

Movement, habitat use, and early life history of fishes in novel river-reservoir complexes

by

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Abstract

Reservoirs and associated river-fragments are novel ecosystems now common across the globe. Riverine habitats have been transformed and fragmented by dams creating mixed lotic-lentic habitats used as introduction points for non-native species. This has resulted in altered habitats and fish assemblages consisting of species that do not share an evolutionary history. The Colorado River basin is fragmented by dams that create a complex of river fragments and reservoir habitats used by native fishes, such as razorback sucker (*Xyrauchen texanus*). Low survival of early life stage (ELS) razorback sucker in the Colorado River Basin, USA is thought to cause a recruitment bottleneck, but conservation efforts are limited by a complete mechanistic understanding of causal factors. I used a combination of lab and field studies to examine potential limiting factors contributing to the lack of recruitment by razorback sucker, assessed distribution patterns of the fish assemblage along the San Juan River inflow to Lake Powell, and evaluated movement potential across the entire upper Colorado River basin including between reservoir and riverine habitats. To explore discrepancies in survival of razorback sucker compared to other co-occurring sucker species, I used museum-cataloged fish specimens collected from the San Juan River, Utah to quantify trophic resource use of co-occurring ELS suckers. I evaluated diet diversity and composition using gut content and stable isotope analysis, expecting high overlap in diets among sucker species. Razorback sucker had the lowest diet richness. Although they were smaller and less developed than the other two species, differences in diet item occurrence across sizes and species reflect differences in resource acquisition among ELS suckers that might be related to recruitment bottlenecks. In the next chapter, I assessed species distributions along a 20 km reach of the San Juan River-Lake Powell inflow with the prediction that fish abundance would increase upstream with increasing energy inputs. I

identified strong patterns in total number of species and individuals captured with both increasing towards the river inflow by systematically sampling shoreline habitats with trammel nets. Changes in assemblage structure were driven mainly by increases in relative abundance of benthic omnivores, including razorback sucker, towards more transitional and riverine habitats, but also by increases in predatory species, such as striped bass (*Morone saxatilis*). River-reservoir inflow areas might provide high-quality feeding areas for both benthic omnivores and piscivores. Lastly, I assessed movement potential of adult razorback sucker across reservoir and river habitats in the upper Colorado River basin using a multi-agency tagging database. Given unimpeded access to upstream riverine habitats, I expected fish to move long distances and readily exchange between riverine and lacustrine habitats. Of 722 fish captured in the Colorado River inflow, 261 were re-encountered and 107 of those were subsequently encountered upstream in the Colorado and Green river systems, or in the San Juan River inflow, with 11 individuals moving at least 586 km. The proportion of fish moving between lacustrine and riverine habitats was estimated in the San Juan River inflow. Within a year of being captured in the reservoir, 29% and 20% of fish in 2017 and 2018, respectively, were detected 30 km upstream in the San Juan River. In 2016-2017, we translocated a total of 303 fish upstream of a 6 m tall waterfall into the San Juan River. Generally, fish did not reside long in the river as 80% were re-encountered downstream of the waterfall within a year. These data show long-distance movements are not limited to a few individuals and illustrate how large river fish can maintain population connectivity in highly altered ecosystems. Managing for the maintenance of diverse movement syndromes (e.g., river-resident versus transient fish) will likely increase population resilience to environmental change. Collectively, this work contributes to an increased

knowledge of the ecology and life history of a highly imperiled species and sheds light on fish assemblage use of novel riverine and reservoir habitats that are widespread across the globe.

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Dedication

“You don’t beat it. You never beat the river.”
—Lewis Medlock, *Deliverance* by John Boorman.

I would like to dedicate this dissertation to all of my friends who shared time with me on the river.

Preface

The three data chapters of this dissertation have been prepared in submission format and include co-authors. Chapter 2 is formatted for *Transactions of the American Fisheries Society*. Chapter 3 is formatted for *Canadian Journal of Fisheries and Aquatic Sciences*. Chapter 4 is formatted for *Aquatic Conservation: Marine and Freshwater Ecosystems*. Chapter 2 has been adapted with permission from **John Wiley and Sons**: License number: 4652600540761, *Transactions of the American Fisheries Society*, Pennock et al. 2019. Chapter 4 is under review at *Aquatic Conservation: Marine and Freshwater Ecosystems*.

Chapter 1 - Fish conservation in novel ecosystems

Lentification of flowing waters has occurred across the globe (Sabater 2008). Humans have fragmented river networks through dam construction causing a loss of lotic habitat and increased lentic habitat (Grill et al. 2019). Damming rivers creates novel ecosystems (*sensu* Hobbs et al. 2006) through coupled human-driven processes of habitat alteration and species introductions that lead to new assemblages of species that have not shared an evolutionary history. Along with altering lotic habitat and providing impetus for non-native fish introductions (Havel et al. 2005), destruction of riverine habitat through dam construction has caused declines in water quality and aquatic biodiversity (Moyle and Leidy 1992; Minckley et al. 2003; Dudgeon et al. 2006; Olden 2016), altered downstream flow and temperature regimes (Poff et al. 1997), isolated populations (Winston et al. 1991; Perkin et al. 2015), and reduced dispersal ability (Rolls et al. 2013). Fish conservation in novel ecosystems has been limited by a lack of information on basic ecology and life history information due to rapidly declining populations (Minckley and Deacon 1991; Cooke et al. 2012), the continued proliferation of water development and use by an increasing human population, and the synergistic effects of a changing climate without a full mechanistic understanding of the factors causing fish species declines (Closs et al. 2016).

Declines in populations of big-river fishes of the Colorado River basin

The Colorado River, and associated tributaries, in the southwestern United States is one of the most heavily managed river systems in the world (Christensen et al. 2004; Castle et al. 2014), that provides municipal water to approximately 40 million people and irrigation water for almost 5.5 million acres of land (United States Bureau of Reclamation 2012). As a result of water development, populations of endemic fishes have declined to the point that all four

endemic “big-river” species have been listed under the Endangered Species Act. Additionally, other endemic species have also experienced declines such as flannelmouth sucker (*Catostomus latipinnis*), which has been extirpated from 50% of its historical range but maintain self-sustaining populations (Bezzerdies and Bestgen 2002; Budy et al. 2015). In the upper Colorado River basin, intense conservation efforts are implemented by two federal recovery programs that include habitat and flow management, non-native fish removal, and supplemental stocking of endangered fishes (Frannsen et al. 2014; Pennock et al. 2018). Razorback sucker (*Xyrauchen texanus*), one of the species of intense management, is thought to experience a recruitment bottleneck in early life stages, and populations are maintained exclusively through supplemental stocking despite the yearly production of wild-spawned larval fish (Barkstedt et al. 2018; Farrington et al. 2018). Recovery efforts for razorback sucker continue to be limited by an incomplete mechanistic understanding of the recruitment bottleneck, but hypothesized factors include habitat loss, non-native fish predation or competition, habitat and flow alteration, and starvation. For the second Chapter of this dissertation, I investigated differences in diet among early life stage suckers to potentially explain differential survival among co-occurring sucker species including flannelmouth and bluehead sucker (*Catostomus discobolus*), which maintain self-sustaining populations in the San Juan River, Utah. I found differences in diet among species using gut content and stable isotope analysis that suggest differences in feeding ecology and could potentially explain differences in survival among species. These differences included a complete lack of certain diet items from the guts of razorback sucker and large intraspecific variation in frequency of occurrence of diet items among individuals of this species.

Fish use of river-reservoir inflows

Reservoirs can be thought of as “river-lake hybrids” because they experience a longitudinal gradient of physicochemical and biological properties along three generally defined, but spatially and temporally dynamic zones: riverine, transitional, and lacustrine (Thornton et al. 1990). Several general patterns can be observed in river-reservoir inflow areas due to this spatial transition among zones. Typically, there is a transition from shallow, higher velocity waters in the riverine zone to deeper, low-velocity waters in the lacustrine zone. Sediment and nutrient availability are high in the riverine zone, and sedimentation and nutrient availability peak in the transition zone as water velocity slows and sediment and associated nutrients are deposited. Nutrient availability declines into the lacustrine zone because a lack of new inputs, increased reliance on within-zone nutrient recycling, biological consumption, as well as deposition and denitrification. The transition zone of a reservoir can experience high levels of volumetric primary production and oxygen demand due to inflow of available nutrients and increases in light penetration, which typically limits productivity in the riverine zone (Thornton et al. 1990). River-reservoir inflow areas (e.g., deltas; Volke et al. 2015) can support diverse communities because they represent heterogeneous edge habitats (i.e., an ecotone; Kaemingk et al. 2007; Spindler et al. 2009; Buckmeier et al. 2014; Volke et al. 2015, 2019). Seasonal inflow dynamics that form delta areas and flooded off-channel habitats in the riverine and transitional zones of reservoirs could be serving as important (supplementary or complementary; Tilman 1982; Dunning et al. 1992) habitats for riverine species currently limited in highly developed river systems (e.g., Colorado River basin; Bestgen et al. 2011; Volke et al. 2015, 2019).

Non-native fish are hypothesized to negatively impact populations of native fishes in the Colorado River basin (Tyus and Saunders 2000; Franssen et al. 2014; Pennock et al. 2018), and

reservoir systems often are comprised of a suite of native and non-native species (Cowx and Gerdeaux 2004; Miranda et al. 2008). Currently, razorback sucker only recruit to adulthood in detectable numbers in one place in the entire Colorado River basin, Lake Mead, which is home to a fish assemblage dominated by non-native species (Albrecht et al. 2010, 2018). This presents a conundrum for managers of this endangered species (Albrecht et al. 2010).

For my third Chapter, I sampled the fish assemblage along the longitudinal axis of the San Juan River-Lake Powell inflow area to identify changes in assemblage structure and assess overlap in species distributions. I found strong increases in species richness and total number of individuals captured closer to the river inflow that are consistent with previously published studies (Buckmeier et al. 2014; Nobile et al. In press). I also found interannual variation in species-specific patterns. Increased relative abundance of benthic omnivores including razorback sucker towards the river inflow contributed most to changes observed at the level of the entire assemblage. Some predatory species also showed significant increases in relative abundance towards the riverine zone. Increased fish abundance towards the reservoir inflow suggest these areas could be providing ample food resources for both benthic omnivores and piscivores, despite differences in habitat use by these two disparate groups. Because samples were collected in spring, it is also possible fish move into those areas to spawn. Coexistence in river-reservoir inflow areas by native and non-native species presents opportunities to manage these areas more holistically for the conservation of native fish species.

Prior to construction of the Laguna Dam on the lower Colorado River in 1903, fish species in the Colorado River basin had access to the Colorado River Delta, which covered 780,000 ha and supported hundreds of plant species in vast areas of floodplain habitat (Sykes 1937; Glenn et al. 1996). Access to floodplain habitat might have been important to the

successful completion of Colorado River fishes' life histories (i.e., provided complimentary habitat). Construction of large water storage reservoirs has further fragmented the Colorado River basin and restricted access to potentially important habitat types for native imperiled fishes. Restricted access to and loss of the Colorado River Delta and other floodplain habitats across the Colorado River basin hinders the recovery of endangered fish, including razorback sucker. In Chapter 4 of this dissertation, I assess the movement ability of razorback sucker across the entire upper Colorado River basin, including Lake Powell, quantify proportions of fish moving between reservoir and riverine habitats, and assess the post-translocation behavior of fish moved upstream of a 6 m tall waterfall barrier on the San Juan River. This study shows razorback sucker move vast distances (>600 km) across the entire river basin, including through Lake Powell, and these movements are not just made by a few individuals as was previously thought. Moreover, about a third of sampled individuals made movements between reservoir and riverine habitat over the course of a year, and although most translocated individuals returned back downstream within a year some first moved upstream at least 100 km. These results suggest that maintaining and improving connectivity will ensure fish are able to freely move throughout upper basin rivers which can increase the long-term viability of populations.

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Chapter 2 - Feeding ecology of early life stage Razorback Sucker relative to other sucker species in the San Juan River, Utah

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Introduction

Recruitment of freshwater fishes can be greatly influenced by trophic interactions of juveniles (Houde 1994). These early life stage (ELS) fish experience drastic ontogenetic shifts with size and trait development (e.g., gut development, fins, mobility) over relatively short time periods, creating a “critical period” when newly hatched larval fish must acquire resources after yolk absorption to support rapid growth and escape predation (Hjort 1914; Miller et al. 1988; Holzman et al. 2015). Failure to do so can diminish fish survival and potentially cause a recruitment bottleneck (Werner and Gilliam 1984). Interspecific differences in ELS fish responses to abiotic and biotic factors can also influence recruitment success (Miller et al. 1988). For instance, some species might be more susceptible to starvation due to lower energy reserves in their yolks (Hunter 1981), while other species might be more susceptible to predation due to smaller size or delayed mobility (Bailey and Houde 1989). Despite the importance of ELS fish survival to population stability (Starrett 1951; Schlosser 1985; Freeman et al. 2001), studies of the trophic ecology of fishes during this life stage are limited (Ross 1986; Childs et al. 1998; Pease et al. 2006; Starks et al. 2016). Increasing our understanding about trophic ecology of co-occurring fishes could help predict why some species, might not be able to successfully transition through this critical period of early life in altered ecosystems.

Colorado River Basin fishes in the American southwest are highly imperiled due to intense water development that has caused range-wide population declines. Consequently, many

species were listed under the Endangered Species Act following the construction of large hydropower dams (Minckley and Deacon 1991; Minckley et al. 2003). Native fishes must now contend with highly altered habitats and heavily managed flow regimes that include changes in geomorphology following non-native plant establishment and artificially restricted movements and habitat loss from river fragmentation (Tyus and Karp 1990; Franssen et al. 2014; Cathcart et al. 2018). Additionally, a suite of nonnative species have been introduced throughout the basin and are hypothesized to prey on and compete with native fishes, increasing their imperilment in altered habitats (Minckley et al. 2003). These altered conditions have led to some species experiencing a recruitment bottleneck despite intensive recovery efforts (Schooley and Marsh 2007).

Razorback Sucker *Xyrauchen texanus* is an endangered “big-river” species that is maintained in the wild through intense stocking efforts throughout the Colorado River Basin. Evidence of successful recruitment (i.e., survival to adulthood) of wild-spawned Razorback Sucker in remnant river fragments is almost nonexistent (except for Lake Mead; Albrecht et al. 2010). Conversely, two native sucker species that co-occur with Razorback Sucker, Bluehead Sucker *Catostomus discobolus* and Flannelmouth Sucker *C. latipinnis*, have relatively stable, self-sustaining populations, despite also being extirpated from most of their historical range (Bezzerrides and Bestgen 2002; Budy et al. 2015). Currently, there is no confirmed mechanism explaining the recruitment bottleneck experienced by Razorback Sucker, but investigations into why other native suckers are recruiting could further our understanding of species’ resistance to habitat degradation. Several competing hypotheses have been proposed to explain a lack of recruitment to maturity by Razorback Sucker, including reduced habitat availability (Tyus and Saunders 2000; Clarkson et al. 2005; Bestgen 2008), altered flow and temperature regimes

(Bestgen 2008), introduction of non-native species (Minckley et al. 2003; Marsh and Pacey 2005), habitat degradation (Horn 1996; Franssen et al 2014), and food limitation (Papoulias and Minckley 1990; Papoulias and Minckley 1992; Horn 1996). The presence of multiple and potentially compounding mechanisms affecting recruitment of imperiled fishes makes it difficult for researchers and managers to mitigate, any single factor.

In the San Juan River of New Mexico, Colorado, and Utah, wild-spawned ELS Razorback Sucker have been collected during annual monitoring efforts in every year since 1998 (Barkstedt et al. 2018); yet, survival of these fish past their first winter is extremely rare. Early life stages of Bluehead Sucker and Flannelmouth Sucker are also collected during these surveys, but age 1+ fish of these species are commonly collected (Farrington et al. 2018). The limited detection of juvenile and sub-adult Razorback Sucker suggests high mortality is occurring in early life (Guttermuth et al. 1994; Modde 1996; Bestgen et al. 2017). Other studies have been conducted on trophic resource use of ELS Bluehead, Flannelmouth, and Razorback Suckers, but these studies have either been conducted in lentic habitats (i.e., for Razorback Sucker in reservoirs; Marsh and Langhorst 1988) or did not include some species because of a lack of occurrence (Muth and Snyder 1995; Childs et al. 1998; Seegert et al. 2014). To our knowledge, this is the first study to assess trophic resource use of ELS Razorback Sucker from riverine habitats. As adults and juveniles, Bluehead, Flannelmouth, and Razorback Suckers generally overlap in diet, but also have differences in morphology that allow specialization on particular food items. For instance, Bluehead Sucker have been described as feeding mainly on attached algae using specialized mouth parts adapted for scraping (Taba et al. 1965; Muth and Snyder 1995; Snyder and Muth 2004), but also consume macroinvertebrates, detritus, and terrestrial vegetation (Seegert et al. 2014). Flannelmouth Sucker are considered the most general feeder of

the three species and their diets include macroinvertebrates, algae, organic matter, zooplankton, terrestrial vegetation, and bottom ooze (Taba et al. 1965; Muth and Snyder 1995; Seegert et al. 2014). Razorback Sucker feed on a variety of items including algae, bottom ooze, zooplankton, macroinvertebrates, and detritus (Marsh 1987; Horn 1996), and are thought to be more planktivorous, relative to the other two species, aided by a larger number of gill rakers and a slightly less terminal mouth (Snyder and Muth 2004). Given these differences in morphologies as juveniles and adults, it is possible that varying morphologies exist in ELS fishes allowing species to specialize on particular food items.

Co-occurring sucker species (family Catostomidae) are common throughout North America and their continued persistence is challenged by a multitude of threats (Cooke et al. 2005). Increasing knowledge on the natural history and ecology of members of this diverse and imperiled family may help conservation efforts (Cooke et al. 2012; Matthews 2015; Courchamp et al. 2015). Our objective was to compare trophic resource use among co-occurring ELS Bluehead, Flannelmouth, and Razorback Suckers using museum-vouchered specimens collected from the San Juan River, Utah. Using gut content and stable isotope analysis, we tested for differences in diet richness and composition among these three species. Based on previous studies that found high diet overlap among Bluehead and Flannelmouth Suckers (Childs et al. 1998; Seegert et al. 2014), we predicted to find minimal differences in trophic resource use among species. We expected to find a higher proportion of empty stomachs in Razorback Sucker because overwinter survival (i.e., survival to age-1) has been extremely limited in the wild for this species. However, they also hatch at smaller sizes compared to Bluehead and Flannelmouth Suckers (Snyder and Muth 2004), which might also limit foraging success due to gape limitation. Size-dependent effects on ELS fish can be very important for survival, likely differ among

species, and are not well understood for many species (Werner and Gilliam 1984; Graeb et al. 2004; Bestgen et al. 2006). Furthermore, early life-stage fish are typically limited in the size of prey items available to them (Graeb et al. 2004).

Methods

Study area and larval fish collections

The San Juan River begins in the southern Rocky Mountains of Colorado and flows south and west before its eventual confluence with the Colorado River in southern Utah. Along its course, the San Juan River is fragmented by a major dam (forming Navajo Reservoir) and several smaller low-head weirs designed to divert water for agricultural and industrial use (Figure 2.1). The historical confluence of the San Juan River and the Colorado River is now inundated by Lake Powell, the second largest reservoir in the United States (volume at full capacity > 32 km³; USBR 2018, <https://www.usbr.gov/uc/rm/crsp/gc/>). The San Juan River is a snowmelt driven system; however, contemporary flows in the San Juan River are highly managed by dam operations at Navajo Reservoir (Propst and Gido 2004; Franssen et al. 2007; Gido et al. 2013). Undammed tributaries still provide natural flow regime cues (e.g. Animas River) and spawning habitat (e.g., McElmo Creek) for some of the native fishes (e.g., Cathcart et al. 2015). Recovery efforts for endangered fishes in the San Juan River include non-native predator removal (Franssen et al. 2014; Pennock et al. 2018), flow management (Propst and Gido 2004; Gido and Propst 2012), and stocking of hatchery reared fish (Furr 2016).

As part of an effort to document spawning and recruitment by native fishes occurring in the San Juan River, larval fish monitoring has been conducted every year from 1991-2018 (Farrington et al. 2018). These collections consist of seining all available low-velocity habitats along the course of the river to document the occurrence and relative abundance of ELS fish in

the San Juan River. Collections are generally made from April to August from 220 km of river (see Barkstedt et al. 2018 for more details). The first collection of Razorback Sucker larvae during these monitoring efforts occurred in 1998. All collections are catalogued in the Division of Fishes, Museum of Southwestern Biology, University of New Mexico in the research collection and made available for use. Throughout, we use the term early life stage to describe fish at various stages of larval development and recently transformed juveniles (Snyder and Muth 2004).

