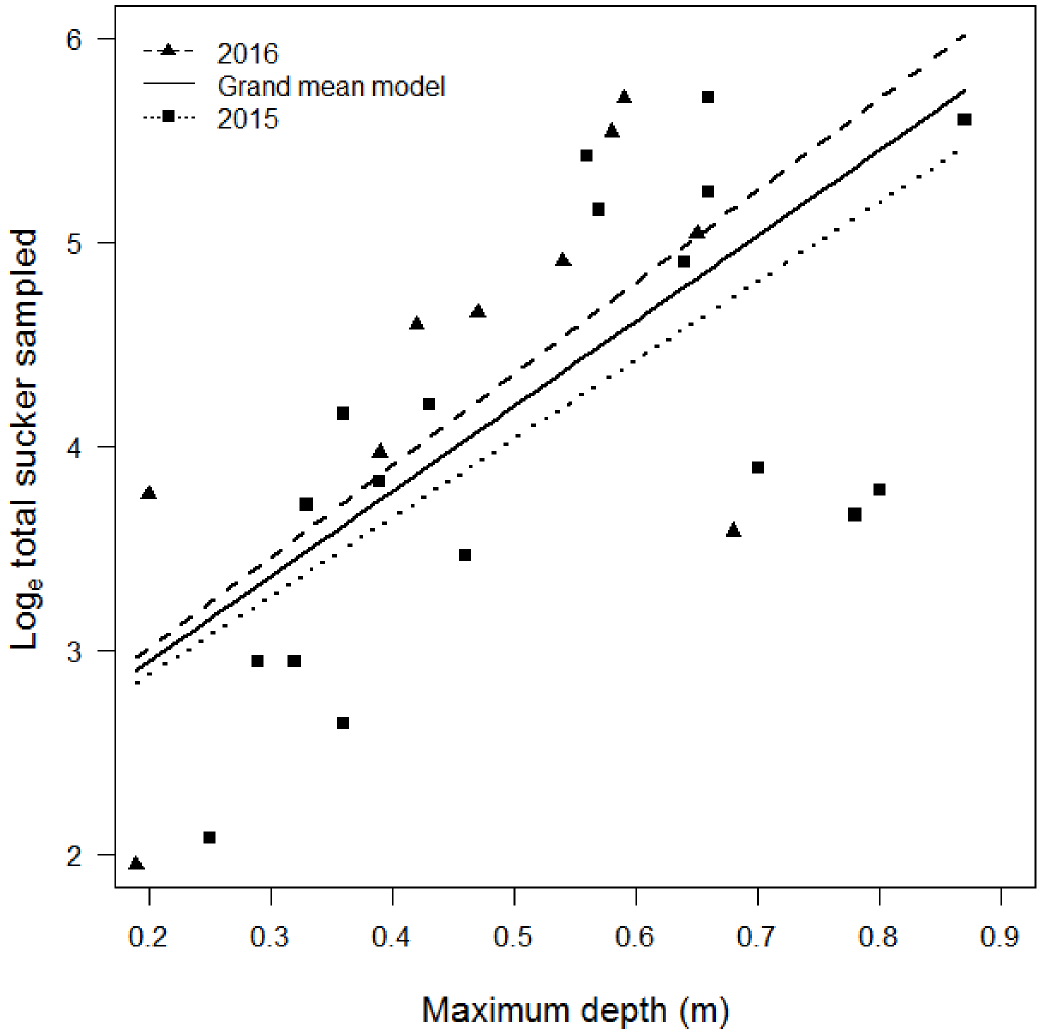

FIGURE 12.—Model results for backwater sampling linear mixed-effects regression. Log$_e$ total sucker sampled are plotted against backwater maximum depth. The solid line indicates the grand mean model prediction. The different points and dashed and dotted lines indicate the model predictions for the two years of the study. The fact that more sucker juveniles are sampled in 2016 than in 2015 is likely due to the fact I sampled more thoroughly in 2016 (i.e., backpack electrofished in addition to seining).

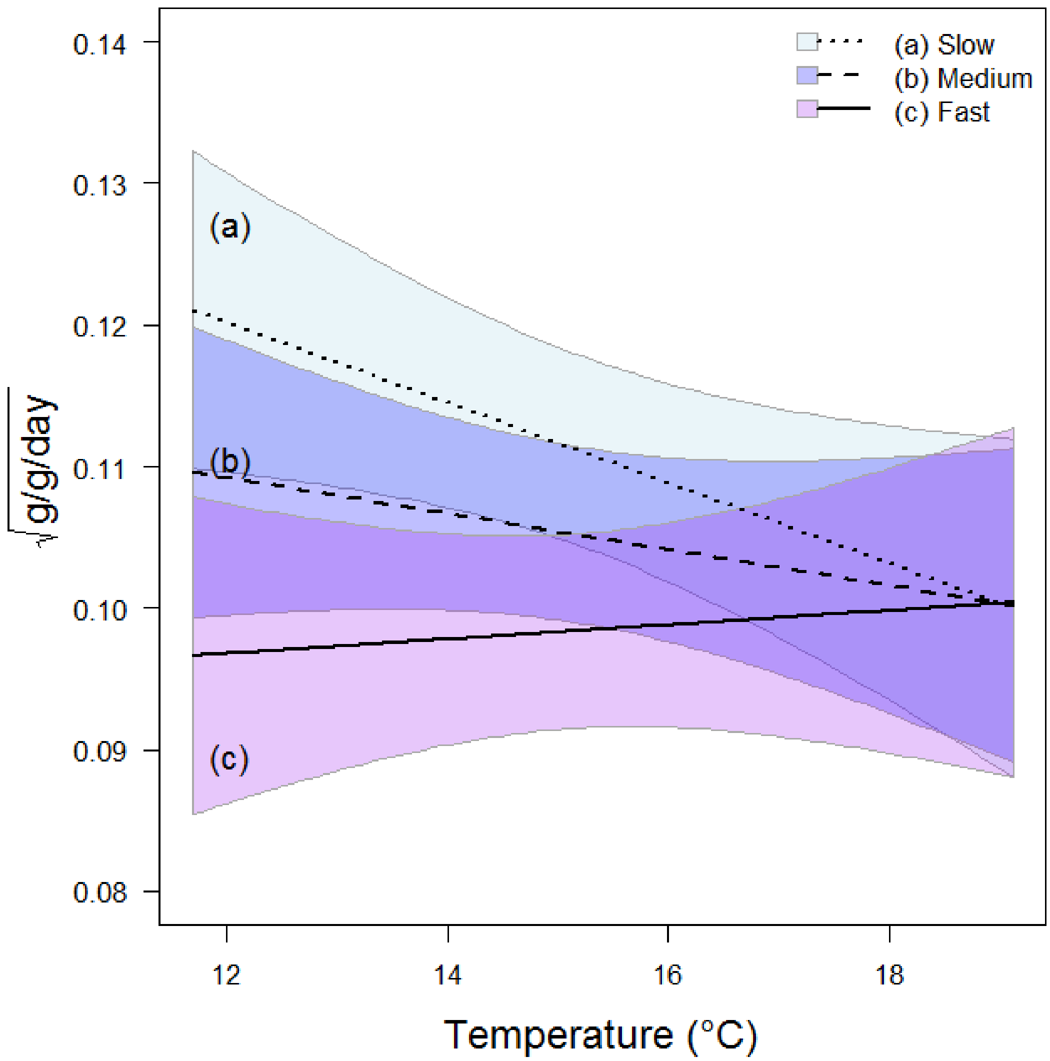

FIGURE 13.—Full model juvenile growth predictions plotted across water temperature. Lines represent model predictions for the mean of each velocity treatment, measured as tank discharge (slow, medium, and fast). Colored polygons represent standard error around the prediction for the mean of each velocity treatment. Juvenile growth differed significantly between the slow and fast velocity treatments at cooler temperatures but not at warmer temperatures.