Gut content analysis

To assess differences in diets among the three sucker species, we first identified collections listed in the FishNet2 online database housed at the Museum of Southwestern Biology where all three species were captured from the same locality (e.g., backwater) on the same date. We further limited collections to those that contained at least 10 individuals of each species (Table 1). In hopes of reducing variation in observed diets due to spatial or temporal differences in available trophic resources, we chose collections that occurred close together in both space and time. The specimens we chose were collected in May ($n = 1$) and June ($n = 4$) 2007 from five sites. From these five collections, we chose 10 individuals of each species that represented the range of standard lengths (SL) of captured fish if more than 10 fish were collected. Individuals were classified by stage of development following Snyder and Muth (2004) and measured to the nearest mm SL prior to gut content analysis ($n = 50$ per species; Figure 2.2). The entire digestive tract was removed from each fish and contents were placed on a microscope slide. Gut contents were viewed under a compound microscope at 40x-200x magnification. Because of subjective limitations with quantifying diets (Baker et al. 2014), we chose to describe diet composition using frequency of occurrence. This involved recording the

presence of various diet items for each individual fish. Diet items were classified into 12 categories and items occurring in < 5% of all individuals were grouped into the “rare” category (Table 2). The “detritus” category included all unidentifiable organic material.

Stable isotopes

Stable isotopes are commonly used to assess energy flow in aquatic systems relative to trophic resource use (Finlay 2001; Gido et al. 2006; Pease et al. 2006). Unlike gut content analysis, which provides a snapshot in time of an individual’s diet, stable isotopes typically reflect resource use over longer time periods. Relative amounts of ¹⁵N in fish tissue can provide an estimate of trophic level (Vander Zanden et al. 1997). While ¹³C varies little across trophic levels, it allows for differentiation among organic matter sources (e.g., benthic algae versus detritus). After dietary tracts were removed, whole bodies of fish (minus the heads) were retained for isotope analysis. Fish were dried (60° C ~8 h), either ground whole after freezing with liquid nitrogen or broken up into small pieces, packed into tin capsules, and weighed. Samples were analyzed for carbon and nitrogen stable isotope ratios at the Stable Isotope Mass Spectrometry Laboratory, Kansas State University, using an Elementar vario Pyro cube Elemental Analyzer coupled to an Elementar Vision mass spectrometer with continuous flow capabilities (Elementar Americas, Mt. Laurel, NJ). Data are reported on a per mil basis (‰) in delta (δ) notation. Delta values were calculated using the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}})-1 \times 1000$$

where R is equal to ¹³C/¹²C and ¹⁵N/¹⁴N. We used laboratory standards calibrated against international standards, Pee Dee Belemnite as the standard for carbon and atmospheric molecular nitrogen for nitrogen. Measurement error on routine analysis of laboratory standards was less

than 0.1‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Because formalin fixation and ethanol preservation predictably affects carbon and nitrogen isotopic signatures in fish tissue, we corrected isotopic ratios of our samples by adding 1.1‰ to observed $\delta^{13}\text{C}$ and by subtracting 0.5‰ from $\delta^{15}\text{N}$ (Edwards et al. 2002).

Statistical analysis

All analyses were conducted in Program R version 3.5.1 (R Core Team 2018). Fish length data did not meet parametric assumptions, so differences in SL among species were tested with a Kruskal-Wallis one-way ANOVA on ranks and pairwise comparisons assessed with Tukey's HSD. Using individual fish as replicates, we tested for differences in mean diet richness (number of diet item categories in gut contents) among species using generalized linear mixed effects models with a Poisson distribution and log-link function, including site as a random effect. Although we were mainly interested in assessing differences among species, fish size can be a strong determinant of diet and ELS fish in our study exhibited a wide range of SL and minimal overlap among species; therefore, we compared models including only the fixed effect of species against models with fixed effects of both species and SL and their interactive effects using likelihood ratio tests. We used the *glmer* function in the *lme4* package (Bates et al. 2015) to build and run generalized mixed effects models. We used the *lrtest* function in the *lmtest* package to compare nested models and an intercept-only model with likelihood ratio tests (Zeileis and Hothorn 2002). We assessed model fit using the *rsquared* function in the *piecewiseSEM* package (Lefcheck 2016) which calculates the proportion of variance explained by only fixed factors (marginal R^2) and by both fixed and random factors combined (conditional R^2). We report least squares means and 95% confidence intervals for species calculated using the *effect* function from the *effects* package (Fox and Weisberg 2018; Fox and Weisberg 2019). We

also assessed the relationship between diet richness and SL for each species independently using general linear models with a Poisson distribution and log-link function.

To assess differences in diet composition among species, we used discriminant function analysis (DFA) in the *flipMultivariates* package (accessed from URL:

<https://github.com/Displayr/flipMultivariates/>). To assess model accuracy, we first split our dataset into a testing and training portion by randomly selecting 70% ($n=105$) of observations with replacement to train the model, and we used the remaining “out-of-sample data” ($n=45$) to test the model. Significance of individual predictor variables (i.e., diet item categories) was assessed with MANOVA and corrected P -values for multiple tests with a false discovery rate correction (Benjamini and Hochberg 1995).

We also assessed differences in diet composition based on isotope samples. Differences in sample size existed among species, because some samples were either too small or were lost during processing, but at least 47 individuals of each species were analyzed. We analyzed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with linear mixed effects models with site as a random effect. We used the *lme* function in the *nlme* package (Pinheiro et al. 2018) to build and run mixed effects models. As with diet richness, we used likelihood ratio tests to compare models with species as a fixed effect to models including the effects of SL. Visual inspection of residual plots revealed heterogeneity of residuals and slight deviations from normality for $\delta^{13}\text{C}$. No obvious deviations from homoscedasticity or normality were apparent for $\delta^{15}\text{N}$. We \log_{10} transformed the absolute value of $\delta^{13}\text{C}$ (because all values were negative) which improved normality, but did not improve heterogeneity. To account for heterogeneity, we modeled variance by including the *varIdent* statement in the model, using site as the stratum. Again, we calculated marginal and conditional R^2 values to assess the approximate variance explained by the models. We report least squares

means and 95% confidence intervals for estimates. Estimates for $\delta^{13}\text{C}$ were back-transformed for ease of interpretation. To assess the relationship between $\delta^{13}\text{C}$ and SL, we used separate generalized least squares models for each species which allowed us to again account for heterogeneous variance as above. We again analyzed transformed $\delta^{13}\text{C}$, but report back-transformed estimates. We used simple linear regression to analyze patterns of $\delta^{15}\text{N}$ and SL.

Results

Collection composition, fish lengths, and diet richness

Relative abundance of Bluehead, Flannelmouth, and Razorback Suckers was variable across the five collection sites, ranging from 75-95%, and suckers made up 87% of total individuals collected (Table 1). All fish examined had identifiable material in their guts. Lengths of ELS fishes were significantly different among species (ANOVA on ranks: $H = 115.8$, $df = 2$, $P < 0.001$). Lengths of Bluehead (12.0 mm, 11.3-13.0; median, IQR), Flannelmouth (19.5, 15.0–22.0), and Razorback Sucker (9.0, 9.0–10.0) were all significantly different (Tukey HSD: $P < 0.05$; Figure 2.2). Species differed significantly in mean diet richness (Figure 2.3). The model with only the fixed effect of species was significantly different from the intercept-only model (likelihood ratio = 39.65, $df = 2$, $P < 0.001$), and models including the additive or additive and interactive effects of SL were not significantly different from the species-only model ($P > 0.05$; Table 3). Bluehead (5.7, 5.2–6.2; least squares mean, 95% CI) and Flannelmouth Sucker (5.8, 5.3–6.3) had 1.7x higher mean diet richness compared to Razorback Sucker (3.4, 2.9–3.9). The marginal R^2 of the species-only model was 0.22 and conditional R^2 was 0.22, suggesting the proportion of variance explained by the fixed effect of species accounted for nearly all of the variance (>99%) explained by the model. Adding the effect of SL only increased the marginal and conditional R^2 to 0.23-0.24, suggesting the effect of SL explained very little additional

variation. Diet richness for Bluehead Sucker ($df = 48$, $P = 0.029$) showed a significant positive relationship with SL, but there was no significant relationship for Flannelmouth Sucker ($df = 48$, $P = 0.158$) or Razorback Sucker ($df = 48$, $P = 0.460$; Figure 2.3).

Diet composition

The trained DFA model had an overall classification accuracy of 57% on out-of-sample data. The first discriminant function explained 76% of the variation among species, and somewhat separated Razorback Sucker from Bluehead and Flannelmouth Suckers. No diet item categories loaded positively on the first discriminant function axis, and were opposite of the centroid for Razorback Sucker (Figure 2.4). The second discriminant function explained the remaining 24% of the variation and was driven by separation between Bluehead and Flannelmouth Suckers. On the second discriminant function axis, diatoms, pollen, and rare items loaded heavily on the positive end, associated more with Bluehead Sucker, and diptera (i), diptera (a), and sand loaded heavily on the negative end, more aligned with Flannelmouth Sucker. Overall, nine of the twelve diet item categories differed significantly ($P < 0.05$; Table 2) in mean frequency of occurrence among species. This was mostly driven by relatively low frequency of occurrence of all diet items in Razorback Sucker. With the exception of one category (i.e., Ephemeroptera, Plecoptera, Trichoptera; EPT), Razorback Sucker had the lowest frequency of occurrence of all diet item categories.

Stable isotopes

Isotopic signatures also indicated diet differences among species, despite overlap in isotopic space (Figure 2.5). Flannelmouth Sucker had the highest isotopic niche breadth, which was evident from high variation in isotopic space (Figure 2.5, left). Flannelmouth Sucker had the largest standard ellipse area, corrected for sample size. Ellipses for Bluehead and Razorback

Suckers were 33% and 51% that of Flannelmouth Sucker, respectively. Bluehead and Razorback Suckers overlapped most in isotopic space, while differences in Flannelmouth Sucker $\delta^{13}\text{C}$ across sites varied substantially. Species differed significantly in mean $\delta^{13}\text{C}$ (likelihood ratio = 57.88, $df = 2$, $P < 0.001$), and again, models with the effects of SL did not differ significantly ($P > 0.05$) from the species-only model (Table 3). Bluehead Sucker (-21.7, -21.2--22.1; least squares mean, 95% CI) and Razorback Sucker (-20.9, -20.4--21.3) both had higher $\delta^{13}\text{C}$ than Flannelmouth Sucker (-22.2, -21.8--22.7). The fixed effect of species accounted for 63% of the variation explained by the model (marginal $R^2 = 0.45$), and the random effect of site accounted for approximately 37% of the variation (conditional $R^2 = 0.71$). $\delta^{13}\text{C}$ decreased significantly with SL for Bluehead Sucker ($df = 48$, $P = 0.014$), and no significant relationship was found for Flannelmouth ($df = 45$, $P = 0.928$) or Razorback ($df = 46$, $P = 0.723$) Suckers. Species differed significantly in mean $\delta^{15}\text{N}$ (likelihood ratio = 30.06, $df = 2$, $P < 0.001$), and as with diet richness and $\delta^{13}\text{C}$, models including the effects of SL were not significantly different ($P > 0.05$) from the species-only model (Table 3). Bluehead Sucker (12.4, 11.9-12.9) and Razorback Sucker (12.2, 11.7-12.7) had higher $\delta^{15}\text{N}$ compared to Flannelmouth Sucker (10.9, 10.4-11.4). The conditional R^2 for the species-only $\delta^{15}\text{N}$ model was 0.24, and the fixed effect of species accounted for 75% of the variation explained by the model (marginal $R^2 = 0.18$). Similar to $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ of Bluehead Sucker decreased significantly with SL (slope = -0.375, $df = 48$, $P < 0.001$), and did not differ for Flannelmouth (slope = 0.002, $df = 45$, $P = 0.964$) or Razorback (slope = -0.315, $df = 46$, $P = 0.077$) Suckers.

Discussion

Rather than finding high overlap in diets of ELS suckers, we found differences in diet richness and composition among the three species. Specifically, intraspecific variation in diet

item composition across individual Razorback Sucker drove the majority of variation among species. Although diet differences among species was confounded by differences in SL (see below), the complete lack of certain diet item categories from Razorback Sucker gut contents, while being present in the other two species, is particularly interesting to us. For example, adult dipterans (e.g., chironomids) were not present in Razorback Sucker diets, but were present in 20% of Bluehead Sucker and 32% of Flannelmouth Sucker, suggesting these individuals foraged at the water surface. Conversely, sand was also absent from Razorback Sucker but present in 22% and 24% of Bluehead and Flannelmouth Suckers, respectively, suggesting benthic feeding. These results suggest differences in feeding ecology of ELS suckers might include differential habitat use and potentially resource partitioning (Markle and Clauson 2006), whereby Bluehead and Flannelmouth Suckers feed at both the water surface and in the benthos, but Razorback Sucker might be more limited in their foraging behavior. Markle and Clauson (2006) found ontogenetic diet shifts in ELS Shortnose Sucker *Chasmistes brevirostris* and Lost River Sucker *Deltistes luxatus* that suggested a shift from surface to more benthic feeding as fish grew larger. Thus, diet items suggestive of both surface and benthic feeding could be related to a wider range of individuals from different developmental stages and sizes rather than species partitioning resources.

The differences in size and developmental stage exhibited by fishes in our study could explain potential differences in resource use, rather than innate differences in feeding ecology across species. It has been hypothesized that ELS fish increase trophic niche breadth as they grow, which leads to higher chances of survival (Fuiman 2002). Werner and Gilliam (1984) referred to this as the ontogenetic niche, which describes changes in resource use patterns across developmental stages. One potential change in the ontogenetic niche occurs when the range of

prey types (i.e., diet richness) increases with body size, but the niche of larger individuals includes that of smaller individuals (Wilson 1975; Werner and Gilliam 1984; Gill 2003). This idea might apply to results from this study where Razorback Sucker were the shortest, least developed, and had the lowest diet richness. Conversely, Bluehead and Flannelmouth Suckers had the highest diet richness and also had a wider range of SL and developmental stages relative to Razorback Sucker. However, Flannelmouth Sucker were larger on average than Bluehead Sucker, but we did not observe differences in diet richness between these species. Thus, the ontogenetic niche of Bluehead Sucker and Flannelmouth Sucker was larger, but included that of Razorback Sucker. Based on ontogenetic niche shifts, differences in species life history such as egg size, size at hatching, and developmental rate could play an important role in determining resource use in early life which could ultimately affect recruitment.

In addition to differences in diet composition based on gut content analysis, we also found substantial overlap, but still significant differences among species based on stable isotope analysis. Flannelmouth Sucker displayed the most variation in trophic resource use, and this appeared to be driven by variation in $\delta^{13}\text{C}$ across sites. Flannelmouth Sucker at S2 and S4 had lower $\delta^{13}\text{C}$ compared to individuals of all three species across other sites. However, individuals with the lowest $\delta^{13}\text{C}$ of Bluehead and Razorback Suckers also occurred at S4. Gido et al. (2006) found $\delta^{13}\text{C}$ of primary consumers (e.g., EPT) decreased from upstream to downstream in the San Juan River possibly due to differences in current velocity among habitats (Finlay et al. 1999). Because all five sites in the current study occurred in a canyon-bound, high gradient reach of river we might expect minimal variation in $\delta^{13}\text{C}$, but differences in local site characteristics (e.g., connection to the main-channel) could have contributed to observed variation in $\delta^{13}\text{C}$. Another possibility is the contribution of riparian plant resources to the food web could differ spatially

along the river and across sites. Based on $\delta^{15}\text{N}$ of fish in this study, it appears ELS fish are not feeding directly on primary producers and variation in $\delta^{13}\text{C}$ could be driven by variation in diets of lower trophic level groups such as aquatic insects or zooplankton. Pease et al. (2006) hypothesized $\delta^{13}\text{C}$ variation in larval fish could be due to diet switching by invertebrate grazers between benthic algae and other carbon sources such as emergent macrophytes. Benthic algae is thought to be the major carbon source for fish in arid-land rivers (Bunn et al. 2003; King 2004; Pease et al. 2006), but in the San Juan River, Gido et al. (2006) concluded detritus from terrestrial sources were the major source for juvenile and adult fishes. $\delta^{13}\text{C}$ of ELS fish measured in this study suggest carbon sources might vary substantially even within river reaches having similar habitat characteristics, and might be driven by variation in diets of lower trophic level consumers.

Differences in $\delta^{15}\text{N}$ among species was consistent across sites, but seems related to ontogenetic stage rather than diet. Specifically, larger Flannelmouth Sucker had significantly lower $\delta^{15}\text{N}$ relative to Bluehead and Razorback Suckers. Although we lack data on baseline trophic resources, higher $\delta^{15}\text{N}$ in Bluehead and Razorback Suckers suggest these species might be feeding at a higher trophic level, which was not supported by gut content data. Alternatively, smaller and less developed ELS fish might be more susceptible to starvation (i.e., in the “critical period”), such that, higher mean $\delta^{15}\text{N}$ in Bluehead and Razorback Suckers could be a result of catabolism of body tissues (Gannes et al. 1997; Gaye-Siessegger et al. 2007). Gaye-Siessegger et al. (2007) found starved Nile Tilapia *Oreochromis niloticus* and those fed a maintenance-only ration had higher $\delta^{15}\text{N}$ compared to fish fed above maintenance. Another and more likely alternative is, ELS fishes have high $\delta^{15}\text{N}$ and experience rapid depletion of the heavy nitrogen isotope as they transition to juveniles (Vander Zanden et al. 1998). Vander Zanden et al. (1998)

found a strong pattern in ELS Smallmouth Bass *Micropterus dolomieu* where embryos had high $\delta^{15}\text{N}$, but $\delta^{15}\text{N}$ declined rapidly until larvae made the transition to the juvenile stage. Parental contributions of $\delta^{15}\text{N}$ were predicted to be the cause of this pattern. A similar phenomenon was observed in penguins, where chicks have higher $\delta^{15}\text{N}$ relative to juveniles and adults (Forero et al. 2002). Although we only found a significant relationship between $\delta^{15}\text{N}$ and fish size for Bluehead Sucker, lower mean $\delta^{15}\text{N}$ of Flannelmouth Sucker might be caused by individuals being farther along in development relative to the other two species. Flannelmouth Sucker spawn earlier, have larger eggs, and are typically larger per developmental stage compared to other catostomids in the Colorado River Basin (Weiss et al. 1998; Snyder and Muth 2004). Assessing the relative trophic level of ELS fish might be problematic because $\delta^{15}\text{N}$ can be biased by lag effects from maternal signatures and can change rapidly across developmental stages (Vander Zanden et al. 1998).

During annual monitoring efforts in the San Juan River, few if any juvenile Razorback Sucker have been collected while all stages of Bluehead and Flannelmouth Suckers, including age 1+ fish, are common. This lack of more developed Razorback Sucker in ELS fish collections has been consistent over the entirety (1998-present) of larval fish monitoring in the San Juan River (Barkstedt et al. 2018). In 2007, when fish in this study were assessed, only 200 Razorback Sucker were collected compared to 16,535 Flannelmouth Sucker and 7,996 Bluehead Sucker. Whether this low relative abundance of Razorback Sucker is due to differences among species in their propensity to drift, use of different spawning habitats (i.e., main-channel vs. tributaries; Tyus 1987; Cathcart et al. 2015), a lack of spawning adults (Diver and Wilson 2018), or other factors is unknown. Few data exist on resource availability and potential limitation in rivers of the Colorado River Basin, but the timing and amount of trophic resources are critically important

to the success of ELS fishes (Cushing 1990; Humphries et al. 2013). Future studies might consider linking dynamics of resource availability and ELS fish success in rivers of the Colorado River Basin.

Currently in the San Juan River (and elsewhere in the Colorado River Basin), nursery habitats for ELS fishes (e.g., backwaters) are rare as a result of flow regime modification and establishment of non-native riparian vegetation. The closing of Navajo Dam brought on decreased spring discharge and increased summer flows, in addition to lowered water temperatures from hypolimnetic water releases (Franssen et al. 2007). In the San Juan River, invasive saltcedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia*) have displaced native tree species such as cottonwood (*Populus fremontii*) and black willow (*Salix gooddingii*). A change in bank vegetation coupled with reduced annual flow peaks has contributed to armoring of river banks and the loss of backwater habitats (Nagler et al. 2011; Franssen et al. 2014). This loss of rearing habitat has reduced available space and likely concentrated ELS fish into remaining habitats where competition or predation could be intense. Alterations to mainstem rivers elsewhere have been linked directly to recruitment bottlenecks experienced by imperiled species (Humphries et al. 2002; Guy et al. 2015), but our understanding of how river regulation has impacted ELS fish is lacking for many species.