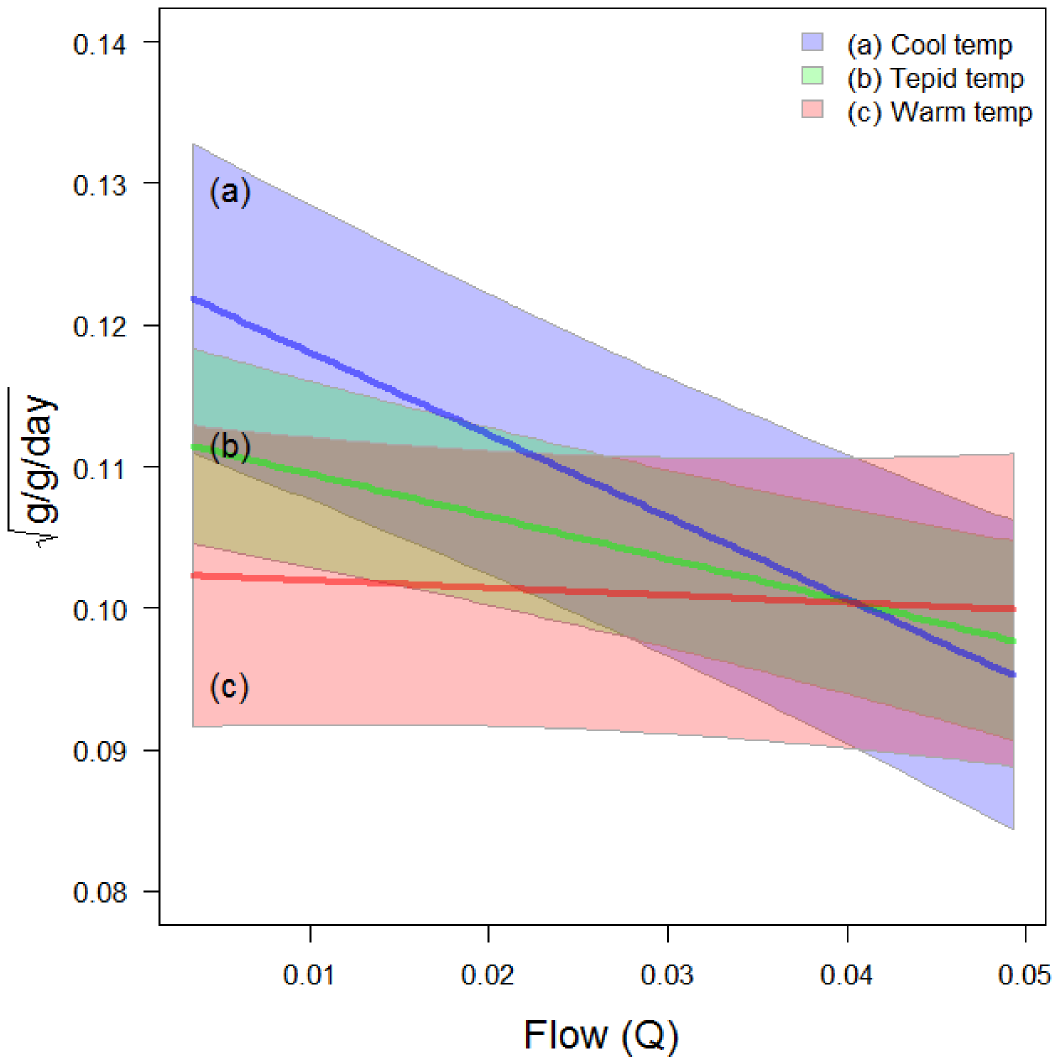

FIGURE 14.—Full model juvenile growth predictions plotted across tank discharge (Q; m^3/s). Colored lines represent model predictions for the mean of each temperature treatment (cool, tepid, and warm). Colored polygons represent standard error around the prediction for the mean of each temperature treatment. Juvenile growth differed significantly between slow and fast velocity treatments in the cool temperature treatment only.

APPENDICES

TABLE 8.—Weber River, UT spawning reach location (UTM zone 12 N coordinates, center of reach), abundance of ripe bluehead sucker (BHS) sampled, linear reach distance, channel width, abundance of large woody debris (LWD; small, medium, and large), and abundance of LWD jams. See Methods section for definitions of LWD size classes. I surveyed spawning reaches in June-September 2015 and May-June 2016.

Spawning reach number	Location (UTM); X, Y	BHS sampled; ripe (total)	Reach length (m)	Channel width (m); wetted (bankfull)	LWD abundance (Sm, Md, Lg)	Number of LWD jams (area; m^2)
297	465779, 4528403	5 (22)	350	16.3 (17.0)	84 (42, 30, 12)	1 (50)
293	465689, 4529222	11 (35)	400	16.4 (20.5)	57 (20, 20, 17)	1 (9)
250	459767, 4539623	6 (7)	300	19.9 (22.3)	16 (13, 3, 0)	1 (5)
234	457260, 4542408	17 (29)	600	18.6 (21.8)	9 (3, 6, 0)	1 (105)
198	449867, 4544728	11 (16)	300	20.0 (23.1)	13 (7, 5, 1)	0 (0)
197	449647, 4544896	4 (15)	300	15.4 (18.7)	10 (5, 4, 1)	0 (0)
190	448684, 4544237	8 (10)	300	20.0 (22.3)	24 (16, 8, 0)	0 (0)
187	447967, 4544123	2 (3)	300	20.1 (23.2)	20 (14, 6, 0)	0 (0)
82	428218, 4554561	5 (6)	300	13.0 (23.1)	18 (8, 7, 3)	0 (0)
54	420914, 4554477	10 (13)	300	15.1 (21.3)	22 (7, 14, 1)	0 (0)
50	419971, 4554884	3 (5)	300	17.2 (22.4)	43 (36, 6, 1)	1 (25)
49	419726, 4555127	2 (2)	300	17.4 (21.2)	20 (15, 5, 0)	0 (0)
37	417022, 4556693	5 (5)	300	14.2 (30.5)	36 (19, 11, 6)	2 (215)
32	416185, 4557823	9 (10)	300	14.3 (21.2)	23 (18, 3, 2)	1 (36)
31	416188, 4558204	7 (10)	375	17.0 (24.5)	24 (17, 7, 0)	0 (0)
26	416788, 4559447	2 (4)	300	17.2 (25.7)	24 (14, 9, 1)	0 (0)
24	416827, 4560176	5 (10)	300	15.7 (19.8)	33 (24, 9, 0)	0 (0)
22	416870, 4560789	10 (13)	300	17.9 (28.9)	36 (23, 10, 3)	1 (50)

TABLE 9.—Weber River, UT spawning reach geomorphic complexity, number of geomorphic units, and percent (%) fines, gravel, cobble, and boulders. See Methods section for definitions of geomorphic complexity and substrate size classes. I surveyed spawning reaches in June-September 2015 and May-June 2016.

Spawning reach number	Geomorphic complexity (%) (riffles, pools)	Number of geomorphic units; pools, riffles, backwaters	Fines (%)	Gravel (%)	Cobble (%)	Boulders (%)
297	25.4 (18.3, 7.1)	3, 3, 6	18.9	37.8	38.7	4.5
293	38.1 (24.4, 13.7)	3, 4, 4	20.2	51.9	25.0	2.9
250	7.5 (2.3, 5.2)	1, 2, 0	126	42.0	42.0	3.4
234	0.5 (0.5, 0.0)	0, 1, 1	6.6	62.3	29.2	1.9
198	10.4 (10.4, 0.0)	0, 2, 0	21.7	39.1	34.8	4.3
197	7.1 (2.3, 4.8)	1, 1, 0	17.0	34.9	37.7	10.4
190	6.0 (3.5, 2.5)	1, 2, 0	36.3	17.6	46.1	0.0
187	8.0 (0.9, 7.1)	1, 1, 0	33.9	30.4	34.8	0.9
82	27.1 (27.1, 0.0)	0, 3, 1	2.5	49.2	20.8	27.5
54	10.0 (10.0, 0.0)	0, 2, 0	17.6	46.6	35.1	0.8
50	13.7 (4.0, 9.7)	2, 1, 0	17.0	30.4	42.0	10.7
49	19.3 (7.9, 11.4)	1, 1, 0	14.6	28.5	48.8	8.1
37	11.2 (10.0, 1.1)	1, 2, 2	29.8	52.6	17.5	0.0
32	13.5 (13.5, 0.0)	0, 4, 2	21.1	52.3	23.9	2.8
31	24.2 (15.7, 8.5)	4, 3, 1	10.7	41.8	46.7	0.8
26	11.6 (6.9, 4.7)	1, 1, 0	14.5	37.6	34.2	13.7
24	27.5 (19.0, 8.5)	2, 2, 0	13.2	50.9	24.6	11.4
22	42.9 (38.4, 4.5)	2, 2, 1	4.2	45.8	49.2	0.8

TABLE 10.—Weber River, UT non-spawning reach location (UTM zone 12 N coordinates, center of reach), linear reach distance, channel width, abundance of large woody debris (LWD; small, medium, and large), and abundance of LWD jams. See Methods section for definitions of LWD size classes. I surveyed non-spawning reaches in June-July 2015.

Non-spawning reach number	Location (UTM); X, Y	Reach length (m)	Channel width (m); wetted (bankfull)	LWD abundance (Sm, Md, Lg)	Number of LWD jams (area; m^2)
320	467035, 523660	300	14.6 (17.3)	22 (11, 10, 1)	1 (25)
318	466970, 524090	300	17.1 (24.9)	26 (20, 5, 1)	2 (250)
317	466890, 524355	300	16.6 (29.0)	32 (25, 4, 3)	1 (75)
316	466880, 524620	300	19.1 (31.4)	54 (25, 16, 13)	1 (25)
41	417942, 556340	300	16.3 (57.5)	64 (30, 29, 5)	3 (275)
34	416460, 557410	300	19.9 (28.2)	27 (15, 7, 5)	1 (50)
27	416697, 559170	300	15.5 (21.7)	35 (26, 7, 2)	0 (0)
18	416874, 561770	300	18.6 (22.3)	27 (14, 12, 1)	0 (0)
13	416885, 563170	300	17.7 (22.6)	41 (21, 17, 3)	1 (50)
4	416346, 564557	300	15.7 (22.9)	35 (21, 10, 4)	1 (210)

TABLE 11.—Weber River, UT non-spawning reach geomorphic complexity, number of geomorphic units, and percent (%) fines, gravel, cobble, and boulders. See Methods section for definitions of geomorphic complexity and substrate size classes. I surveyed non-spawning reaches in June-July 2015.

Non-spawning reach number	Geomorphic complexity (%) (riffles, pools)	Number of geomorphic units; pools, riffles, backwaters	Fines (%)	Gravel (%)	Cobble (%)	Boulders (%)
320	8.8 (7.8, 1.0)	1, 2, 4	17.4	28.4	50.5	3.7
318	19.5 (14.0, 5.4)	2, 3, 3	6.1	32.5	61.4	0.0
317	25.6 (21.5, 4.0)	1, 4, 1	13.4	22.3	63.4	0.9
316	31.8 (29.8, 2.0)	1, 5, 1	26.1	18.3	55.7	0.0
41	20.8 (19.5, 1.3)	1, 3, 3	12.0	35.2	50.0	2.8
34	16.2 (0.0, 16.2)	2, 0, 0	24.8	23.9	15.6	35.8
27	21.5 (19.7, 1.8)	1, 4, 0	11.9	33.0	41.3	13.8
18	12.7 (11.7, 1.0)	1, 1, 0	14.3	55.5	25.2	5.0
13	17.6 (12.3, 5.4)	1, 2, 0	18.0	55.0	24.3	2.7
4	16.4 (9.3, 7.1)	4, 4, 2	7.0	64.9	22.8	5.3

TABLE 12.—Ferron Creek, UT spawning (sp) and non-spawning (non) reach location (UTM zone 12 N coordinates, center of reach), abundance of ripe bluehead sucker (BHS) sampled (reported only for spawning reaches), linear reach distance, channel width, abundance of large woody debris (LWD; small, medium, and large), and abundance of LWD jams. See Methods section for definitions of LWD size classes. I surveyed reaches in July-August 2016.