In this study, diet differences among seemingly similar ELS fishes suggest differences in feeding ecology. How fish respond to the critical period of early life, whether they succumb to it or survive it, can influence population and community dynamics (Houde 1994; Freeman et al. 2001). Early life stage fishes are largely presumed to rely on similar resources, but differences among species during these delicate life stages could explain differential responses at the population level to habitat alteration and repatriation efforts (e.g., Mueller and Wydoski 2004).

Negative interactions with nonnative fishes are the most commonly hypothesized factor contributing to imperilment of native fishes in the Colorado River Basin (Minckley et al. 2003). If predation by nonnative fishes is the primary cause for the complete lack of recruitment by Razorback Sucker, then why have Bluehead Sucker and Flannelmouth Sucker not suffered similar fates? Habitat alteration and loss have also been hypothesized as contributing to the decline of “big-river” species in the Colorado River Basin, but thus far mechanistic understanding of specific factors limiting recruitment of species such as Razorback Sucker remains elusive. Along with altering habitats for fishes, river regulation has impacted prey communities of ELS fishes (e.g., Kennedy et al. 2016), potentially leading to mismatches in ELS fish occurrence and prey availability. Other studies have assessed trophic resource use of ELS Razorback Sucker in artificial habitats (e.g., reservoirs; Marsh and Langhorst 1988; Papoulias and Minckley 1992), but this is the first study to quantify trophic resource use in riverine habitats and compare it to other native species. Comparative studies that include similar species showcasing differential responses to habitat alteration can help place results in context that would otherwise be lacking from single-species investigations.

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Figures

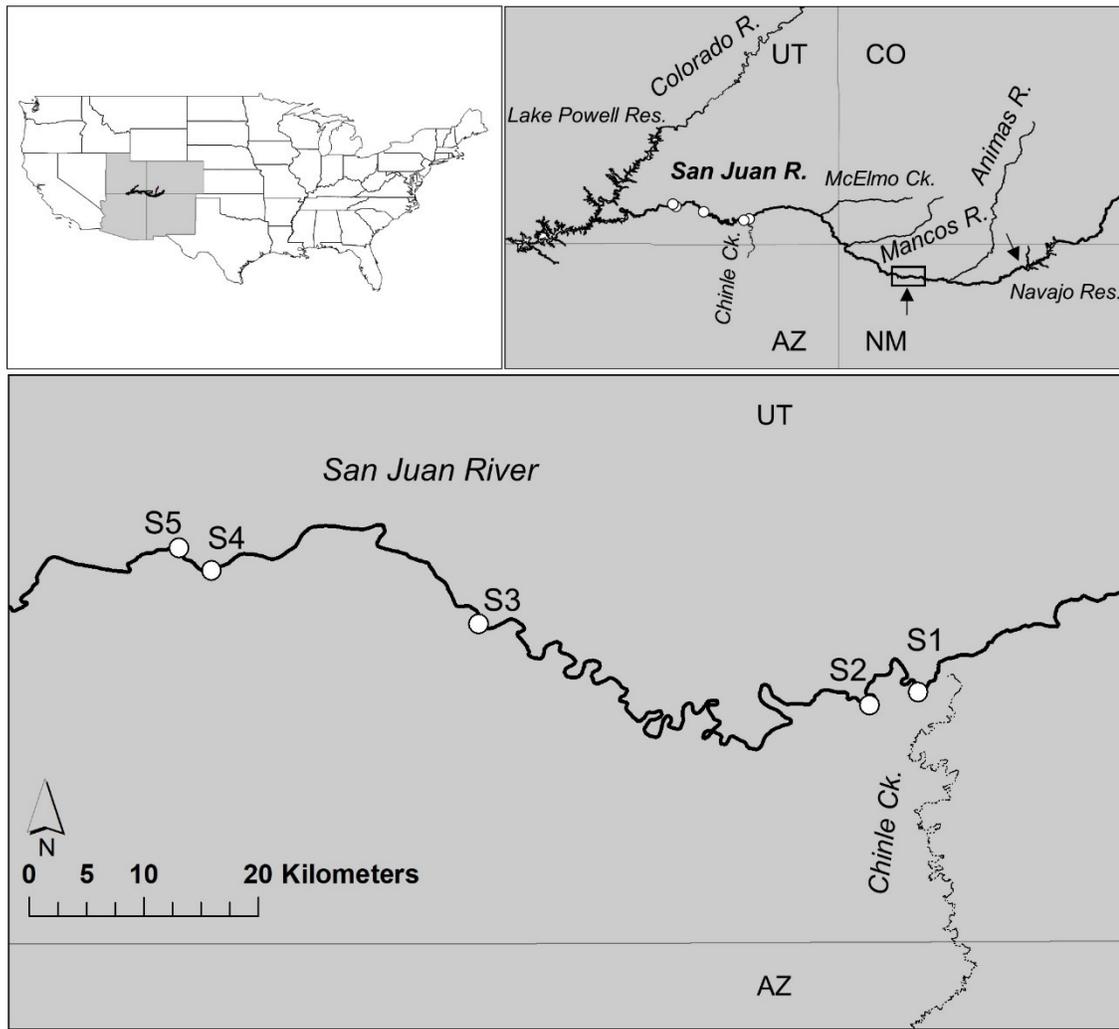


Figure 2.1—The San Juan River basin is located in the four corners region of the American Southwest (top left). The San Juan River is fragmented by a hydropower dam and associated water storage reservoir (i.e., Navajo Reservoir) and several smaller weirs located between the Animas and Mancos river confluences (top right, identified with arrows). Sites of larval fish collections occurred in a downstream, canyon-bound portion of the river (bottom

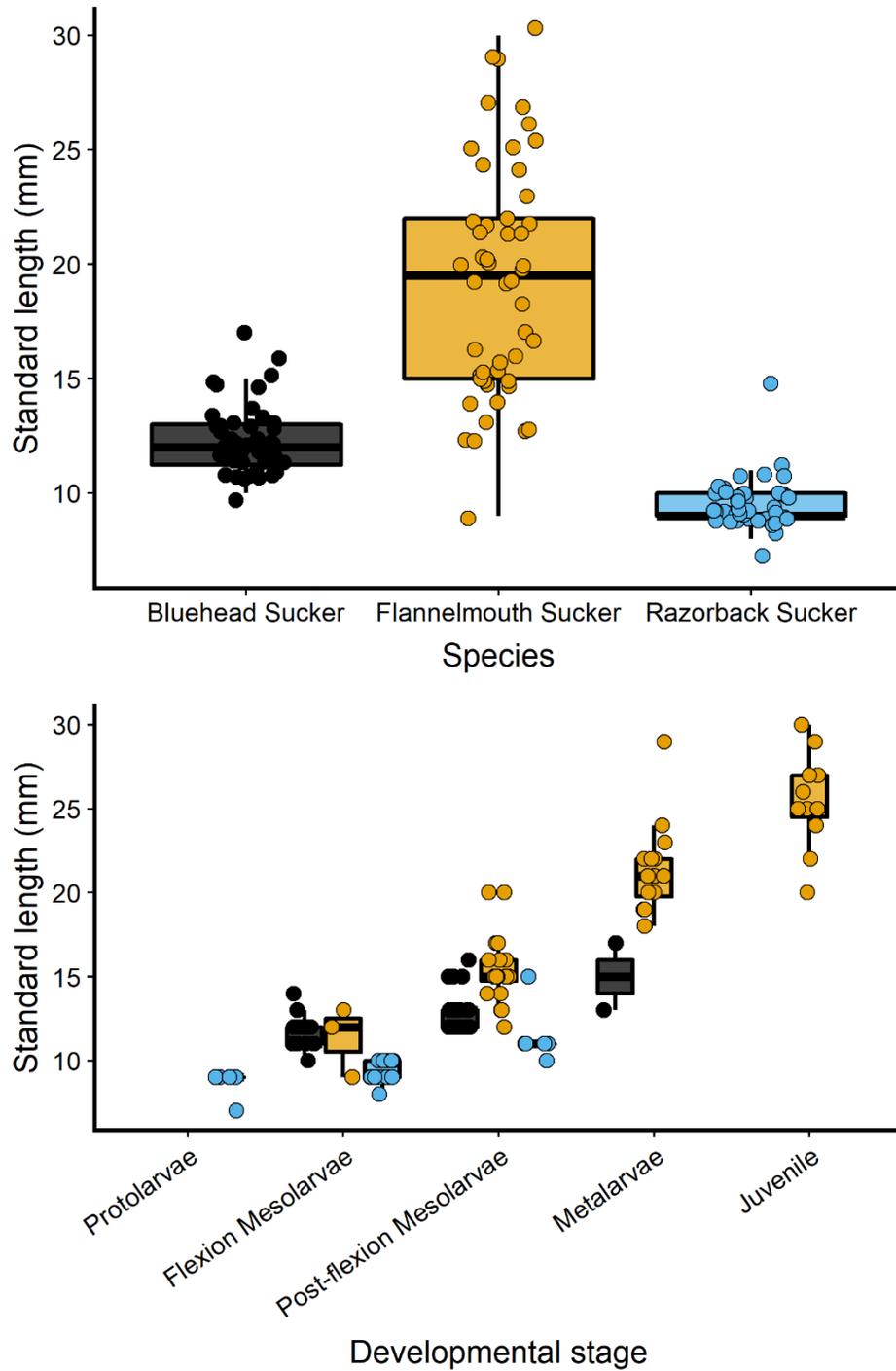


Figure 2.2—Standard length (mm) was significantly different (ANOVA on ranks: $P < 0.001$) among all species (top). Razorback Sucker always had the shortest standard length per developmental stage (bottom). Solid lines represent medians

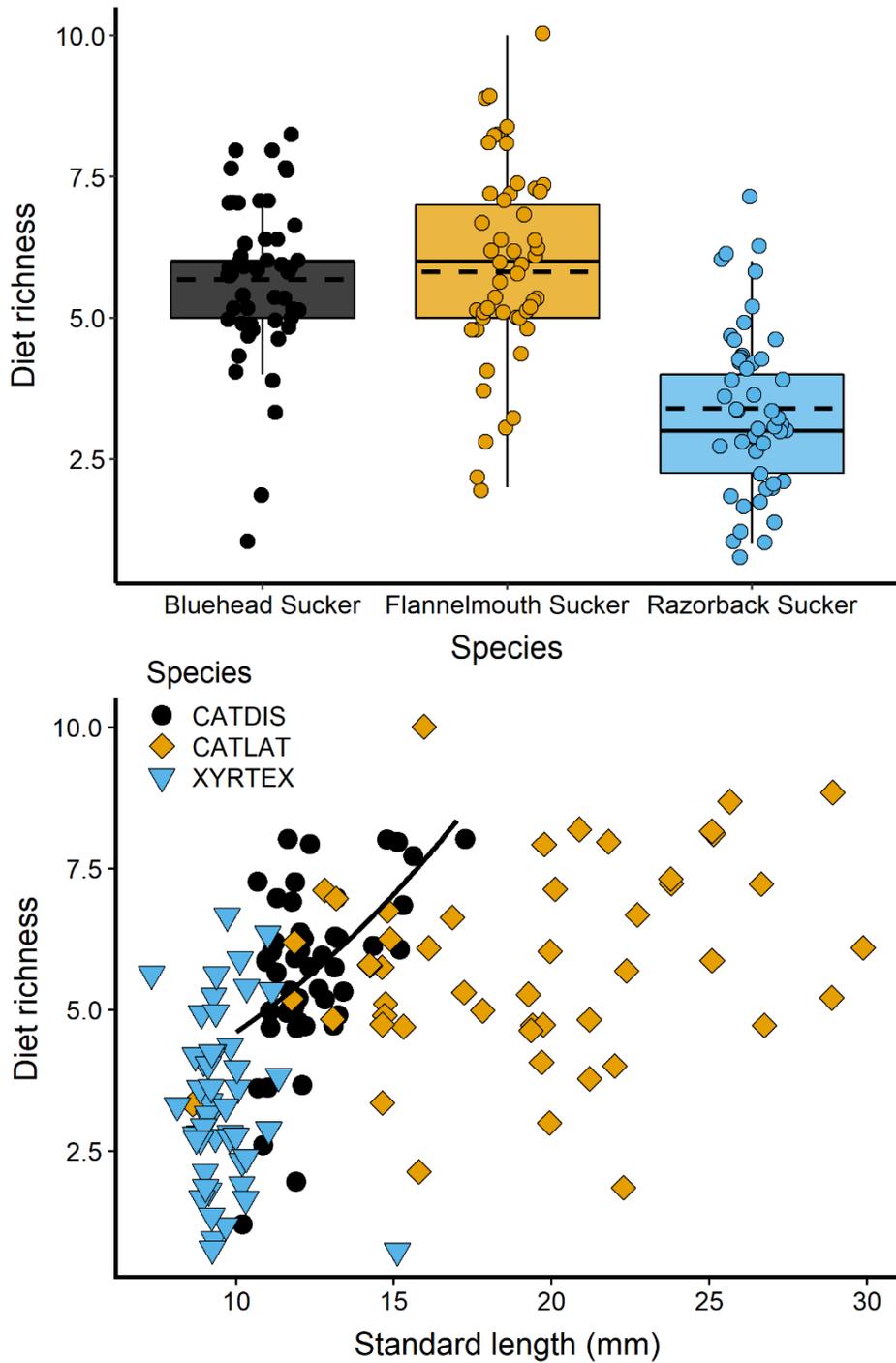


Figure 2.3—Top panel) Diet richness (number of diet item categories in gut) differed significantly among species (likelihood ratio: 39.7, $P < 0.001$) with Razorback Sucker being lower than both Bluehead and Flannelmouth Suckers. Solid lines represent medians and dashed lines represent

means. The 95th, 75th, 25th, and 5th percentiles are represented respectively by the upper whisker, upper box edge, lower box edge, and lower whisker. Top panel) Diet richness increased significantly with length for Bluehead Sucker ($P = 0.029$), but not Flannelmouth ($P = 0.158$) or Razorback ($P = 0.460$) Suckers. A small amount of jitter was added to individual points in both panels to reduce overlap and show sample sizes

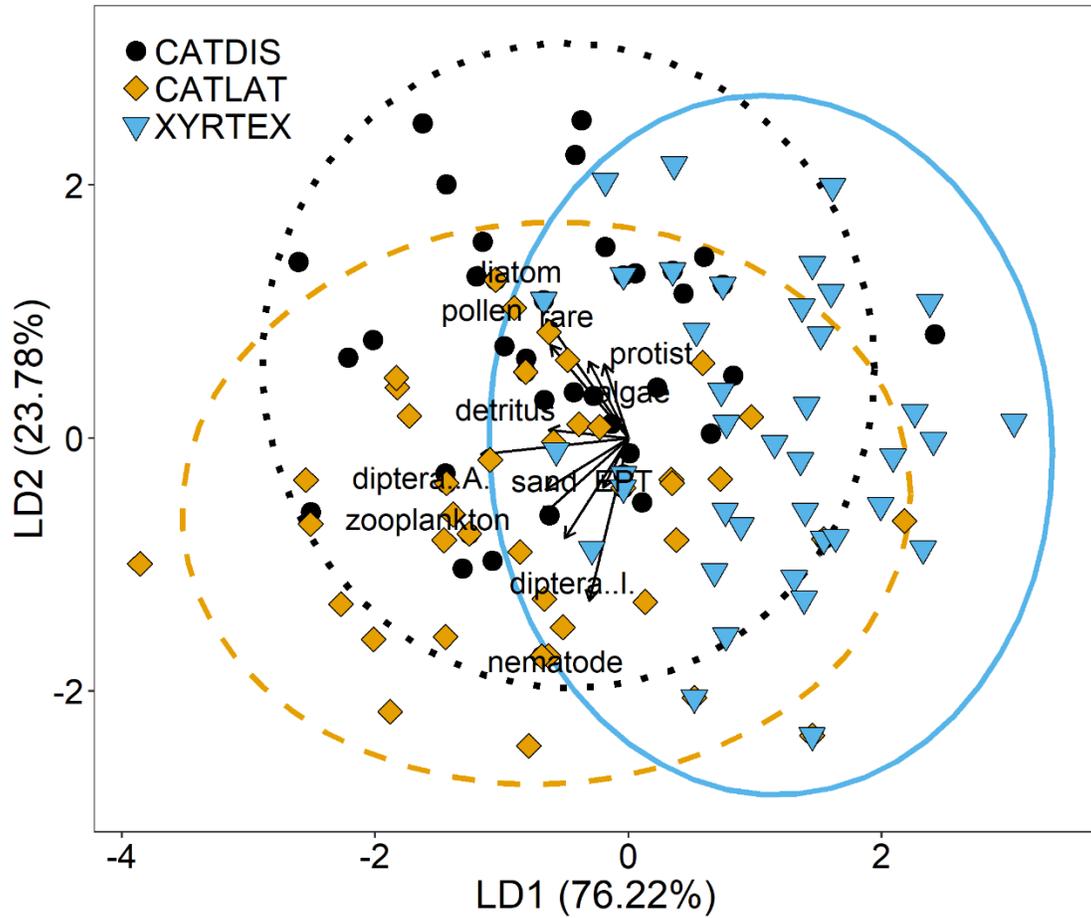


Figure 2.4—Discriminant function analysis biplot of early life-stage diet compositions among Bluehead (CATDIS), Flannelmouth (CATLAT), and Razorback Suckers (XYRTEX). The first discriminant function explained 76.22% in variation among groups and largely separated Razorback from both Bluehead and Flannelmouth Suckers. The second discriminant function separated Bluehead Sucker from Flannelmouth Sucker, and explained the remaining 23.78% of variation. See Table 2 for significance of individual diet item categories. Ellipses are 95% confidence ellipses calculated from a multivariate normal distribution

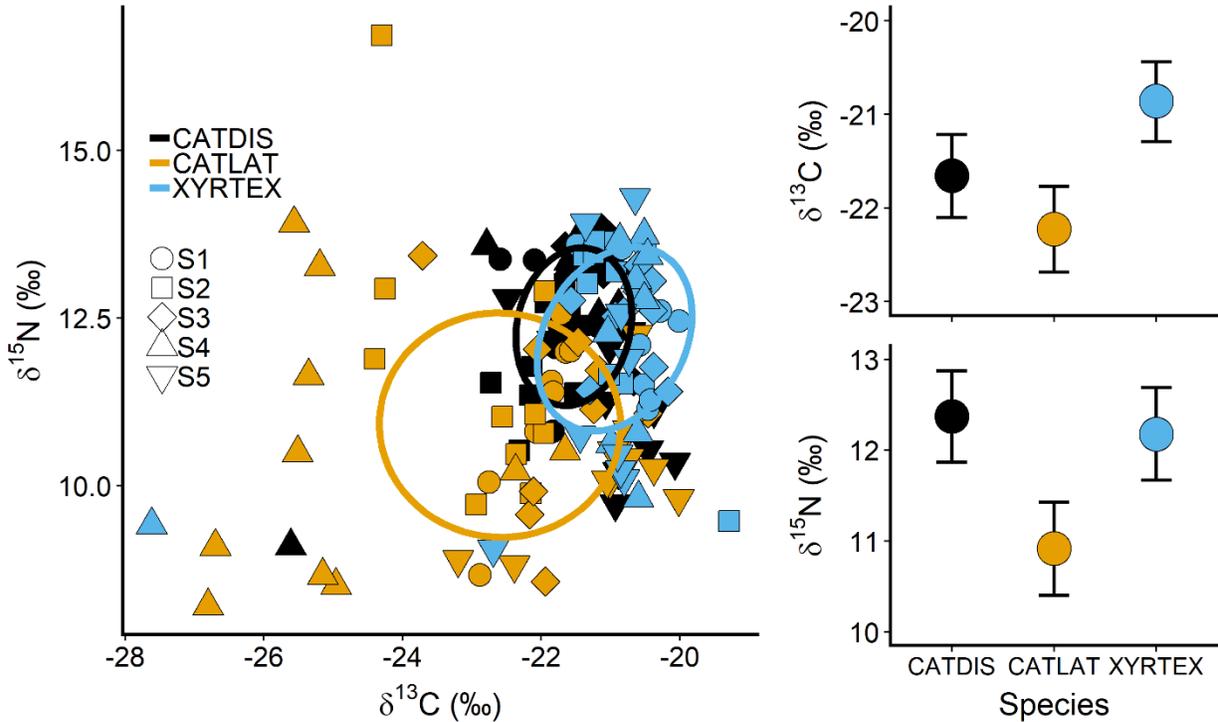


Figure 2.5–Bivariate plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (left) of co-occurring early life stage Bluehead (CATDIS), Flannelmouth (CATLAT), and Razorback (XYRTEX) Suckers from five sites in the San Juan River, Utah. Sites are represented by different symbols and standard ellipses were corrected for sample size (SEAc) and calculated using the SIAR package (Parnell and Jackson 2013) in Program R. Flannelmouth Sucker had the largest isotopic niche breadth (SEAc = 9.15) compared to Bluehead Sucker (3.06) and Razorback Sucker (4.65). $\delta^{13}\text{C}$ (top right) differed among species. Bluehead and Razorback Suckers had higher $\delta^{15}\text{N}$ (bottom right) compared to Flannelmouth Sucker. Values represent least squares means \pm 95% CI

Tables

Table 2.1—Abundance (relative abundance, %) of early life-stage Bluehead, Flannelmouth, and Razorback Suckers collected in five backwaters from the San Juan River, Utah. River kilometers were calculated using the Piute Farms Waterfall (Cathcart et al. 2018) as zero to match river maps used by biologists with the San Juan River Basin Recovery Implementation Program. The total abundance of all fish and the percent sucker abundance is also presented. Specimens were catalogued in the Division of Fishes, Museum of Southwestern Biology (MSB) research collection.