	Reach number	Location (UTM; X, Y)	BHS sampled; ripe (total)	Reach length (m)	Channel width (m); wetted (bankfull)	LWD abundance (Sm, Md, Lg)	Number of LWD jams (area; m^2)
Spawning reaches	11 (sp)	476965, 331716	3 (5)	300	7.4 (12.1)	20 (8, 7, 5)	0 (0)
	10 (sp)	477098, 4331244	3 (3)	300	8.4 (9.4)	5 (2, 2, 1)	0 (0)
	9 (sp)	477234, 4331015	2 (4)	300	8.7 (11.7)	24 (16, 4, 4)	0 (0)
	8 (sp)	477394, 4330798	4 (6)	300	7.7 (12.0)	22 (13, 3, 6)	0 (0)
	7 (sp)	477615, 4330344	2 (2)	300	6.6 (10.3)	8 (5, 2, 1)	0 (0)
	6 (sp)	478480, 4329778	6 (7)	300	7.5 (9.5)	14 (6, 5, 3)	0 (0)
	5 (sp)	478866, 4329421	8 (19)	670	9.0 (11.6)	0 (0, 0, 0)	0 (0)
	4 (sp)	479832, 4328890	2 (3)	300	5.9 (8.0)	12 (10, 2, 0)	1 (5)
	3 (sp)	480088, 4328631	4 (6)	300	7.9 (12.6)	6 (4, 2, 0)	0 (0)
	2 (sp)	480326, 4328501	8 (17)	700	6.8 (9.3)	3 (3, 0, 0)	0 (0)
	1 (sp)	481244, 4328342	10 (13)	360	9.2 (17.1)	4 (3, 0, 1)	0 (0)
Non-spawning reaches	10 (non)	476946, 4331460	-	270	7.1 (12.6)	7 (0, 1, 6)	0 (0)
	9 (non)	477464, 4330563	-	270	7.5 (12.8)	11 (7, 2, 2)	0 (0)
	8 (non)	477865, 4330192	-	330	5.7 (8.9)	3 (2, 1, 0)	0 (0)
	7 (non)	478090, 4330079	-	330	6.7 (11.2)	17 (10, 5, 2)	0 (0)
	6 (non)	478327, 4330019	-	330	8.3 (11.3)	10 (6, 3, 1)	1 (15)
	5 (non)	479188, 4329231	-	275	7.3 (9.9)	4 (2, 1, 1)	0 (0)
	4 (non)	479446, 4329140	-	275	7.3 (9.8)	4 (2, 1, 1)	0 (0)
	3 (non)	479690, 4329114	-	275	5.2 (9.6)	2 (1, 1, 0)	0 (0)
	2 (non)	480702, 4328191	-	330	5.4 (10.2)	1 (0, 1, 0)	0 (0)
	1 (non)	480927, 4328289	-	330	6.4 (11.2)	1 (0, 0, 1)	0 (0)

TABLE 13.—Ferron Creek, UT spawning (sp) and non-spawning (non) reach geomorphic complexity, number of geomorphic units, and percent (%) fines, gravel, cobble, and boulders. See Methods section for definitions of geomorphic complexity and substrate size classes. I surveyed reaches in July-August 2016.

	Reach number	Geomorphic complexity (%) (riffles, pools)	Number of geomorphic units; pools, riffles, backwaters	Fines (%)	Gravel (%)	Cobble (%)	Boulders (%)
Spawning reaches	11 (sp)	34.9 (22.9, 12.0)	4, 4, 0	37.0	25.0	36.0	2.0
	10 (sp)	9.4 (1.9, 7.5)	3, 1, 0	25.7	40.6	32.7	1.0
	9 (sp)	23.4 (13.6, 9.9)	4, 2, 1	20.2	40.4	39.4	0.0
	8 (sp)	24.9 (4.3, 20.6)	8, 1, 0	16.3	55.1	28.6	0.0
	7 (sp)	43.9 (7.4, 36.5)	5, 3, 0	16.0	57.0	26.0	1.0
	6 (sp)	8.2 (2.5, 5.8)	2, 1, 0	10.8	47.1	39.2	2.9
	5 (sp)	9.1 (3.5, 5.6)	11, 2, 0	11.0	36.0	47.0	6.0
	4 (sp)	8.1 (5.6, 2.5)	2, 2, 0	9.1	42.4	40.4	8.1
	3 (sp)	4.7 (0.0, 4.7)	2, 0, 0	6.9	48.5	42.6	2.0
	2 (sp)	18.6 (3.8, 14.9)	11, 2, 0	12.0	48.0	33.0	7.0
	1 (sp)	36.4 (26.5, 10.0)	6, 2, 0	14.9	43.6	37.6	4.0
Non-spawning reaches	10 (non)	12.6 (8.1, 4.5)	2, 2, 0	18.0	36.0	45.0	1.0
	9 (non)	17.3 (8.6, 8.7)	4, 3, 0	17.0	38.0	45.0	0.0
	8 (non)	24.2 (10.9, 13.3)	4, 3, 0	29.7	40.6	29.7	0.0
	7 (non)	15.7 (1.5, 14.2)	5, 2, 0	25.5	40.8	32.7	1.0
	6 (non)	0.0 (0.0, 0.0)	0, 0, 0	13.0	52.0	34.0	1.0
	5 (non)	6.1 (0.0, 6.1)	2, 0, 0	22.2	31.3	34.3	12.1
	4 (non)	9.3 (1.8, 7.4)	2, 2, 0	29.7	39.6	25.7	5.0
	3 (non)	0.6 (0.0, 0.6)	1, 0, 0	31.4	41.9	25.7	1.0
	2 (non)	5.5 (5.5, 0.0)	0, 1, 0	29.8	26.0	32.7	11.5
	1 (non)	4.9 (0.0, 4.9)	1, 0, 0	15.8	39.6	31.7	12.9