MSB catalogue numbers	Site	River km	Sucker abundance			Assemblage abundance	
			Bluehead Sucker	Flannelmouth Sucker	Razorback Sucker	Total abundance	Percent sucker
63698, 63699, 63700	1	109.0	331 (73)	22 (5)	17 (4)	454	81%
63712, 63713, 63714	2	100.3	602 (89)	29 (4)	13 (2)	680	95%
63496, 63497, 63498	3	39.4	45 (49)	11 (12)	13 (14)	92	75%
63530, 63531, 63532	4	18.5	58 (52)	10 (9)	19 (17)	112	78%
63460, 63461, 63462	5	16.1	36 (18)	109 (56)	17 (9)	196	83%

Table 2.2—Mean frequency of occurrence of diet item categories for Bluehead, Flannelmouth, and Razorback Suckers collected from five backwaters in the San Juan River, Utah. Diet item categories were used as predictor variables in a discriminant function analysis (DFA) to classify sucker species. Overall, the DFA model classified sucker species correctly 65% of the time. Multiple comparisons were corrected using a false discovery rate correction (Benjamini and Hochberg 1995).

Diet item category	Species			<i>P</i> -value	<i>Total frequency of occurrence</i>	Coefficients of linear discriminants	
	Bluehead Sucker <i>n</i> =50	Flannelmouth Sucker <i>n</i> =50	Razorback Sucker <i>n</i> =50			<i>LD1</i>	<i>LD2</i>
algae	0.80	0.78	0.58	0.019	0.72	-0.15	0.22
detritus	0.90	0.94	0.68	< 0.001	0.84	-0.78	0.08
diatom	0.80	0.58	0.46	0.002	0.61	-0.81	1.17
diptera (a) ^a	0.20	0.32	0.00	< 0.001	0.17	-1.46	-0.16
diptera (i) ^b	0.62	0.84	0.42	< 0.001	0.63	-0.63	-0.99
EPT ^c	0.02	0.12	0.12	0.114	0.09	-0.25	-0.49
Nematode	0.14	0.24	0.06	0.061	0.15	-0.39	-1.61
pollen	0.60	0.44	0.20	< 0.001	0.41	-0.77	0.92
protist	0.42	0.28	0.20	0.065	0.30	-0.24	0.73
sand	0.22	0.24	0.00	< 0.001	0.15	-0.81	-0.51
zooplankton	0.72	0.84	0.62	0.076	0.73	-0.87	-0.78
rare ^d	0.24	0.20	0.06	0.037	0.17	-0.39	0.76

Table 2.3—Model comparison results using likelihood ratio tests to sequentially compare nested mixed models for diet richness, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. Marginal R^2 values represent the proportion of variation explained by only fixed factors and conditional R^2 values are the proportion of variation explained by fixed and random effects.

Models	marginal R^2	conditional R^2	χ^2 df	Likelihood ratio	P -value
Diet richness ~ 1 + (1 Site)					
Diet richness ~ Species + (1 Site)	0.22	0.22	2	39.65	<0.001
Diet richness ~ Species + SL + (1 Site)	0.23	0.23	1	3.32	0.068
Diet richness ~ Species + SL + Species*SL + (1 Site)	0.24	0.24	2	3.77	0.152
$\delta^{13}\text{C}$ ~1 + (1 Site)					
$\delta^{13}\text{C}$ ~Species + (1 Site)	0.45	0.71	2	57.88	<0.001
$\delta^{13}\text{C}$ ~Species + SL + (1 Site)	0.45	0.71	1	0.02	0.876
$\delta^{13}\text{C}$ ~ Species + SL + Species*SL + (1 Site)	0.44	0.73	2	2.72	0.256
$\delta^{15}\text{N}$ ~1 + (1 Site)					
$\delta^{15}\text{N}$ ~Species + (1 Site)	0.18	0.24	2	30.06	<0.001
$\delta^{15}\text{N}$ ~Species + SL + (1 Site)	0.18	0.25	1	1.13	0.289
$\delta^{15}\text{N}$ ~ Species + SL + Species*SL + (1 Site)	0.20	0.29	2	5.44	0.066

Chapter 3 - Reservoir inflow areas as hotspots for fish conservation: shifts in arid-land fish assemblage structure across an aquatic ecotone

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Introduction

Reservoir and river fragments are now common in lotic systems (Sabater 2008; Poff 2014; Grill et al. 2019). Despite calls to embrace a more holistic approach that acknowledges the structural and functional connections between rivers and reservoirs, these systems continue to be managed independently (Cowx and Gerdeaux 2004; Miranda et al. 2008; Buckmeier et al. 2014; Wurtsbaugh et al. 2015). Formation of delta areas where rivers flow into reservoirs mimics historically available habitats in unregulated river reaches (Buckmeier et al. 2014; Volke et al. 2015, 2019). Reservoir inflow areas might not be conducive to some species life histories such as drifting early life stages of pallid sturgeon (*Scaphirhynchus albus*) (Guy et al. 2015) or pelagic broadcast spawning minnows (Dudley and Platania 2007; Perkin and Gido 2011; Hoagstrom et al. 2015). However, recent discoveries of recruitment of wild-spawned fish in reservoir inflow areas suggest these habitats could play a role in conservation for some native species in contemporary riverscapes (Albrecht et al. 2010, 2018; Gilbert and Pease 2019). It is not clear what limits species distributions in river-reservoir inflows, but evaluating fish species

distributions along gradients of biotic and abiotic variables where rivers transition to reservoirs might help identify those physical or biological factors that determine species' success.

Reservoirs blend characteristics of lentic and lotic habitats that vary along a gradient of ecosystem novelty from river inflows to the dam (Thornton et al. 1990; Falke and Gido 2006; Gandy and Rehage 2017). This leads to turnover in species distributions as lotic-adapted species are commonly found in upstream riverine and transitional habitats, while more lentic-adapted species are found in downstream lacustrine habitats (Matthews et al. 2004; Yang et al. 2012; Nobile et al. In press). Some species adapted to use both lentic and lotic habitats can occur throughout reservoirs but still might use resources available at the lotic-lentic interface that are now limiting in upstream river fragments (Bestgen et al. 2011; Volke et al. 2015, 2019). There is a need to understand mechanisms governing species distributions and potential interactions in river-reservoir systems where native and non-native species co-occur (Gido et al. 2002; Clarkson et al. 2005; Oliveira et al. 2005). One potential mechanism of coexistence is resource partitioning (Werner et al. 1977; Edds et al. 2002), but a first step in understanding how species partition resources is to measure spatial overlap by quantifying species distributions across environmental gradients (Prchalova' et al. 2008).

Reservoirs are traditionally managed for the production of sport fishes, such as largemouth bass (*Micropterus salmoides*), that are successful in lentic habitats (Hall and Van Den Avyle 1986; Cowx and Gerdeaux 2004; Fischer and Quist 2019). However, successful species in reservoirs also include non-game fishes that possess traits allowing them to use both lentic and lotic habitats, such as benthic omnivores (Gido 2001; Miranda et al. 2008). These traits include the ability to feed in both clear and turbid conditions on pelagic and benthic food resources, and many species move into lotic habitats to spawn (Matthews et al. 2004; Gido et al.

2009; Da Silva et al. 2015). In reservoirs, this group includes rheophilic species (e.g., suckers, carp, catfish, gar) that evolved in large river systems with high habitat complexity and spatiotemporal heterogeneity (Cooke et al. 2005; Miranda et al. 2008). Because of their evolutionary history in complex riverine environments, some species possess traits that allow them to be successful in river-reservoir inflow areas (Edds et al. 2002).

One instance of native fish successfully using river-reservoir inflows occurs in the Colorado River basin in the American Southwest (Albrecht et al. 2018). In reservoirs of the Colorado River basin, razorback sucker (*Xyrauchen texanus*), an endemic, “big-river” species is able to use a variety of habitats including mainstem rivers, smaller tributaries, volcanically impounded waters, and reservoirs (Dalrymple and Hamblin 1998; Albrecht et al. 2018; Cathcart et al. In press) and is the focus of intense conservation and recovery efforts (Schooley and Marsh 2007; Franssen et al. 2014; Marsh et al. 2015). This species now occurs in most major reservoirs in the Colorado River basin, including Lake Havasu, Lake Mohave, Lake Mead (where spawning and recruitment occurs), and Lake Powell (Albrecht et al. 2010; 2018). Although impacts of non-native species and habitat alteration are the leading hypothesized reasons for the decline and continued imperilment of Colorado River basin fishes (Tyus and Saunders 2000; Minckley et al. 2003; Pennock et al. 2018), turbid river-reservoir inflow areas might provide adequate habitat to promote co-existence of multiple life stages of non-native and native species (Johnson and Hines 1999; Albrecht et al. 2018).

There is a need to further understand factors governing the use of river-reservoir inflows by native species and potential negative interactions with non-native predators or competitors that requires assessing the use of these areas by entire fish assemblages. In this study, we asked two overarching questions: 1. How does fish assemblage structure change along the inflow

gradient of the San Juan River and Lake Powell?, and 2. Is there synchrony in distributions of different feeding groups, such as benthic omnivores? We expected to find higher numbers of species and individuals upstream towards the river inflow based on well-documented transitions in habitat, turbidity, and trophic resources that occur along river-reservoir inflows (Thornton et al. 1990; Gido et al. 2002; Buckmeier et al. 2014). We also expected to find overlap in the distribution of species, based on similar habitat and trophic resource use. We predicted that relative abundances of benthic omnivores would be highest towards more riverine portions of the inflow while site-feeding predators would increase moving away from the inflow area.

Methods

Study area

Lake Powell, located in southern Utah and northern Arizona, is the second-largest reservoir in the United States (volume: over 32 billion m³; surface area: over 65,300 ha). The reservoir formed after Glen Canyon Dam on the Colorado River closed in 1963, and first filled to full pool in June 1980. Lake Powell is primarily managed for water storage and hydropower production (<https://www.usbr.gov/uc/water/crsp/cs/gcd.html>). There are two major tributaries that form the main arms of Lake Powell, the Colorado and San Juan rivers (Figure 1). Water levels in the reservoir are seasonally dynamic as natural river flows in the basin are primarily driven by snowmelt run-off. Lowest water levels during the year typically occur in April immediately prior to run-off and peak in July after run-off is complete. There is also considerable variation in water levels among years. For instance, the water level at the start of sampling efforts during this study differed by 11.9 m between 2018 and 2019 (Figure 2). Since filling to capacity, the water level has generally declined (inset Figure 2) as a result of regional drought across the upper Colorado River basin as well as increasing water consumption downstream of

Glen Canyon Dam. Dynamic water levels from variable river inflows have created unique geomorphic structures at the San Juan River inflow including a 6 m tall waterfall that block all upstream movement of fish approximately 30 km upstream of our study area (Cathcart et al. 2018), and multiple decadal droughts have increased riverine habitat upstream of Lake Powell. We used the lower end of Neskahi Bay (0 river kilometers; rkm; Figure 1) as a fixed landmark within the reservoir as a reference point to characterize changes in fish assemblages upstream towards the river inflow along the historic river channel (rkm). Because we ended our sampling in the riverine zone of the reservoir where it was too shallow to access by boat, the distance sampled upstream of that reference point was 8 km farther upstream in 2018 than 2019.

During this study, we sampled fishes along the longitudinal axis of the San Juan River inflow area including two major habitats, the Great Bend of the San Juan River (hereafter Great Bend) and Neskahi Bay (Figure 1). These two areas differed in habitat complexity and in proximity to the riverine, transition, and lacustrine zones of the reservoir (*sensu* Thornton et al. 1990). The riverine zone generally consists of lotic habitat with slowing water velocities and well-mixed water with limited light penetration from inorganic sediments. Sedimentation happens rapidly in the transition zone as water velocities continually slow and light penetration increases such that trophic resources (i.e., phytoplankton and zooplankton) reach their highest levels. This zone is also the most dynamic in spatial location and extent as river inflows and reservoir water level change within and among years. The lacustrine zone occurs farther down-reservoir and is characterized by an increase in light penetration, lower concentrations of available nutrients, and longer water residence time. The Great Bend was more representative of the riverine and transition zones with habitat becoming more lacustrine downstream towards the lower end of Neskahi Bay. The Great Bend is canyon-bound, shorelines are relatively

homogenous, and substrates mainly consist of sand and silt deposited by river-inflows. Neskahi Bay has more complex shorelines that differ between the north and south sides. The north shoreline has coarser boulder-sized substrates with steeper slopes, while the south shoreline has many coves and inlets with relatively fine gravel-sized substrates and shallower slopes (Figure 1). The main environmental gradients from the upstream end of the Great Bend to the lower end of Neskahi Bay were turbidity from sediment deposition and primary production and water depth. Distance along the historic river channel from the lower end of Neskahi Bay served as a latent variable representative of well-established environmental gradients (e.g., turbidity, phytoplankton biomass), which were present in our study area (Figure 2).

Fish sampling

Fish sampling took place bi-weekly starting in late April and ending in early June in 2018 and 2019 ($n = 3$ weeks per year). The fish assemblage in the San Juan River inflow area was sampled using stationary trammel nets (45.2 m long x 1.2 m tall with 2.5 cm internal and 30.5 cm external panels) set systematically along the shoreline. Using ArcMap (Esri, Redlands, CA), we delineated the shoreline into 500 m segments (Figure 1). Each 500 m segment was sampled weekly, but the number of segments sampled differed among years because of water level fluctuations in the reservoir (Figure 2). Because shoreline habitat was relatively homogenous in the Great Bend, we alternated which shoreline nets were set at for a given 500 m segment, unlike in Neskahi Bay where every 500 m segment was sampled along both shorelines. Trammel nets could be set at any point within a 500 m segment to allow for flexibility in net placement due to wind and local habitat conditions uncondusive to setting nets (e.g., boulder fields). Both daytime and overnight sets were used in Neskahi Bay, and with few exceptions in the first two weeks in 2018. Only daytime sets were used in the Great Bend because of high fish densities. Nets were

generally set in the morning and retrieved in late-afternoon (i.e., 0900 – 1500 hours) for daytime sets, and set in early-evening and retrieved in early-morning (i.e., 1800 – 0900 hours) for overnight sets. To ensure individual shoreline segments were not sampled only during the daytime or nighttime, we offset our starting point each week. We generally began sampling each week towards the downstream end of our study area and worked upstream; exceptions being when wind conditions were not conducive to starting in the same area. A subset of individuals of each species was measured to the nearest mm for total length (TL). Trammel nets can be selective for larger size classes of fish (Hubert et al. 2012), so we consider our results to be mainly reflective of larger-bodied individuals. Although we did collect individuals < 200 mm TL of most species, 90% of all individuals were > 200 mm TL.

Statistical analysis

Spatial variation in number of species and total individuals captured-All analyses were performed in R version 3.5.1 (R Core Team 2018). We excluded species that occurred in < 3 net sets from all analyses ($n = 3$ species and 1 hybrid sunfish; Table 3.1), retaining 15 species for analyses. To assess assemblage structure along the river-reservoir inflow, we calculated species richness and total individuals captured as the total number of species captured per net and total number of individuals captured per net, respectively. Because fish activity could differ over the diel period, potentially changing susceptibility to capture, we tested for differences ($\alpha = 0.05$) in total individuals captured between daytime and overnight net sets and sites using ANOVA. We analyzed years separately because overnight net sets were not used in the Great Bend in 2019. We included the effects of netting period (day or night), site, and their interactive effects for 2018. We were only able to test the effect of netting period for 2019. We accounted for variable effort among net sets by dividing the number of individuals captured by the number of hours nets

were deployed to obtain the number of individuals captured per hour. We log-transformed (base 2) data to improve normality. To assess changes in assemblage structure along the longitudinal axis of the inflow area, we used distance (rkm) as a continuous predictor variable in least-squares regressions and multivariate GLMs. Years were analyzed separately because of differences in water level. We used linear regression to assess changes in number of species captured per hour and total number of individuals captured per hour along the longitudinal axis of the river inflow. Again, data were log-transformed (base 2) to improve normality.

Fish assemblage composition-We took a modeling-based approach to assess how assemblage structure changed along the longitudinal axis of the reservoir and to quantitatively assess species-specific distributions. The manyGLM function in the mvabund package fits individual GLMs to each species using the same set of predictor variables (Wang et al. 2019). The likelihood ratios (*LR*) of each model are summed together (i.e., *Sum of LR*), and this is used to test for an assemblage-level effect with a *P*-value estimated via resampling (Wang et al. 2012). The significance of individual species GLMs can be determined using permutation-based ANOVA with *P*-values corrected for multiple testing. The contribution of each species to the overall assemblage response can be calculated by dividing the *LR* of species-specific models by the *Sum of LR*, which is similar to a SIMPER procedure (Clarke 1993). We used counts of each species in each net set as response variables and river distance along the longitudinal axis of the inflow as a predictor variable in manyGLMs. We modeled raw count data assuming a negative binomial distribution with a log link function, accounting for variable effort by including effort as a covariate. This allowed us to correct for effort within the model rather than prior to by transforming data to catch per unit effort, but still resulted in a measure of species abundance corrected for effort (i.e., relative abundance).

Results

In both years, turbidity from sedimentation (brown) was visible upstream, transitioning to turbidity from presumed phytoplankton production (green), and finally to lowered turbidity (clear water, black in color) downstream, which is suggested by decreased light availability towards the river inflow and can be seen in satellite photos (Figure 1 & 2). In 403 net deployments, we captured a total of 7,218 individuals representing 18 species and one hybrid (Table 1). Only four species were native to the Colorado River basin. Fifteen species made up >99 % of all individuals. Of those 15 species, threadfin shad (*Dorosoma petenense*) were only caught in 2018. On average, we captured 64 % more fish per hour in the Great Bend compared to Neskahi Bay in 2018, and 57 % more in 2019 (Figure 3.3). In 2018, there was a statistically significant interaction between netting period and site (ANOVA: $F_{1,215} = 8.1, P = 0.005$), and there were more fish captured per hour in overnight net sets in Neskahi Bay. There was also a significant main effect of site ($F_{1,215} = 90.6, P < 0.001$). In 2019, the main effect of site was significant ($F_{1,181} = 36.3, P < 0.001$), but day and overnight sets appeared to catch similar numbers of fish in Neskahi Bay. Species captured per hour increased as we sampled closer to the river inflow in both 2018 (Least-squares regression: $F_{1,217} = 60.7, P < 0.001$) and 2019 ($F_{1,217} = 72.9, P < 0.001$; Figure 3.4). Similarly for both 2018 and 2019, total number of individuals captured per hour increased with distance from lower Neskahi Bay (2018: $F_{1,217} = 144.9, P < 0.001$; 2019: $F_{1,182} = 49.8, P < 0.001$; Figure 3.5).

Fish assemblage composition changed along the longitudinal axis of the San Juan River inflow to Lake Powell. Many GLMs suggested there were clear differences (2018: $Sum-of-LR = 529.4, df = 217, P = 0.001$; 2019: $Sum-of-LR = 129.2, df = 182, P = 0.001$) in assemblage structure along the longitudinal gradient of the San Juan River inflow, but there were variable

species-specific patterns among years (Table 2). In 2018, individual GLMs were significant for eight species that contributed to 97.7% of the explained variation in assemblage structure. These included a mix of non-native species and razorback sucker, which increased in relative abundance towards the river inflow (Figure 6). Responses of three species, channel catfish (*Ictalurus punctatus*), gizzard shad (*Dorosoma cepedianum*), and common carp (*Cyprinus carpio*), explained 60.2% of the variation in assemblage structure, and these species also showed clear increases in relative abundance as we sampled closer to the river inflow that mimic the pattern observed for total number of individuals captured (Figure 5 & 6). Only one species, smallmouth bass (*Micropterus dolomieu*), had a statistically significant decrease in relative abundance moving closer to the river inflow and explained 12.1% of the variation in assemblage structure. Many species with relatively high counts in the Great Bend in 2018 exhibited decreased relative abundance in 2019. In 2019, only four individual species GLMs were significant and contributed to 89.7% of the variation in assemblage structure (Table 2). Three species increased moving towards the river inflow, and similar to 2018, included channel catfish and common carp, but also yellow bullhead (*Ameiurus natalis*) (Figure 6). Again, smallmouth bass showed a significant decline in relative abundance moving towards the river inflow.

Discussion

Our study identified clear changes in fish assemblage structure along the longitudinal axis of the San Juan River inflow to Lake Powell with the most striking patterns being predictable increases in number of species and total catch in upstream reaches towards the river inflow. This pattern is consistent with other studies that found increasing reservoir fish density with proximity to tributary inflows (Matthews et al. 2004; Mueller and Horn 2004; Vašek et al. 2004). An increase in species richness towards river inflows is also a pattern commonly found in river-

reservoir inflows and further supports the characterization of these areas as aquatic ecotones (Buckmeier et al. 2014; Da Silva et al. 2019; Nobile et al. In press).

Species-specific distributions differed among years, and this might be explained by lower water level in 2019. Specifically, the transition zone might have extended farther into Neskahi Bay, but the lower end of our study area remained fixed leading to fewer samples from the lacustrine zone in 2019 compared to 2018. This shift in the transition zone is supported by assessing aerial imagery and light intensity data that matches changes in water color associated with a transition of turbidity. Perhaps the resource gradient between the lacustrine and riverine-transition zones was more pronounced in 2018 than 2019. For instance, gizzard shad showed a strong increase in relative abundance in 2018, but in 2019 did not display a statistically significant pattern. If resources associated with the transition zone encompassed more of Neskahi Bay in 2019, and species were tracking resources or water conditions, they would be more likely to be more dispersed throughout our study area in 2019. Consequently, interannual variation in reservoir water level likely influences the spatial distribution of fishes in river-reservoir inflows.

Sampling for this study was only conducted during spring, but seasonal variability in physicochemical variables and local habitat conditions also exist in river-reservoir systems. Indeed, some studies have found high intra-annual variation in fish community structure as a result of highly variable habitat conditions, including water level and connection among habitats in river-reservoir deltas (Buckmeier et al. 2014; Gilbert and Pease 2019; Nobile et al. In press). Because Lake Powell is part of a network of dams across the Colorado River basin primarily managed for hydropower production and downstream water use, water level fluctuates drastically within years, which impacts local habitat conditions and causes shifts in environmental gradients in large reservoirs (Matthews et al. 2004). Annual maximum and annual

minimum water levels in Lake Powell have differed by 7 to 16 m from 2014-2019. Additionally, species distributions in river-reservoir systems shift throughout the year as species complete their life history, moving between reservoirs and inflowing rivers. Some species dwelling in reservoirs or natural lakes undertake spawning migrations into inflowing rivers (Hladík and Kubečka 2003; Childress et al. 2014), and inflow areas can be highly productive nursery habitats and recruitment dynamics can influence fish assemblage structure (Acre 2015; Gilbert and Pease 2019), which we did not assess in this study.

Benthic omnivores drove most of the variation in community structure along the longitudinal gradient of the inflow area. These included species such as common carp, channel catfish, gizzard shad, and yellow bullhead (*Ameiurus melas*), but also razorback sucker. Abundant phytoplankton, zooplankton, and benthic invertebrates that exist in river-reservoir inflows (Thornton et al. 1990; Noguera et al. 2008; Slavevska-Stamenković et al. 2012) might attract species that can feed in highly turbid waters (Drenner et al. 1982; Thornton et al. 1990; Miranda and Lucas 2004). Benthic omnivores are often the most common trophic guild in large reservoirs (Matthews et al. 2004) and are represented by species that typically feed at low trophic levels and are habitat generalists (Gido and Franssen 2007; Gido et al. 2009). The species of benthic omnivores found in our study are able to forage successfully in reservoir environments high in plankton resources such as the transition zone, but also garner energy from detritus and associated bacteria found in sediment biofilms that are also abundant in this zone (Šimek et al. 2001; Gido 2002; Mašín et al. 2003). Thus, river-reservoir inflow areas might provide feeding areas for species able to use low-quality, but highly abundant resources (Gido 2001; Herbert and Gelwick 2003).

Patterns in site-feeding predator distribution matched our predictions for some species, but not others. As expected, we found higher relative abundance of smallmouth bass in more lacustrine-type habitat, downstream from the river inflow, in both years. However, we also found significant increases towards the river inflow for some predators such as striped bass and black crappie (*Pomoxis nigromaculatus*); species that are more typical of lacustrine habitats, which might be responding to areas of higher prey availability, rather than habitat, upstream in the transition-riverine zones. For example, striped bass feed primarily on other fish species, including threadfin shad and gizzard shad, in large reservoirs (Matthews et al. 1988). Although our sampling mainly targeted larger-bodied fishes, river-reservoir inflows provide habitat for smaller-bodied species and early life stages that would be susceptible to predation by piscivorous species (Buckmeier et al. 2014; Gilbert and Pease 2019). Additionally, some predatory species might be using river inflow areas as spawning habitat (Gustaveson et al. 1984; Graeb et al. 2009; Gilbert and Pease 2019). Because of high temporal variability in water levels that affects local habitats in reservoirs (Matthews et al. 2004; Klobucar and Budy 2016), use of river-reservoir inflows by predators might differ substantially among years and be influenced by spawning success of other species and potential spawning migrations.

Habitat heterogeneity created at the upstream end of aging reservoirs by inflowing rivers mimics that of historical river conditions (Volke et al. 2015; 2019) and might provide adequate, albeit somewhat artificial, habitat for the completion of species life histories. This appears to be the case for razorback sucker in nearby Lake Mead (e.g., Albrecht et al. 2010; 2018). Although reservoirs might hinder species with obligate riverine life stages (Guy et al. 2015; Pelicice et al. 2015), there are some species that appear well adapted to the mix of lotic and lentic habitats present in river-reservoir systems (Miranda et al. 2017). For example, species in the family

Catostomidae (suckers) commonly occur in mixed lotic-lentic environments such as reservoirs and floodplain lakes (Miranda and Lucas 2004; Cooke et al. 2005; Miranda et al. 2008). Some species in this family have incurred vast range losses, and many remain unprotected and understudied (Cooke et al. 2005; Budy et al. 2015; Lackmann et al. 2019). Even for those that are protected, such as razorback sucker, understanding of mechanisms allowing their successful use of river-reservoir habitats is limited (Keggeries et al. 2017; Albrecht et al. 2018). River-reservoir inflows might provide refuge habitat where fish can utilize turbid water for cover and also for abundant food resources. Fish also might use these areas if they provide optimal seasonal temperatures. For instance, average monthly water temperature in Lake Powell is generally warmer than the San Juan River inflow from September-February, by as much as 9°C in December (W. Gustaveson, Utah Division of Wildlife Resources, unpublished data; USGS gage data). Finally, river-reservoir inflows can have high vegetation production, which could provide cover and rearing habitat for early life stages (Volke et al. 2015; Strakosh et al. 2009). One potential management strategy in river-reservoir inflows could be to adjust water level to promote growth of vegetation by wetting and subsequently drying river deltas (e.g., Volke et al. 2015). Once vegetation was established water levels could be adjusted to inundate vegetated areas to provide cover and rearing habitat for fish (Strakosh et al. 2009). Habitat loss and degradation caused by dam construction obviously impact native fish populations and assemblages (Guy et al. 2015; Pelicice et al. 2015; Agostinho et al. 2016), but river-reservoir inflows might still provide useful habitats to some native species, such as suckers, and play a role in the conservation of imperiled fishes in modern riverscapes (Miranda and Dembkowski 2016; Miranda et al. 2017).

Reservoirs are common in riverscapes of the Anthropocene epoch and understanding factors governing species-specific distributions along environmental gradients is fundamental to the success of implementing meaningful conservation and management actions in these novel ecosystems (Irz et al. 2006; Miranda et al. 2010; Fischer and Quist 2019). Upstream effects of dams have been understudied relative to downstream effects (Franssen and Tobler 2013; Guy et al. 2015), but upper riverine portions of reservoirs offer complex habitats that can attract fish with diverse habitat and trophic requirements (Miranda et al. 2017; Da Silva et al. 2019; this study). Although dams and reservoirs present challenges for obligate riverine species, some fishes are able to complete their life cycle within these novel habitats. The success of future conservation and management efforts requires identification of specific factors allowing species to be successful in river-reservoir systems. Strategies for conservation and management of native fishes is continually evolving, and by incorporating river-reservoir inflows into management actions, such as management of riverine habitat upstream of reservoirs or stocking of extirpated species in reservoirs (Miranda et al. 2017), it might be possible to assist the recovery of some species.

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Figures

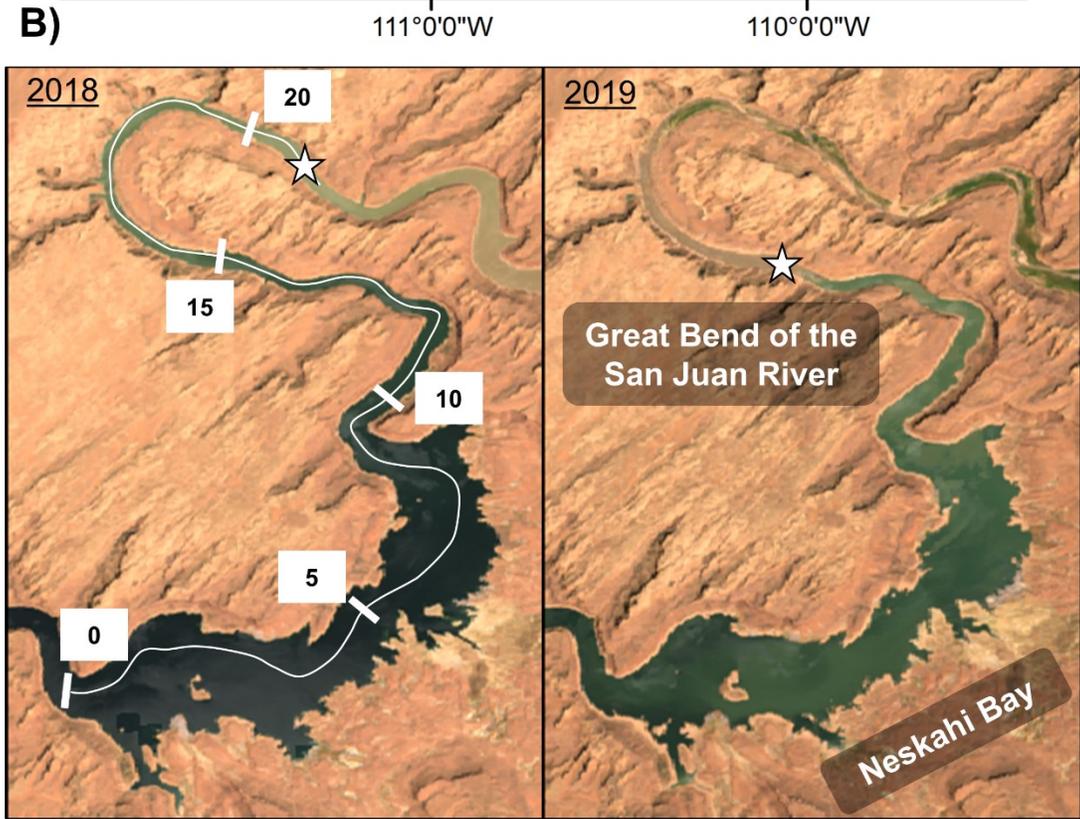
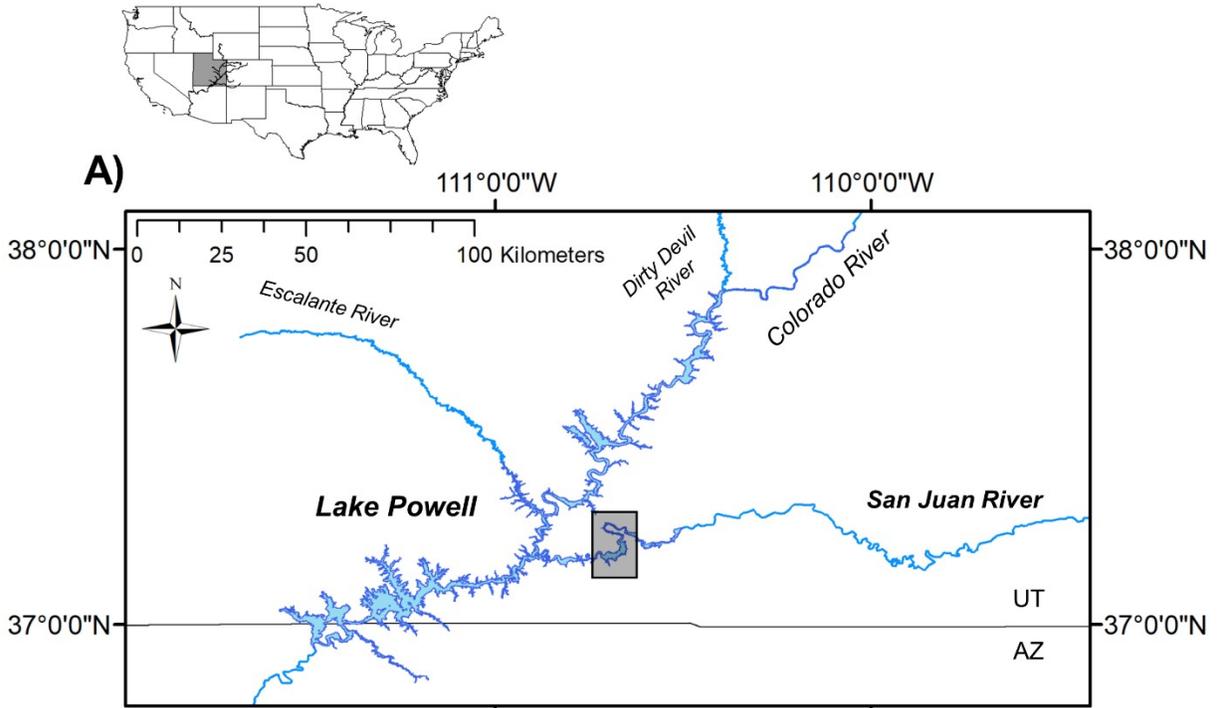


Figure 3.1: Study area map showing: A) the location of Lake Powell in southern Utah and northern Arizona, USA and its major tributaries, and B) the San Juan River inflow where systematic shoreline trammel netting took place in 2018 and 2019 (inset in panel A). There are two major habitats, the Great Bend of the San Juan River and Neskahi Bay, where sampling took place. The white line and associated numbers in panel B represent the historical river channel and were used to calculate river kilometers from the lower end of Neskahi Bay (rkm 0) from a standardized stream layer available from the STReaMS database (available at <https://streamsystem.org/>). Stars represent the upstream extent of sampling in each year.

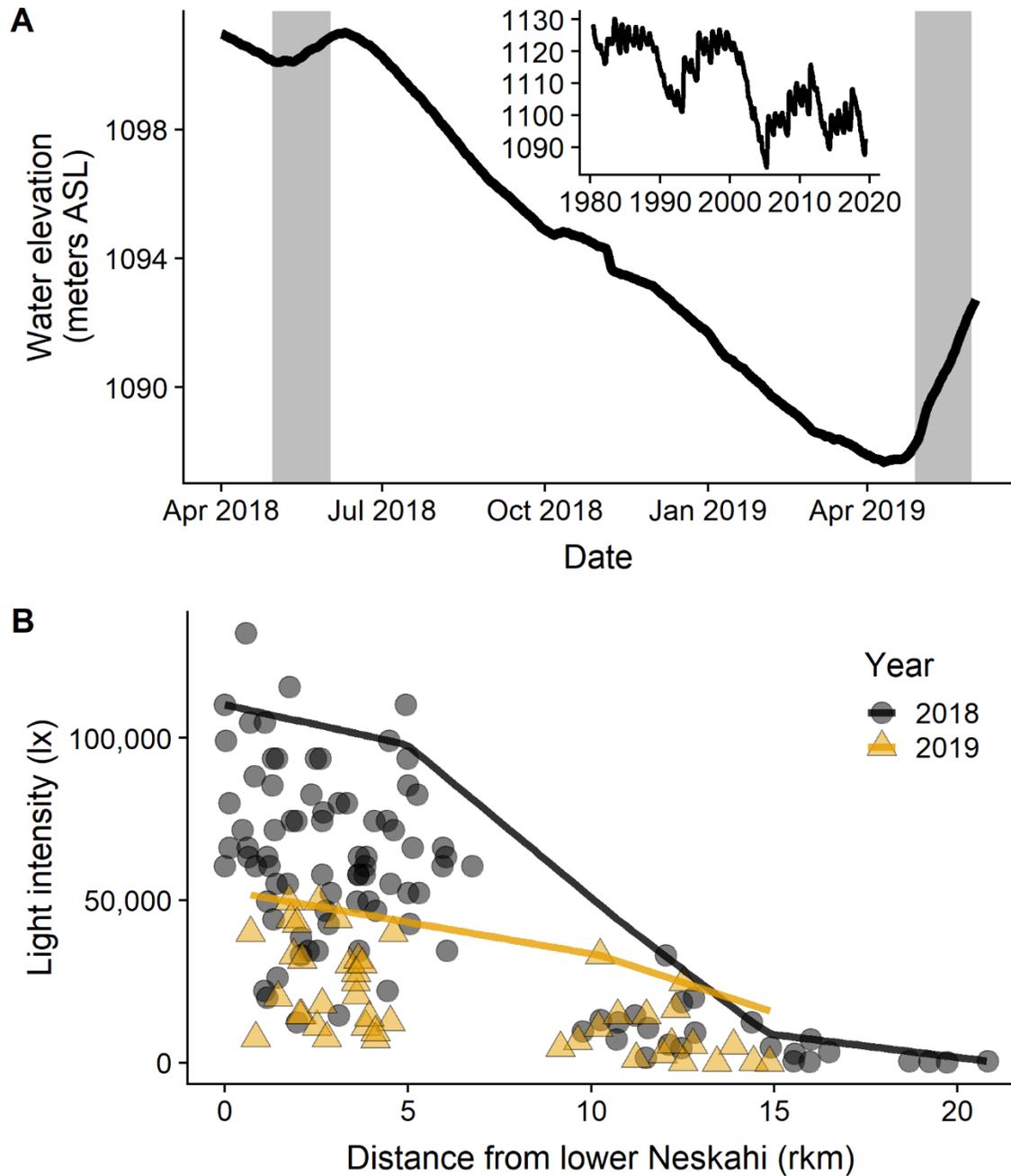


Figure 3.2: A) Daily water elevation (meters above sea level) at Glen Canyon Dam on Lake Powell from April 2018-June 2019. Grey bars represent when sampling occurred in the San Juan River inflow. The inset is water elevation from June 1980, when Lake Powell first reached full pool, to May 31, 2019. B) Light intensity (lx) measured at 1 m depth using HOBO pendants (Onset Computer Corporation, Bourne, MA) during daytime trammel net deployments of the San

Juan River inflow in 2018 and 2019. Measurements were all taken between 1200-1400 h. Lines are 95th additive quantile regressions calculated using the quantreg package in R (Koenker 2019). A small amount of jitter was added to each point to reduce overlap.