TABLE 14.—Laboratory experiment results for juvenile bluehead sucker growth (median; g/g/day) in each velocity or temperature (temp) treatment with 25th and 75th quartiles and sample size (n) shown.

Treatment	Median	25th quartile	75th quartile	n
Slow velocity	0.000233	-0.00125	0.00656	36
Medium velocity	0.00205	-0.00175	0.00445	35
Fast velocity	-0.00107	-0.00320	0.00181	31
Cool temp	-0.000513	-0.00273	0.00309	35
Tepid temp	0.00287	0.00142	0.00619	35
Warm temp	-0.00165	-0.00300	-0.000144	32

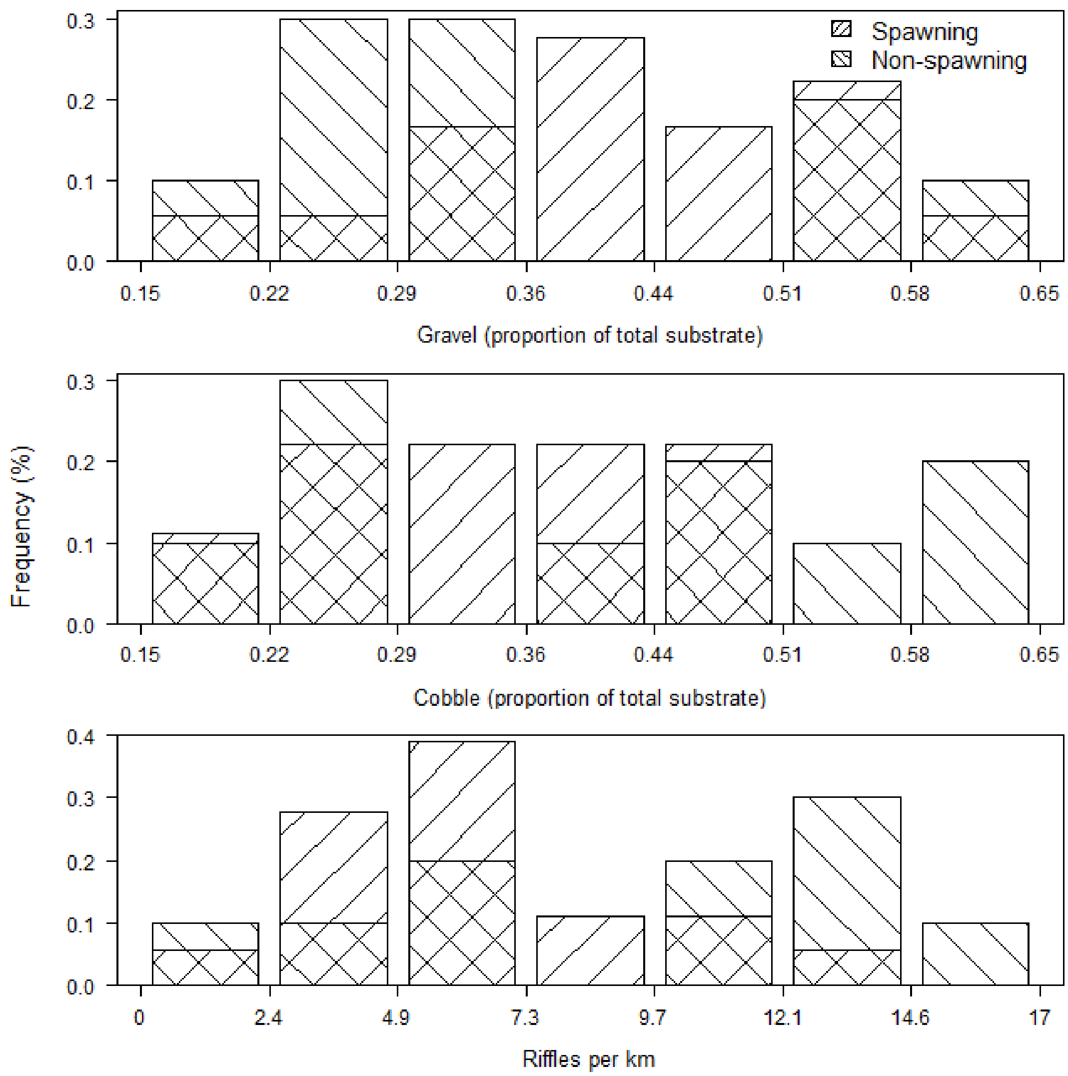

FIGURE 15.—Frequency of the three significant habitat characteristics used to classify spawning and non-spawning reaches in the Weber River, UT, determined using random forest classification.