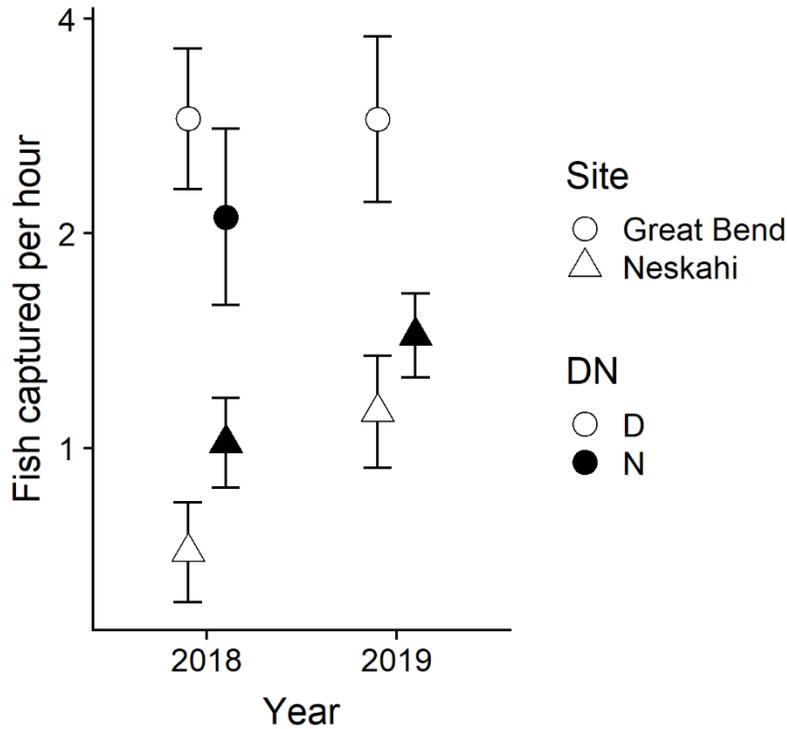


Figure 3.3: A) Number of fish captured per hour during daytime (unfilled) and overnight (filled) trammel net deployments at two major habitats, the Great Bend (circles) and Neskahi Bay (triangles), in the San Juan River inflow to Lake Powell in 2018 and 2019. Y-axis is on a log-scale. In 2018, there was a significant interaction between site and netting period (ANOVA: $F_{1,215} = 8.1, P = 0.005$), where we captured more fish per hour in the Great Bend regardless of netting period but captured more fish in overnight sets in Neskahi Bay. Overnight net sets were not used in the Great Bend in 2019 so we could not test for an interaction, but we captured more fish per hour in the Great Bend ($F_{1,182} = 36.3, P < 0.001$). Statistics were ran on log-transformed data.

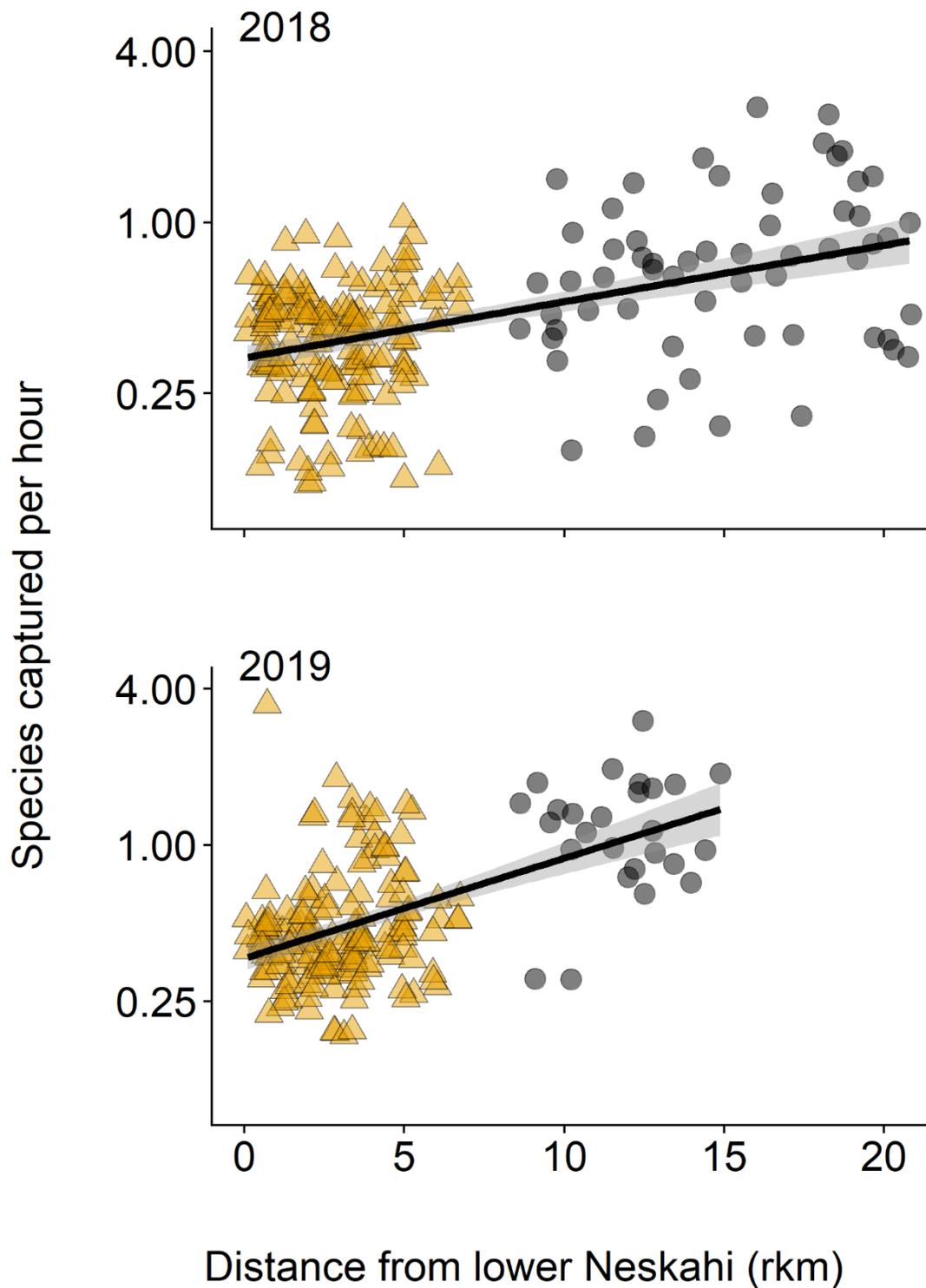


Figure 3.4: Scatter plots of number of species captured per hour as a function of distance from lower Neskahi Bay in 2018 (top) and 2019 (bottom). Y-axes are on a log-scale. Lines and shaded

regions are model estimates and 95% CI from least squares regressions. There was a statistically significant increase in species per hour with distance in 2018 ($F_{1,217} = 60.7, P < 0.001$) and 2019 ($F_{1,182} = 72.9, P < 0.001$). Shapes represent nets deployed in the two major sampling areas, Neskahi Bay (triangles) and the Great Bend (circles). Statistics were run on log-transformed data. A small amount of jitter was added to each point to reduce overlap.

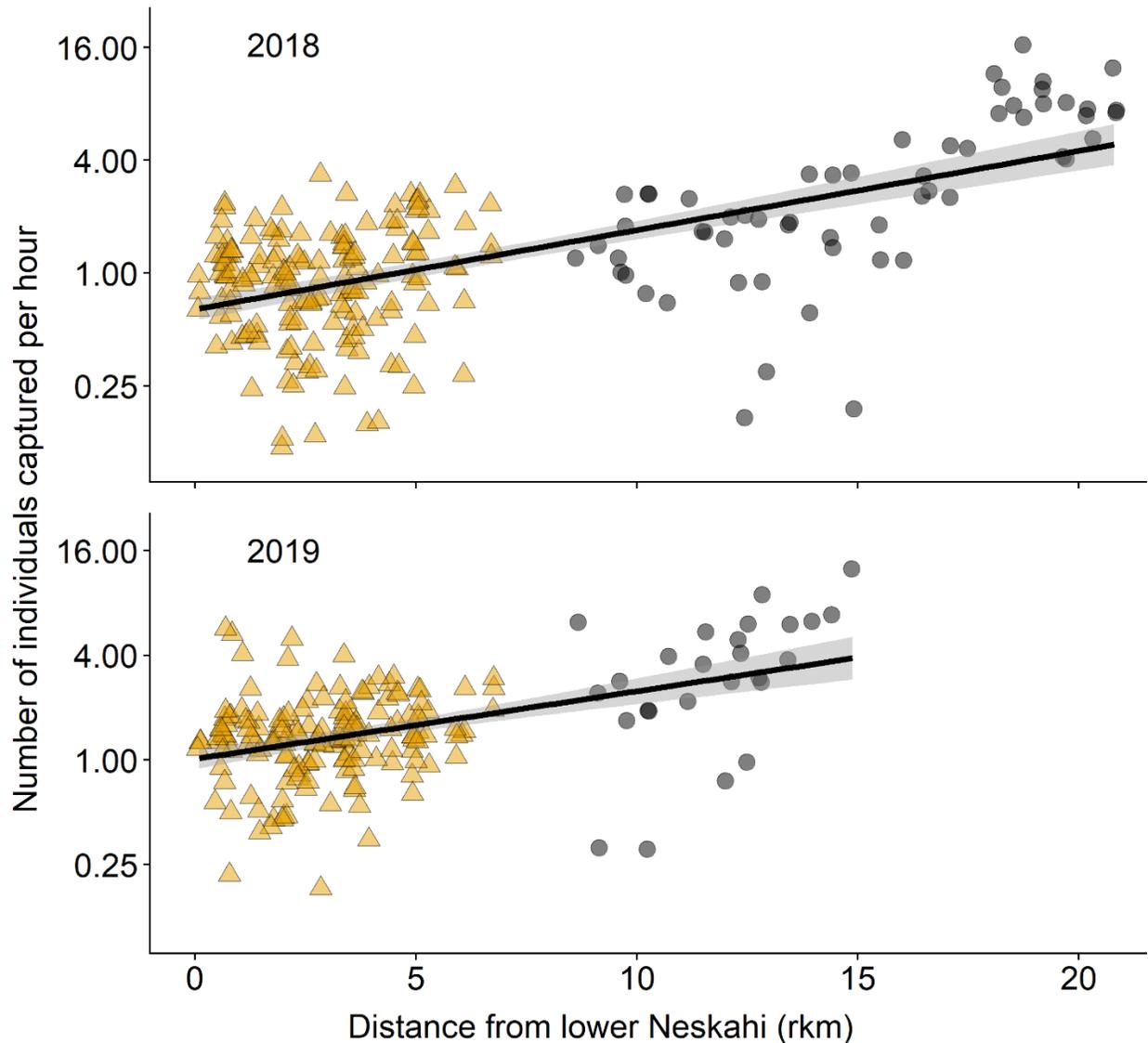


Figure 3.5: Scatterplots of total number of individuals captured per hour as a function of distance from lower Neskahi Bay. Y-axes are on a log-scale. In both 2018 (top; $F_{1,217} = 144.9$, $P < 0.001$) and 2019 (bottom; $F_{1,182} = 49.8$, $P < 0.001$) there was an increase in number of individuals captured per hour as we sampled closer to the river inflow after correcting for effort. Lines and shaded regions are model estimates and 95% CI from least squares regressions of log-transformed data. Shapes represent nets deployed in the two major sampling areas, Neskahi Bay

(triangles) and the Great Bend (circles). A small amount of jitter was added to each point to reduce overlap.

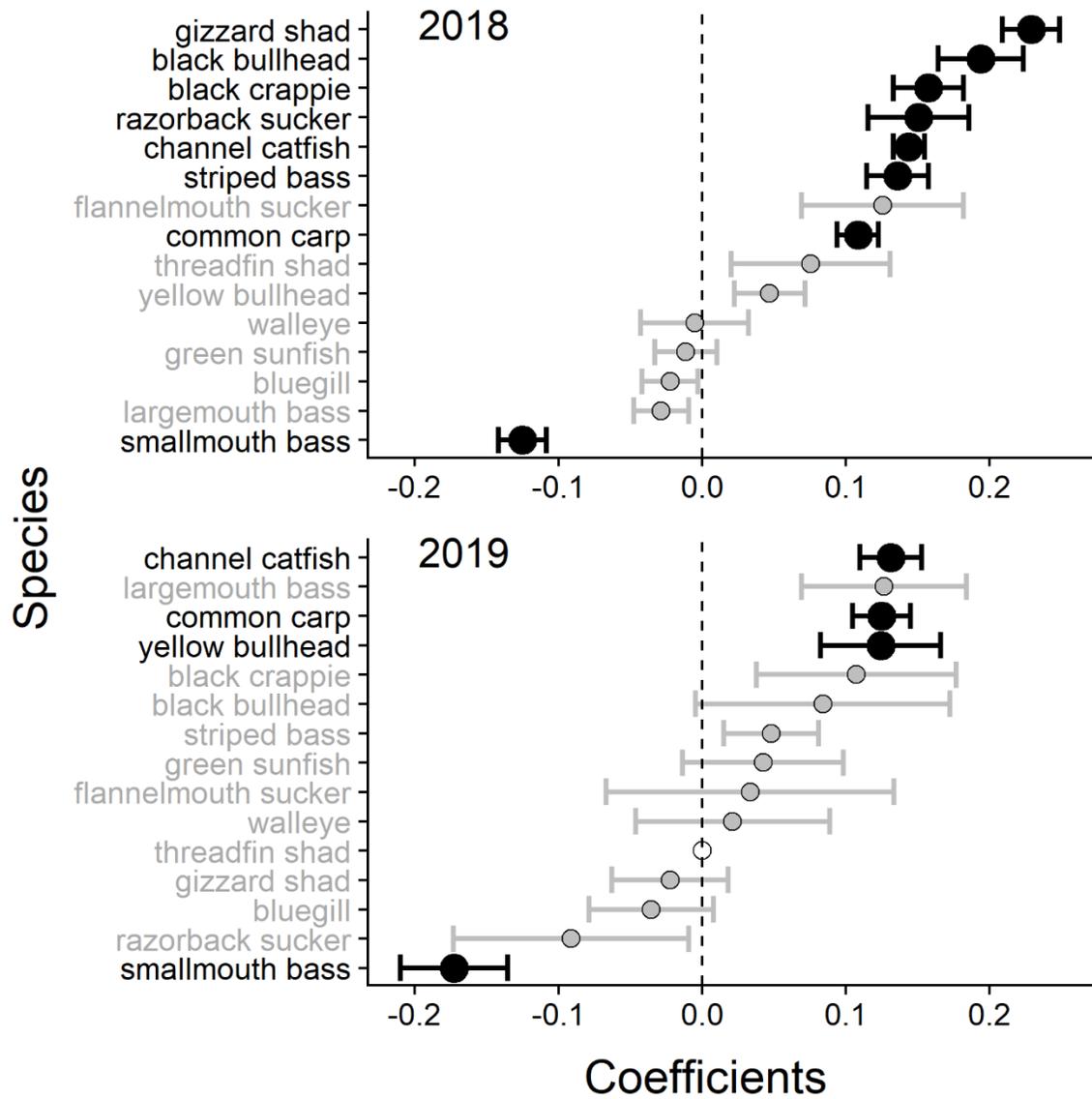


Figure 3.6: Coefficient plots from manyGLM models assessing the effect of distance towards the river inflow on species relative abundance in 2018 (top) and 2019 (bottom). Points are coefficient estimates and error bars represent one SE. Species with a significant ($P < 0.05$) relationship after correcting for multiple testing are shown in black. Threadfin shad were not captured in 2019. The order of Y-axes differs among panels.

Tables

Table 3.1: Total number of individuals, occurrence in nets (n = 403), and sub-sampled total lengths (mm) of species captured during trammel netting in the San Juan River inflow area, Lake Powell, Utah during 2018 and 2019.

Species	Total count	Occurrence in Nets (%)	Total length (mean \pm SD)	Total length (range)	Number in sub-sample (%)
common carp (<i>Cyprinus carpio</i>) ^I	1644	310 (77)	471 \pm 61	146 - 680	989 (60)
channel catfish (<i>Ictalurus punctatus</i>) ^I	1537	297 (74)	299 \pm 74	173 - 750	1067 (69)
gizzard shad (<i>Dorosoma cepedianum</i>) ^I	1454	204 (51)	391 \pm 111	147 - 570	949 (65)
smallmouth bass (<i>Micropterus dolomieu</i>) ^I	615	252 (63)	258 \pm 48	176 - 415	225 (37)
bluegill (<i>Lepomis macrochirus</i>) ^I	432	174 (43)	197 \pm 26	122 - 293	190 (44)
yellow bullhead (<i>Ameiurus natalis</i>) ^I	349	132 (33)	252 \pm 32	154 - 321	263 (75)
striped bass (<i>Morone saxatilis</i>) ^I	344	154 (38)	488 \pm 80	200 - 612	253 (74)
green sunfish (<i>Lepomis cyanellus</i>) ^I	286	129 (32)	185 \pm 29	130 - 295	111 (39)
largemouth bass (<i>Micropterus salmoides</i>) ^I	171	114 (28)	327 \pm 76	202 - 495	61 (36)
black bullhead (<i>Ameiurus melas</i>) ^I	118	51 (13)	221 \pm 34	148 - 310	89 (74)
black crappie (<i>Pomoxis nigromaculatus</i>) ^I	95	61 (15)	191 \pm 52	140 - 370	71 (74)
walleye (<i>Sander vitreus</i>) ^I	80	60 (15)	462 \pm 71	244 - 644	48 (60)
razorback sucker (<i>Xyrauchen texanus</i>) ^N	62	45 (11)	494 \pm 54	345 - 584	58 (94)
flannelmouth sucker (<i>Catostomus latipinnis</i>) ^N	17	17 (4)	410 \pm 54	340 - 493	15 (88)
threadfin shad (<i>Dorosoma petenense</i>) ^I	9	8 (2)	108 \pm 23	94 - 143	4 (44)

^IIntroduced species, ^NNative species

Note: Other species captured, but not included in analyses because they occurred in < 3 nets and had total counts < 2: Hybrid bluegill-green sunfish (*Lepomis macrochirus* x *cyaneus*)^I, rainbow trout (*Oncorhynchus mykiss*)^I, Colorado pikeminnow (*Ptychocheilus lucius*)^N, bluehead sucker (*Catostomus discobolus*)^N.

Table 3.2: Model output from manyGLMs ran separately for each year assessing species relative abundance as a function of increasing distance from lower Neskahi Bay, Lake Powell. Positive coefficients indicate decreasing abundance downstream. P-values were corrected for multiple testing and an effect of effort was included in models as a covariate. Percent of Sum-of-LR is displayed for species with significant relationships ($P < 0.05$) and was calculated by dividing the LR of each species model by the LR summed across species (Wang et al. 2012). Threadfin shad were not captured in 2019.