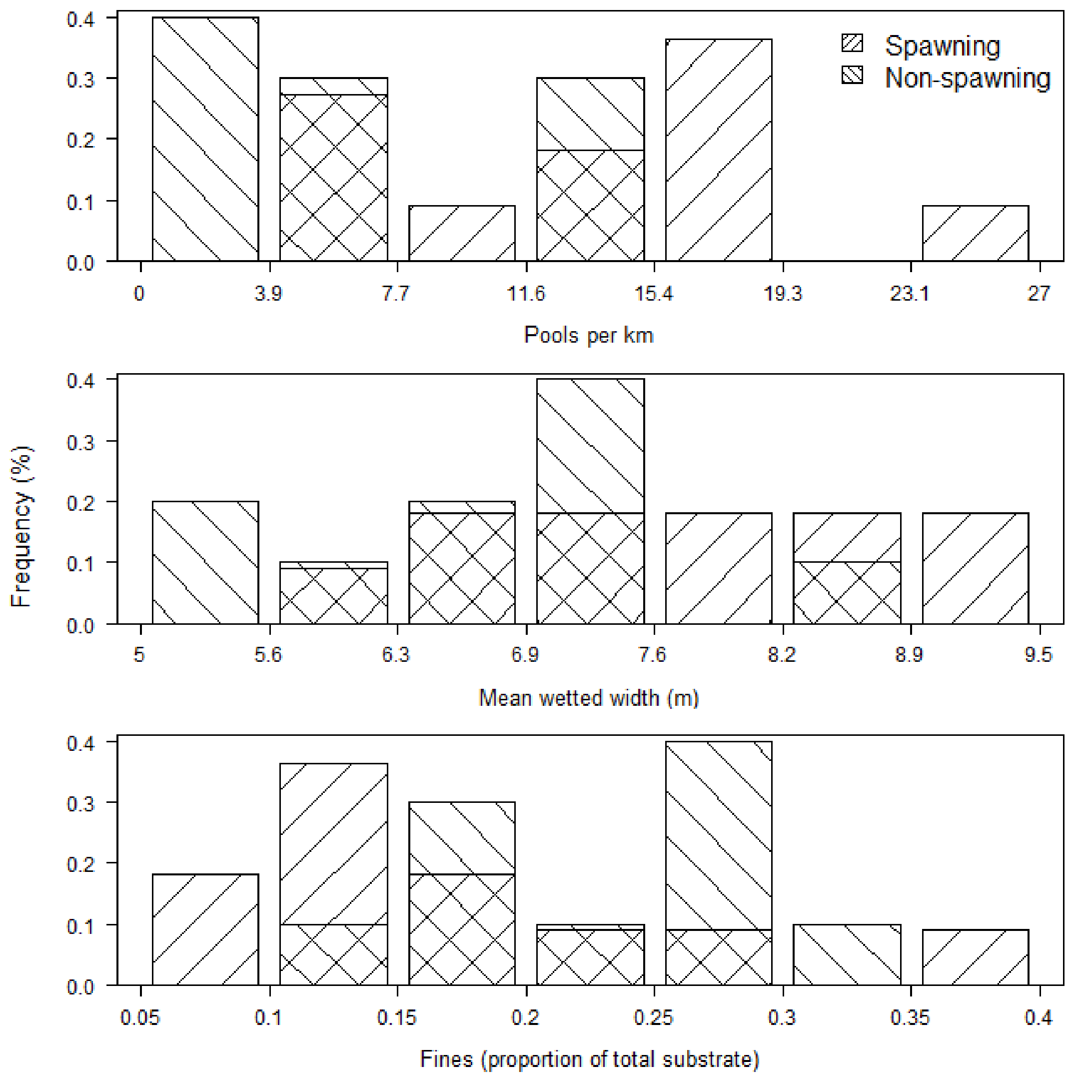

FIGURE 16.—Frequency of the three significant habitat characteristics used to classify spawning and non-spawning reaches in Ferron Creek, UT, determined using random forest classification.