Year	Species	Coefficient (SE)	LR	P-value	Percent of Sum-of-LR
2018	channel catfish (<i>Ictalurus punctatus</i>) ^I	0.14 (0.01)	134.87	0.001	25.5%
	gizzard shad (<i>Dorosoma cepedianum</i>) ^I	0.23 (0.02)	114.96	0.001	21.7%
	common carp (<i>Cyprinus carpio</i>) ^I	0.11 (0.01)	68.30	0.001	13.0%
	smallmouth bass (<i>Micropterus dolomieu</i>) ^I	-0.13 (0.02)	64.05	0.001	12.1%
	black bullhead (<i>Ameiurus melas</i>) ^I	0.19 (0.03)	40.92	0.001	7.7%
	striped bass (<i>Morone saxatilis</i>) ^I	0.14 (0.02)	38.46	0.001	7.3%
	black crappie (<i>Pomoxis nigromaculatus</i>) ^I	0.16 (0.02)	38.27	0.001	7.2%
	razorback sucker (<i>Xyrauchen texanus</i>) ^N	0.15 (0.04)	17.02	0.002	3.2%
	flannelmouth sucker (<i>Catostomus latipinnis</i>) ^N	0.13 (0.06)	4.60	0.234	
	yellow bullhead (<i>Ameiurus natalis</i>) ^I	0.05 (0.02)	3.33	0.395	
	largemouth bass (<i>Micropterus salmoides</i>) ^I	-0.03 (0.02)	2.17	0.551	
	threadfin shad (<i>Dorosoma petenense</i>) ^I	0.07 (0.06)	1.44	0.686	
	bluegill (<i>Lepomis macrochirus</i>) ^I	-0.02 (0.02)	0.86	0.768	
	green sunfish (<i>Lepomis cyanellus</i>) ^I	-0.01 (0.02)	0.20	0.880	
walleye (<i>Sander vitreus</i>) ^I	-0.002 (0.04)	<0.01	0.948		
2019	common carp (<i>Cyprinus carpio</i>)	0.13 (0.02)	41.07	0.001	31.8%
	channel catfish (<i>Ictalurus punctatus</i>)	0.13 (0.02)	40.47	0.001	31.3%
	smallmouth bass (<i>Micropterus dolomieu</i>)	-0.17 (0.04)	24.87	0.001	19.2%
	yellow bullhead (<i>Ameiurus natalis</i>)	0.13 (0.04)	9.59	0.03	7.4%
	largemouth bass (<i>Micropterus salmoides</i>)	0.13 (0.06)	4.39	0.352	
	black crappie (<i>Pomoxis nigromaculatus</i>)	0.11 (0.07)	2.33	0.735	
	striped bass (<i>Morone saxatilis</i>)	0.05 (0.03)	2.22	0.735	
	razorback sucker (<i>Xyrauchen texanus</i>)	-0.09 (0.08)	1.30	0.884	
	black bullhead (<i>Ameiurus melas</i>)	0.09 (0.09)	1.27	0.884	
bluegill (<i>Lepomis macrochirus</i>)	-0.04 (0.04)	0.63	0.941		

green sunfish (<i>Lepomis cyanellus</i>)	0.05 (0.06)	0.62	0.941
gizzard shad (<i>Dorosoma cepedianum</i>)	-0.02 (0.04)	0.16	0.968
walleye (<i>Sander vitreus</i>)	0.03 (0.07)	0.14	0.968
flannelmouth sucker (<i>Catostomus latipinnis</i>)	0.03 (0.10)	0.10	0.968

^IIntroduced species, ^NNative species

Chapter 4 - Movement ecology of imperiled fish in a novel ecosystem: River-reservoir exchanges by razorback sucker and translocations to aid conservation

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Introduction

Many freshwater fishes occupy novel ecosystems (*sensu* Hobbs et al., 2006) that blend vestiges of natural landscapes with anthropogenic additions. The creation of novel aquatic ecosystems through damming and lenticification of rivers is ubiquitous across the globe (Grill et al., 2019; Sabater, 2008), resulting in altered flow and temperature regimes, decreased floodplain connectivity, and restricted movement of aquatic organisms (Pelicice, Pompeu, & Agostinho, 2015; Reidy Liermann, Nilsson, Robertson, & Ng, 2012). Dams cause reductions in biodiversity (Reidy Liermann et al. 2012), population abundance (Junge, Museth, Hindar, Kraabol, & Vollestad, 2014), dispersal ability (Rolls, Ellison, Faggotter, & Roberts, 2013), and the capacity of populations to buffer themselves against environmental stochasticity (Dunham, Young, Gresswell, & Rieman, 2004; Perkin, Gido, Costigan, Daniels, & Johnson, 2015; Perkin et al., 2019). Reservoirs and river-fragments between reservoirs are novel ecosystems consisting of

altered abiotic conditions and combinations of species that may not have shared an evolutionary history (Havel, Lee, & Vander Zanden, 2005; Hobbs et al. 2006). Given the prevalence (and perhaps permanence) of novel ecosystems, understanding how native species use these systems can improve management of their populations in contemporary riverscapes (Buckmeier, Smith, Fleming, & Bodine, 2014).

The relevance of novel river-reservoir systems to population dynamics of native fishes is unclear but might be clarified within a movement ecology framework (Nathan et al., 2008). Movement is a necessity for freshwater fish to complete their life history, is generally understudied for many species, and the scale at which it is important is unclear and difficult to ascertain (Cooke et al., 2016; Cooke, Paukert, & Hogan, 2012; Fausch, Torgersen, Baxter, & Li, 2002; Schlosser, 1991). Freshwater fish make movements to access patchily distributed resources, critical habitats (e.g., spawning habitat), and capitalize on favorable environmental conditions (Lucas & Baras, 2001). Fish movements influence demographic processes such as immigration and emigration, possible genetic exchange, and functionally connect habitats through transfer of materials and subsidies (Childress, Allan, & McIntyre, 2014; Cooke et al., 2016; Flecker et al., 2010). Conservation of mobile fish species is challenged by continued habitat degradation and blocked migration routes (McIntyre et al., 2016), and a lack of data on species' spatial ecology in river-reservoir systems hinders management efforts (Clarke, Telmer, & Shrimpton, 2007; Cooke et al., 2016).

The Colorado River basin, USA, epitomizes the novel ecosystem. Water storage reservoirs have transformed and fragmented rivers, causing habitat loss and restricting access to potentially important habitat types for native fishes (Minckley & Deacon, 1991). Colorado River basin fishes may have evolved to use spatially and temporally disjunct habitats including the

Colorado River Delta (Glenn, Lee, Felger, & Zengel, 1996; Sykes, 1937), volcanically impounded reaches (Dalrymple & Hamblin, 1998), and other lentic environments created by high water events (i.e., Salton Sea; Minckley 1983), but now must cope with an abundance of lacustrine environments created by anthropogenic barriers that also are habitat for introduced fishes (Clarkson, Marsh, Stefferud, & Stefferud, 2005). Because native fishes no longer have access to a large, diverse network of connected habitats, but are now restricted to fragmented populations in highly altered habitats, there is a need to understand how fish are using and moving throughout these novel ecosystems.

Razorback sucker (*Xyrauchen texanus*) is one of the Colorado River basin's imperiled, endemic species and understanding its movement ecology has been complicated by these above-mentioned habitat alterations. Razorback sucker make movements for spawning, rearing, and refuge, and they use a variety of habitats including mainstem rivers, smaller tributaries, floodplain wetlands, and reservoirs (Albrecht et al., 2018; Bottcher, Walsworth, Thiede, Budy, & Speas, 2013; Cathcart, McKinstry, MacKinnon, & Ruffing, 2019). In the upper Colorado River basin, early studies suggested razorback sucker were sedentary outside of the spawning season, but could move long-distances (> 100 km) to spawn (Modde & Irving, 1998; Tyus & Karp, 1990). The presumed sedentary nature of razorback suckers is cited in recovery documents (e.g., USFWS 1998) and recent studies (e.g., Durst & Francis, 2016). Studies of stocked fish over broader spatial (>1000 km) extents have focused mainly on post-stocking dispersals using physical recapture data, and indicate some individuals move long distances (514-684 km; Durst & Francis, 2016; Zelasko, Bestgen, & White, 2010). For example, Zelasko et al. (2010) determined the longest movements made were those initially following stocking events and movements were mostly in downstream directions. Despite knowledge of how fragmentation and

study design influence interpretations of fish movement (Gowan, Young, Fausch, & Riley, 1994), razorback sucker movement studies are typically limited in spatial extent because of remoteness of study areas and resources needed to tag and recapture enough fish to adequately describe movement patterns. However, by combining passive integrated transponder (PIT) tagging technology across the basin and development of data-sharing programs by multiple agencies, we can begin to synthesize data across a broader geographic extent to discern the scales at which individuals in the upper Colorado River basin are moving among novel reservoir and river habitats, which may lead to a better understanding of population connectivity and furthering conservation of the species.

Assessing movement is critical to evaluate connectivity within a novel ecosystem featuring large river corridors connected to a large reservoir and given tagging and stocking efforts across the entire upper Colorado River basin we can begin to better understand the spatial ecology of razorback sucker. We characterized movements of razorback sucker collected in Lake Powell, into its two main tributary inflows that have contrasting access to upstream riverine habitats. Specifically, Lake Powell is fed by the Colorado River that offers fish unimpeded access to the upper Colorado River and associated tributaries and by the San Juan River that is blocked by a 6 m tall waterfall approximately 30 km upstream of the current river-reservoir transition zone (Cathcart et al., 2018). By linking PIT-tags to encounter records compiled in a multi-agency database and tracking acoustic-tagged fish, we assessed broad dispersal capability, the proportion of fish exchanging between the reservoir and rivers, and responses of razorback sucker translocated upstream of the waterfall barrier. We specifically addressed three questions:

1. Where do razorback sucker captured in the Colorado River arm of the reservoir redistribute?,
2. What is the proportion of fish moving upstream from the San Juan River arm of Lake Powell

to the waterfall?, and 3. What is the post-translocation movement, residence time, and proportion of fish returning below the waterfall? Given unimpeded access, we expected fish to move throughout rivers upstream of Lake Powell, and although movement is impeded by the waterfall, we still expected to find frequent annual movements between the reservoir and river below the waterfall. For translocated fish, we expected individuals to move relatively long distances into upstream riverine habitat deemed suitable for spawning and most fish would remain resident in the San Juan River (Cathcart et al., 2018).

Methods

Study area

The upper Colorado River basin drains parts of Colorado, New Mexico, Utah, and Wyoming before entering Lake Powell, an impoundment that has inundated the historical confluence of the Colorado and San Juan rivers since Glen Canyon Dam was closed in 1963 (Figure 3.1). At full pool, Lake Powell inundates the Colorado River to approximately 30 km downstream of its confluence with the Green River whereas the San Juan River is inundated for approximately 110 km upstream of its historical confluence with the Colorado River.

Management for imperiled fishes consistently occurs in three major river systems (Green, Colorado, and San Juan rivers) of the upper Colorado River basin. These rivers differ in size (i.e., mean annual discharge) and the degree to which small diversion structures impede movement in upstream reaches (Figure 3.1). For instance, mean annual discharge has averaged $144 \text{ m}^3 \text{ s}^{-1}$ in the Green River at Green River, Utah compared to $37 \text{ m}^3 \text{ s}^{-1}$ in the San Juan River at Bluff, Utah from 2014-2018. Fishes in Lake Powell have unimpeded access to upstream riverine habitat on the Colorado River arm of the reservoir. On the San Juan River arm, upstream access is limited by the Piute Farms Waterfall (hereafter referred to as the “waterfall”). The waterfall

recently emerged in the inflow area after reservoir elevations dropped following the reservoir initially filling to capacity in the 1980s and the river cutting a new channel through deposited sediments (see Cathcart et al., 2018 for more details). With the exception of a two-week inundation event in late-July and early August of 2011, the waterfall has presented a complete barrier to upstream fish movement since 2001 and periodically formed in two different places between 1992 and 2001 (Durst & Francis, 2016; Ryden & Ahlm, 1996). In addition to variable access to riverine habitat directly upstream of Lake Powell inflow areas, fishes must also contend with fragmentation issues further upstream, where eight relatively large diversion structures occur on the Green, Colorado, Gunnison, and San Juan rivers with varying degrees of fish passage capability, including no passage structure, non-selective passages, or selective passages (Figure 3.1). Although fish passages can increase functional connectivity of fish populations (McLaughlin et al., 2013; Pennock, Bender, et al., 2018), no quantitative evaluation (e.g., passage efficiency; Noonan, Grant, & Jackson, 2012; Roscoe & Hinch, 2010) of passage structures has been completed in the upper Colorado River basin aside from documenting the presence and relative abundance of fish species captured or detected within, upstream, or downstream of passages.

Recovery and maintenance of razorback sucker is reliant on intense management efforts administered through the Upper Colorado Endangered Fish Recovery Program (<http://www.coloradoriverrecovery.org/>) and the San Juan River Basin Recovery Implementation Program (<https://www.fws.gov/southwest/sjrip/>). These programs include a multidisciplinary group of researchers representing state, federal, tribal and private stakeholders. Coordination between these two programs is crucial to meet basin-wide recovery goals. Accordingly, joint activities include education and outreach, operating hatchery facilities, and the formation of a

centralized tagging database. As part of coordinated stocking efforts, most razorback sucker have been PIT-tagged prior to being stocked into upper Colorado and San Juan rivers (Cathcart et al., 2018), and all research and monitoring efforts working with the programs scan captured fishes for PIT-tags and tag previously untagged individuals. The programs maintain a centralized database, in which all fish stocking, capture, tagging, and tag detection records are compiled from efforts across the entire upper Colorado River basin, including the San Juan River and Lake Powell (STReaMS, 2018).

Where do razorback sucker captured in the Colorado River arm of the reservoir redistribute?

Essentially all razorback sucker occurring in Lake Powell were stocked in upstream rivers, and so, have moved downstream into the reservoir since being stocked. Although untagged fish are captured in the inflow areas, the proportion of untagged fish either matches that from upstream rivers (e.g., tag loss in fishes from the Green, Colorado, and Gunnison rivers; Zelasko et al., 2010), or age estimates of untagged fish overlap with year classes of hatchery fish being stocked without PIT-tags in 2006 and 2007 (e.g., San Juan River arm; Furr, 2016). The lacustrine-transition zones (Thornton, Kimmel, & Payne, 1990) of the Colorado River arm of Lake Powell (CRA in Figure 3.1 & 3.2) were sampled in April, May, and June from 2014-2016 to assess the occurrence and number of razorback sucker in the inflow area (Albrecht et al., 2018). Reservoir-captured fish were sampled with a combination of trammel nets and boat electrofishing. Any captured but previously untagged razorback sucker were PIT-tagged (Biomark, Boise, Idaho, 12-mm full-duplex, 134.2 kHz) before release. Concomitant with sampling events, a total of 44 razorback sucker were tagged with acoustic telemetry tags (Sonotronics, Inc., Tuscon, AZ, CT-05-48). Acoustic-tagged fish were either stocked from a

hatchery ($n = 13$) or captured in the reservoir ($n = 31$) and released. To assess the redistribution of fish tagged in the Colorado River arm, records were identified in the STReAMS database of razorback sucker physically captured in 2014-2016 in the Colorado River arm of Lake Powell. Then, we queried the STReAMS database for all post-capture re-encounters (physical captures, PIT-tag detections, telemetry detections) of these fish across the entire upper Colorado River basin. We calculated the distance between where fish were captured in Lake Powell and their most upstream encounter location. For this objective, re-encounters could have taken place anytime between when a fish was captured in Lake Powell and December 13, 2018, when we queried the database. We used a standard set of river kilometers provided with the STReAMS database to calculate movement distances for all objectives.

Fish sampling efforts occurred throughout the upper Colorado River basin but varied in spatial and temporal distribution and sampling methods depending on goals of individual projects, including sampling for non-native fish removal, Colorado pikeminnow (*Ptychocheilus lucius*) and humpback chub (*Gila cypha*) population estimates, adult native fish monitoring, and various other research projects across >1,800 km of river (Figure 3.1; Cathcart et al., 2018; Franssen et al., 2014; Zelasko et al., 2010). In addition to efforts that physically capture fish, the use of PIT-tag antennas to re-encounter PIT-tagged fishes has increased throughout the basin at mainstem and tributary stream locations (Bottcher et al., 2013; STReAMS, 2018). Thus, our analysis was limited to quantifying the broad dispersal capability of razorback sucker outside of the Colorado River arm of the reservoir because we did not have standardized sampling or representative PIT-tag antenna locations systematically placed throughout the basin.

What is the proportion of fish moving upstream from the San Juan River arm of Lake Powell to the waterfall?

To quantify the proportion of razorback sucker moving between reservoir and river habitats, we used capture data from 2017 and 2018 in the San Juan River arm of Lake Powell (SJRA in Figure 3.1) and PIT-tag detection data from 2017 and 2018 at the waterfall ~30 km upstream on the San Juan River. Fish sampling was conducted in the lacustrine-transition zones of the San Juan River arm of Lake Powell with trammel netting and electrofishing, as previously described for the Colorado River arm. PIT-tag detections were compiled by a submersible antenna (Biomark, Inc., Boise, Idaho) located directly downstream of the waterfall. We felt estimates of exchange between reservoir and riverine habitat would be more robust in the San Juan River arm, because migrating fish aggregate below the waterfall, creating high tag detection probabilities for PIT-tag antennas there (0.6-0.9; Cathcart et al., 2018). We counted fish captured in the reservoir prior to moving upstream to the river below the waterfall and then detected at the PIT-tag antenna within a calendar year (365 days post-capture). We calculated non-parametric confidence intervals for the proportion of fish moving in each year using 10,000 bootstrap iterations.

What is the post-translocation movement, residence time, and proportion of fish returning below the waterfall?

To mimic historical access to riverine habitats in the San Juan River upstream of the waterfall, we translocated razorback sucker upstream of the waterfall in late winter-early spring of 2016 and 2017. We translocated fish during this period because detections and captures indicated abundant sexually mature, ripe fish directly below the waterfall during periods when temperatures and flows were approaching or at observed spawning conditions (Cathcart et al.,

2018). Razorback sucker were captured below the waterfall with raft-mounted electrofishing, scanned for the presence of a PIT-tag, injected with one if one was not present, and translocated by motorized raft up to 3.5 km upstream depending on flow conditions. Although fallback of translocated fish is possible (Hagelin, Calles, Greenberg, Nyqvist, & Bergman, 2016), we assumed fish were motivated to move upstream based on the number of fish in spawning condition (Cathcart et al., 2018). Fish could not be transported further upstream because of a rapid and cobble bar (~1 km long) that were not passible by boat. A subset of fish were also tagged with either acoustic tags in 2016 ($n = 10$) or dual acoustic-radio telemetry tags in 2017 ($n = 32$; ART-01-80). Fish could be re-encountered via a combination of physical re-captures, passive detections (PIT), and active detections in 2017 only (telemetry). We used the term “minimum distance moved” to describe the river distance between the waterfall and the most upstream encounter location. This term is described as a “minimum”, because we only used data on the first and last encounter locations, not any movement between or outside these two points. Similarly, we calculated the “minimum river residence time” as the number of days between when a fish was translocated and when it was last encountered in the river. Because we do not know if a fish left the river after re-encounter, this metric is a conservative estimate. Finally, we assessed whether any of these fish returned downstream of the waterfall via physical re-captures, passive detections (PIT and telemetry), and active detections (telemetry).

Results

Where do razorback sucker captured in the Colorado River arm of the reservoir redistribute?

Between 2014 and 2016, 722 individual razorback suckers (mean \pm SD; 485 ± 57 mm TL) were captured in the Colorado River arm of Lake Powell. Most (87%) of these fish had

stocking records in upper basin rivers (Table 1). The majority, 461 fish (64%), were never re-encountered and so are not reported on further. A total of 261 fish were re-encountered after capture. Fifty-nine percent ($n = 154$) were only re-encountered within the original capture area, and 108 of those individuals were recaptured in multiple years. Forty-one percent ($n = 107$) were either recaptured ($n = 11$), detected ($n = 100$), or both ($n = 3$) outside of the reservoir capture area including in the Green and Colorado river systems as well as across the reservoir in the San Juan River arm of Lake Powell (Figure 3.2). Passive detections on PIT-tag antennas comprised the majority of re-encounters. Sixty-seven fish were encountered in the Green River at a permanent PIT-tag antenna array near the Tusher Diversion weir, approximately 300 km upstream of the Lake Powell capture area (Figure 3.3). After this antenna system was installed in May 2016, cumulative tag detections sharply increased (Figure 3.4). Opportunistically placed PIT-tag antennas in the upper Green River, detected 11 individuals 586-614 km upstream of the Lake Powell capture area. All re-encounters of fish in the San Juan River arm of Lake Powell were passive detections of either PIT-tags ($n = 2$) or acoustic telemetry tags ($n = 17$). Of these 17 acoustically tagged fish, 16 were fish captured from the reservoir and 1 was stocked into the reservoir in 2015.

What is the proportion of fish moving upstream from the San Juan River arm of Lake Powell and the waterfall?

Fish moved annually among reservoir and riverine habitats in the San Juan River arm of Lake Powell, and proportions were relatively consistent across years. In 2017, 147 razorback sucker (496 ± 39 mm TL) were captured in the lacustrine-transition zones of the San Juan River arm of Lake Powell, ~30 km downstream of the waterfall. After being captured in the reservoir, (mean, [95% CI]) 29%, [21-36%] moved upstream towards riverine habitat and were later

detected at the waterfall within a year of being captured in the reservoir. In 2018, 20%, [12-30%] of reservoir-captured fish were detected at the waterfall within a year. Thus, we suggest as many as a third of reservoir-dwelling individuals attempt to move upstream each year, and fish are moving between reservoir and riverine habitats at relatively fine temporal scales.

What is the post-translocation movement, residence time, and proportion of fish returning below the waterfall?