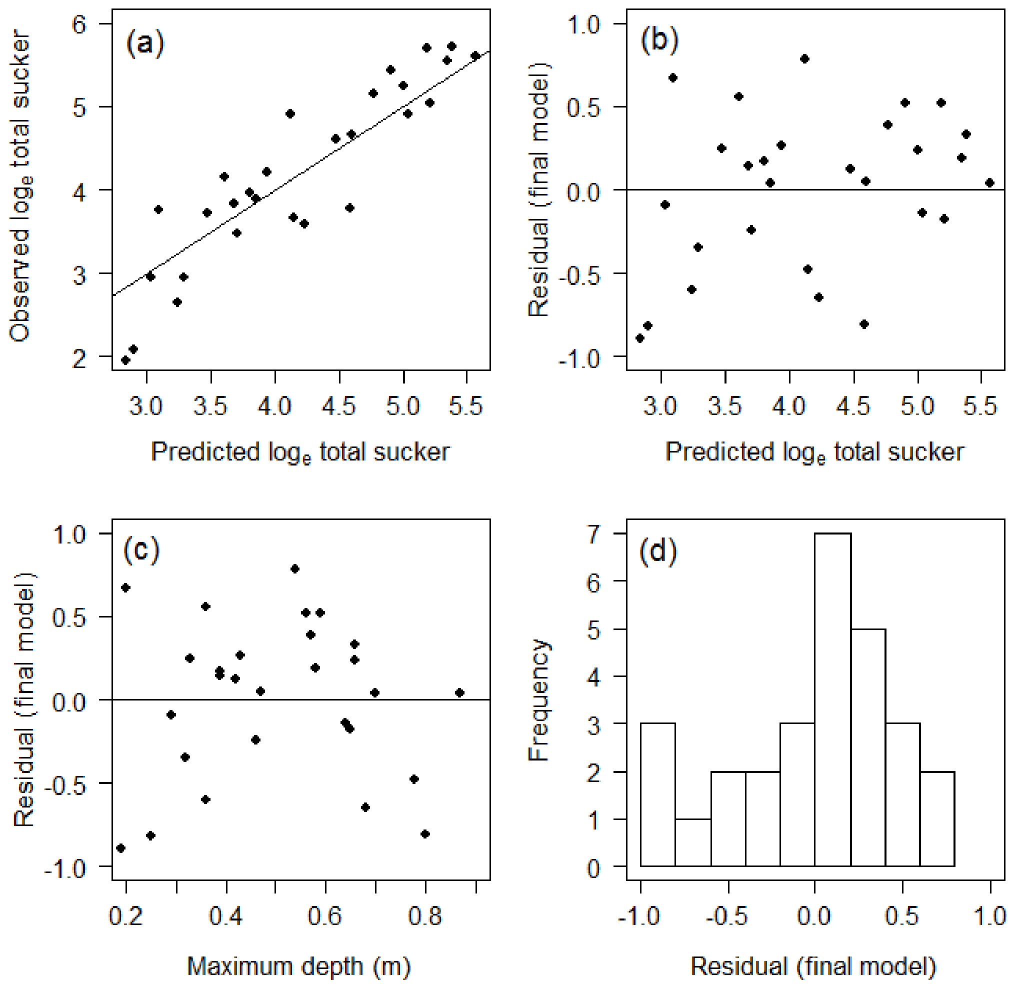

FIGURE 17.—Model fit for the final model evaluating backwater-sampling data. (a) Observed $\log_e$ total sucker plotted against predicted $\log_e$ total sucker. (b) Final model residuals plotted predicted $\log_e$ total sucker. (c) Final model residuals plotted across backwater maximum depth. (d) Histogram of final model residuals.

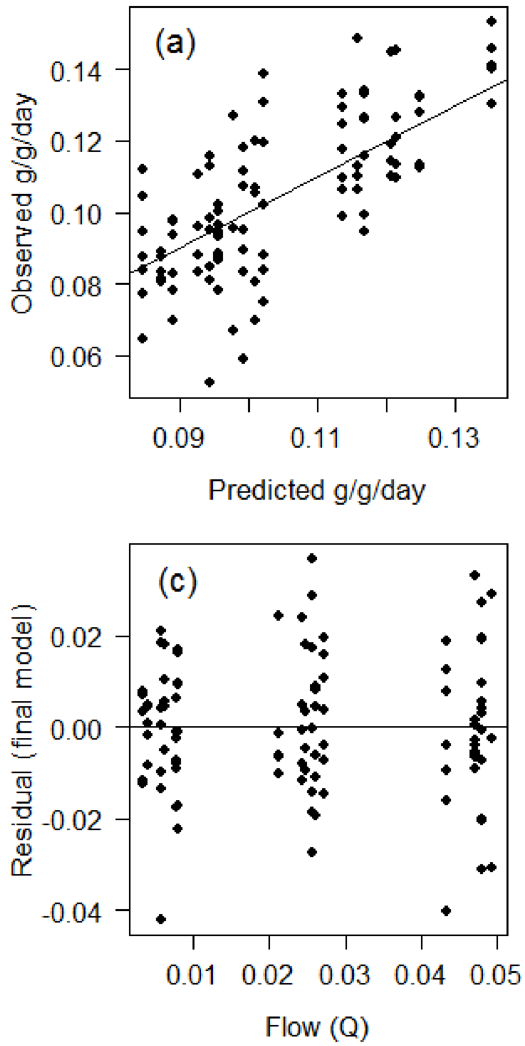

FIGURE 18.—Model fit for the full model evaluating laboratory juvenile growth data. (a) Observed juvenile growth (g/g/day) plotted against predicted juvenile growth. (b) Full model residuals plotted against predicted juvenile growth. (c) Full model residuals plotted across water velocity. (d) Full model residuals plotted across water temperature.