We captured and translocated 152 razorback sucker in 2016 and 151 in 2017 (492 ± 39 mm TL; Table 2). In 2016, 9 of 152 fish were re-encountered in the river (Figure 3.5). Six of those nine fish were physically recaptured, and 3 fish were detected on PIT-tag antennas. These fish all moved at least 99 km upstream, including one fish that moved upstream 307 km to the Public Service Company of New Mexico (PNM) diversion, which has a selective fish passage structure. Minimum distance moved upstream averaged 218 km, and minimum residence time ranged from 17-536 days. In 2017, 20 of 151 fish were re-encountered in the river by physical recapture ($n = 2$), PIT-tag antenna detection ($n = 4$), or telemetry detection ($n = 14$) with a range of minimum distances traveled between 17-186 km and a minimum residence time between 13-132 days. However, fish generally were not detected as far upstream in 2017 (average 90 km) compared to 2016 (Figure 3.5). By July, active telemetry trips covering 290 km of river detected no fish upstream of the waterfall. The same number of fish ($n = 27$) in both years were not re-encountered after translocation. Eighty percent and 79% of translocated fish from 2016 and 2017, respectively, were re-encountered back downstream of the waterfall within a year (Table 2).

Discussion

Razorback sucker movement was quantified across an entire river basin relative to novel habitat types including movements through a large reservoir and upstream into river networks. By quantifying exchanges and movement potential across a broad spatial extent, we built on previous evidence of trans-basin movements (Durst & Francis 2016) and suggest there is connectivity between populations of razorback sucker in major tributary arms of the upper Colorado River basin that is maintained by movement of more than a few individuals. Notably, 17 of 44 acoustic-tagged razorback sucker moved from the Colorado River arm through lacustrine habitat to the San Juan River arm, a distance of at least 170 km. These results suggest razorback sucker have high dispersal capability through both lacustrine and riverine habitats and can move upstream distances of over 600 km where unimpeded in the current riverscape. Results also suggest that about a third of individuals dwelling in the reservoir are moving upstream to riverine habitat and this was consistent among years. This is the minimum proportion of individuals making annual movements from the reservoir to rivers upstream given our assumption that all fish migrating to the waterfall would be detected. Although reservoirs have been considered movement barriers for riverine species (Hudman and Gido, 2013; Pelicice et al., 2015), our data suggest razorback sucker in Lake Powell and its adjoining tributary networks function as metapopulations where there is notable exchange of individuals among major habitats.

Movement among spatiotemporally dynamic habitats is likely important for long-lived, periodic strategists such as razorback sucker, which are thought to have evolved bet-hedging strategies to capitalize on environmental variation (e.g., water temperatures, flows) that plays out over broad spatial and temporal extents (Schindler, Armstrong, & Reed, 2015; Winemiller &

Rose, 1992). Razorback sucker are hypothesized to experience a recruitment bottleneck in early life stages (Pennock, Farrington, & Gido, 2019; Schooley & Marsh, 2007) and this obviously must be remedied to establish genetic flow from migrating individuals. However, if recruitment conditions vary across large spatial and temporal scales, it is important that spawning adults can access as many places as possible to increase chances of successful recruitment (Cathcart, Gido, & Brandenburg, 2019; Lopes et al., 2019). Where fish have the most access to riverine habitat in the upper Colorado River basin, recruitment to adulthood by razorback sucker is still rarely documented (Bestgen et al., 2017), suggesting that connectivity is not the only management action required to recover this fish. While increasing or maintaining connectivity may not override other limiting factors, such as temperature or rearing habitat necessary for successful recruitment of early life stages (Bestgen 2008; Bestgen, Beyers, Haines, & Rice, 2006), it might increase long-term viability of the entire metapopulation by ensuring immigration-emigration pathways are maintained and by allowing access to favorable habitats (Fagan, 2002; Fullerton et al., 2010; Gido, Whitney, Perkin, & Turner, 2016).

Although our study focused on movement of razorback sucker, the occurrence of riverine species in reservoirs, and movement between reservoir arms and their associated river tributaries, is by no means unique to the Colorado River basin. Substantial exchanges of migrant fishes have been documented in other river-reservoir systems (Hladík & Kubečka, 2003; Říha et al., 2014), illustrating that mobile fish functionally connect rivers and reservoirs. For instance, Hladík & Kubečka (2003) found that 26 species and over 11% of all fish biomass in Římov Reservoir, Czech Republic, migrated between the reservoir and the Malše River inflow. These movements were mainly associated with spawning runs into the river by cyprinids such as bleak (*Alburnus alburnus*), roach (*Rutilus rutilus*), and bream (*Abramis brama*) (among others), but also included

Eurasian perch (*Perca fluviatilis*). Thus, reservoir dwelling fishes will readily move between lacustrine and riverine habitats, particularly rheophilic species that might be searching for spawning or feeding habitat. Along with movements for spawning (e.g., Graeb, Willis, & Spindler, 2009), fishes might move among rivers and reservoirs to exploit spatiotemporally dynamic habitats near inflow areas offering abundant food, such as phyto- and zooplankton (Thornton et al., 1990), cover in turbid water from high sedimentation rates (Miranda et al., 2010), and complex habitat structure (deltas, submerged vegetation, higher water temperatures) no longer found or limited in upstream portions of regulated rivers (Bestgen, Haines, & Hill, 2011; Buckmeier et al., 2014; Volke, Scott, Johnson, & Dixon, 2015). Fisheries managers in reservoirs and rivers often have varying objectives (i.e., maximizing sport fish production versus conservation of native species), and these habitats have traditionally been managed as independent systems (Buckmeier et al., 2014). Identifying mechanistic drivers of fish movements within and among river and reservoir habitats could inform managers of ecological costs and benefits (e.g., growth, diet, survival, and spawning productivity) experienced by individuals exhibiting these movements, which would ultimately help manage these systems more holistically (Buckmeier et al., 2014).

The majority of fish translocated upstream of the waterfall barrier on the San Juan River returned to the reservoir within a year. It is not immediately clear why so many fish returned back downstream of the waterfall. One possibility is that translocated fish were searching for suitable habitat (e.g., Carpenter-Bundhoo et al. 2019) but happened to move too far downstream, similar to how fish might have ended up in the reservoir after being stocked in the river. Alternatively, fish might have encountered spawning habitat, contributed to spawning, and purposefully moved back downstream to the inflow area where low-velocity habitat and trophic

resources are presumed to be high. In the San Juan River upstream of the waterfall, spawning habitat might occur only 30-40 km upstream where translocated fish were found to aggregate immediately downstream of rapids and cobble bars in spawning condition (i.e., expressing eggs or milt; B. Hines and C. Pennock, pers. obs.). Translocation of fish is a means to mitigate river fragmentation for native species at places such as the waterfall, where preventing access to upstream riverine habitat by non-native fishes (e.g., striped bass *Morone saxatilis*) is an objective for managers (McLaughlin et al., 2013; Pennock, Durst, et al., 2018; Rahel & McLaughlin, 2018). Downstream movements by most fish in this study suggest annual pre-spawn translocations of razorback sucker would be necessary for fish to access spawning habitat upstream of the waterfall.

We acknowledge the variable efforts used to re-encounter fish across the basin might limit the interpretation of razorback sucker dispersal patterns. For instance, although more translocated fish were encountered in the San Juan River in 2017 than in 2016, efforts to re-encounter fish were greater because of active telemetry tracking. Additionally, the different detection probabilities among various methods used to re-encounter fish in this study (e.g., acoustic telemetry versus PIT-tag antennas) prevented us from more rigorously quantifying the relative proportion of razorback sucker that moved among habitats. Even differences in detection probability using the same method but at different locations (e.g., PIT-tag antennas at Tusher Diversion versus the waterfall) likely exist and complicate quantitative efforts to assess fish movements at the population level. For these reasons, we did not analyze relative differences in the number of encounters among specific locations, such as the number of fish detected at Tusher Diversion versus the waterfall, but instead focused on broad dispersal capabilities of razorback sucker throughout the upper Colorado River basin.

Conservation practitioners must acknowledge the effect of novel ecosystems on population dynamics of imperiled species. Novel aquatic ecosystems are now ubiquitous across the globe (Havel et al., 2005; Reidy Lierrman et al., 2012), and many freshwater fishes contend with altered habitats and species assemblages. Although conservation efforts are challenged by increasing imperilment of species without a full understanding of mechanisms driving their declines (Closs et al., 2016), management might be more effective if efforts account for diverse life history strategies (e.g., movements) that increase population resilience to environmental change (Allen & Singh, 2016; Hilborn, Quinn, Schindler, & Rogers, 2003; Schindler et al., 2015). A more complete understanding of how species employ variable movement syndromes (Comte & Olden, 2018) among habitats in contemporary riverscapes such as between rivers and reservoirs could allow for these habitats being managed more completely for the benefit of imperiled species – especially if management promotes and maintains connectivity.

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Figures

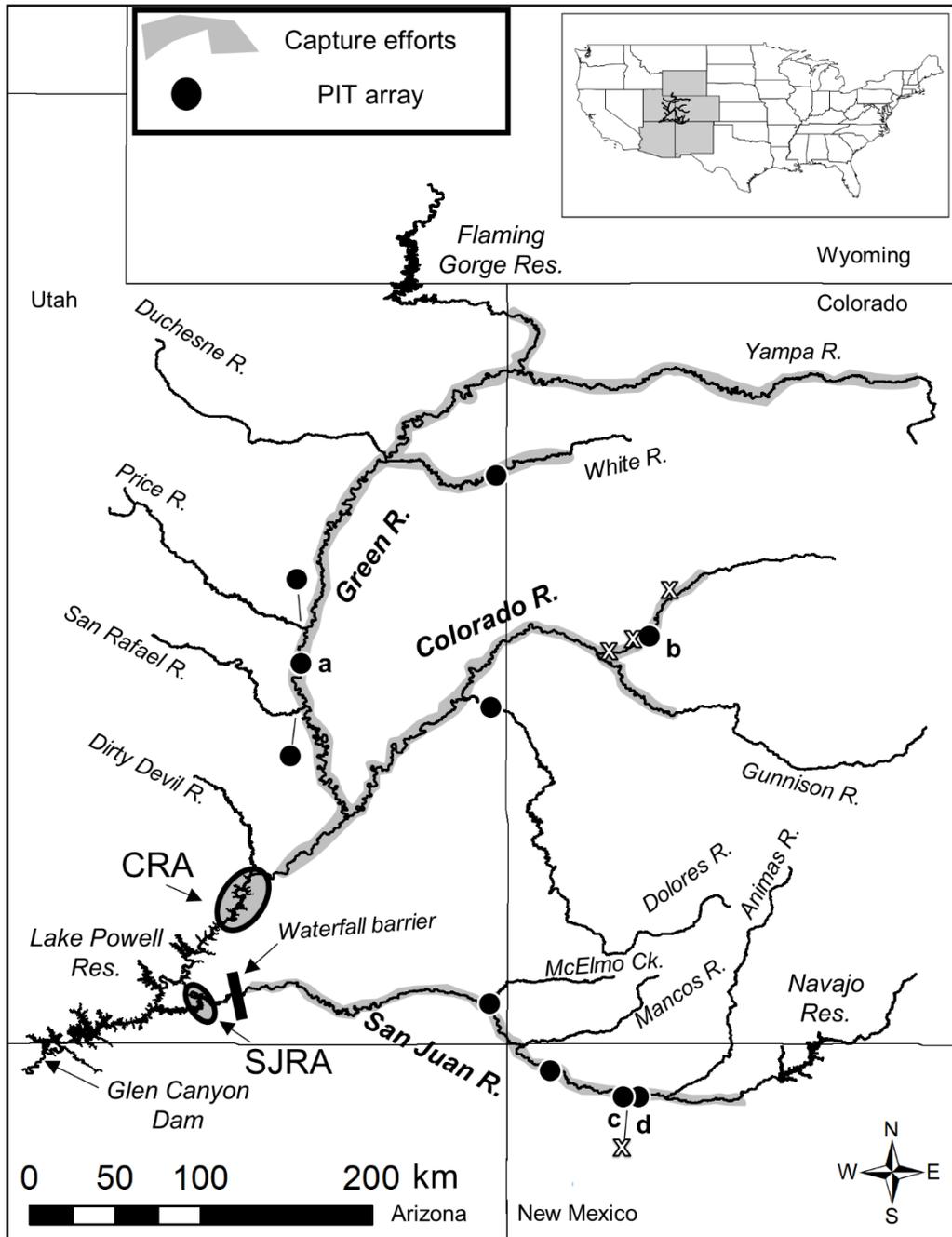


Figure 4.1: Major rivers and reservoirs of the upper Colorado River basin. Sampling for the occurrence of razorback sucker in Lake Powell reservoir inflow areas occurred in 2014-2016 (Colorado River arm, CRA) and in 2017 (San Juan River arm, SJRA). Sampling efforts occur

throughout the basin for various projects (grey shading), and various permanent PIT-tag antenna arrays have been installed (filled dots). Opportunistically placed submersible PIT-tag antennas (not depicted) are also used to detect fish throughout the study area (e.g., Waterfall barrier, upper Green River). Four diversion structures with fish passages and PIT-tag antennas are labeled with letters (a, Tusher Wash; b, Price Stubb; c, Hogback; and d, Public Service Company of New Mexico). Three other diversion structures on the Gunnison (Redlands) and Colorado rivers (Grand Valley Irrigation Company and Grand Valley Project) have fish passages but lack PIT-tag antennas, and one diversion on the San Juan River (APS) lacks both fish passage and antennas (X's). The Piute Farms Waterfall (Waterfall barrier) is located at the upper end of the San Juan River arm of Lake Powell.

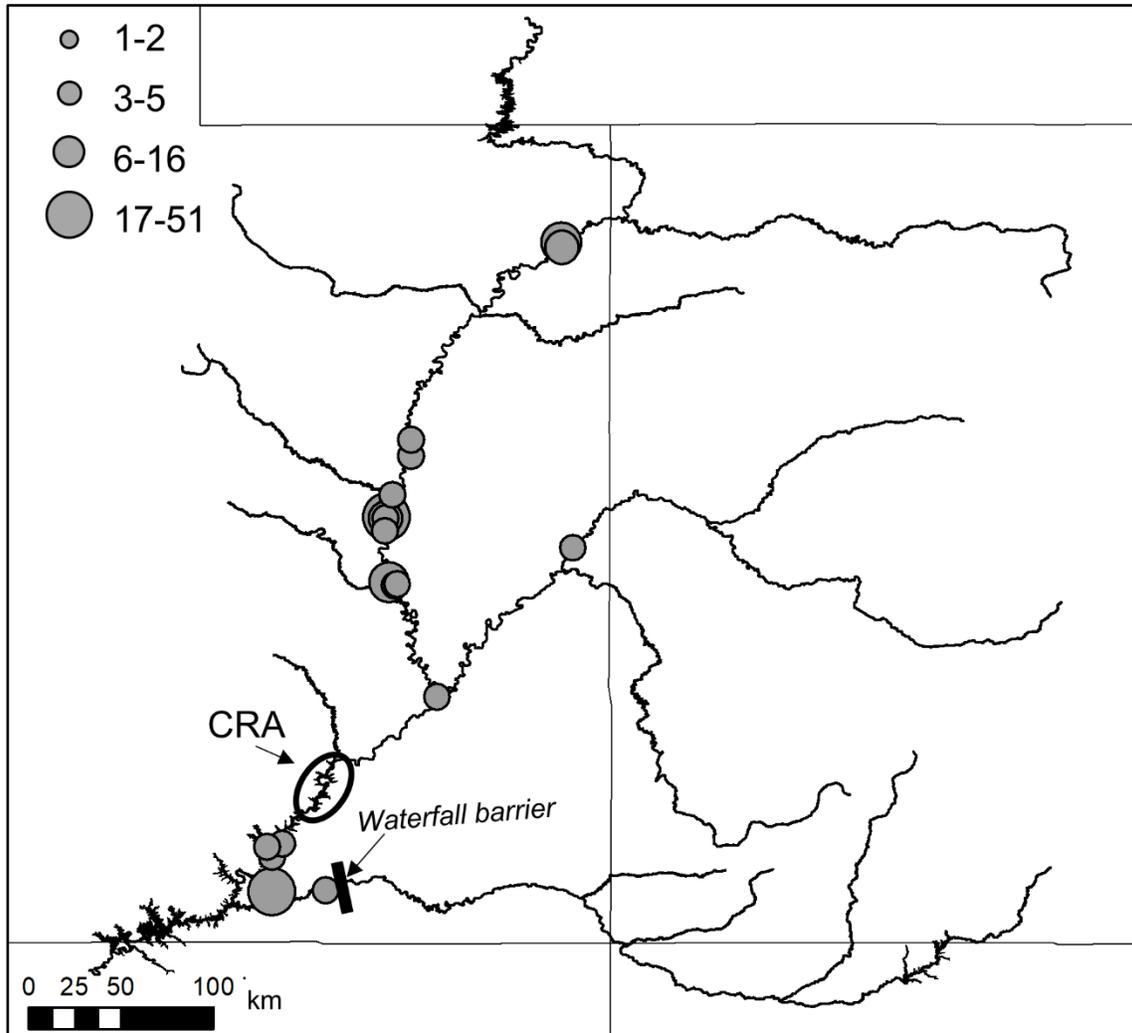


Figure 4.2: Encounter locations (physical captures, PIT-tag detections, and telemetry detections) of individual razorback sucker ($n = 107$) throughout the upper Colorado River basin following physical capture in the Colorado River Arm (CRA) of Lake Powell reservoir in 2014-2016. Upstream movement into the San Juan River is blocked by an impassable waterfall. The size of dots corresponds to the number of individuals encountered at that location (legend). Records accessed from the STReAMS database included any encounters after the date of capture through December, 13 2018.

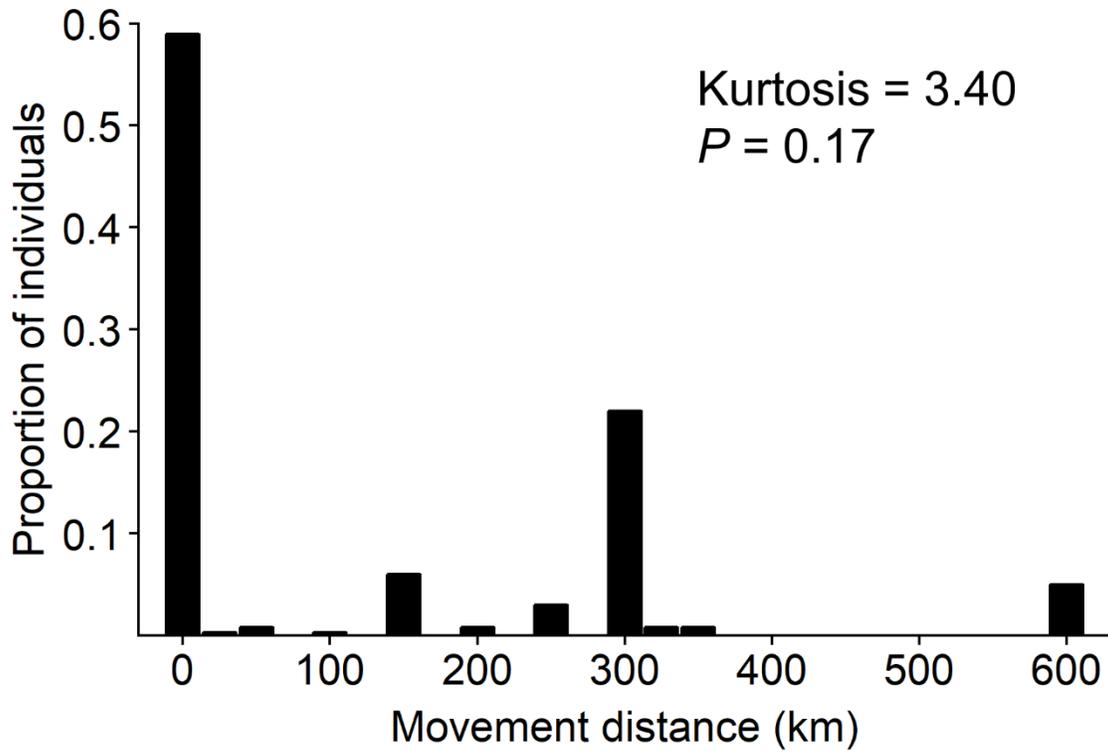


Figure 4.3: Absolute distances moved by razorback sucker ($n = 261$) that were initially captured in the Colorado River arm of Lake Powell and encountered throughout the upper Colorado River basin. Fifty-nine percent were only re-encountered within the original capture area, and forty-one percent were re-encountered outside the original capture area. The distribution did not show significant leptokurtosis.

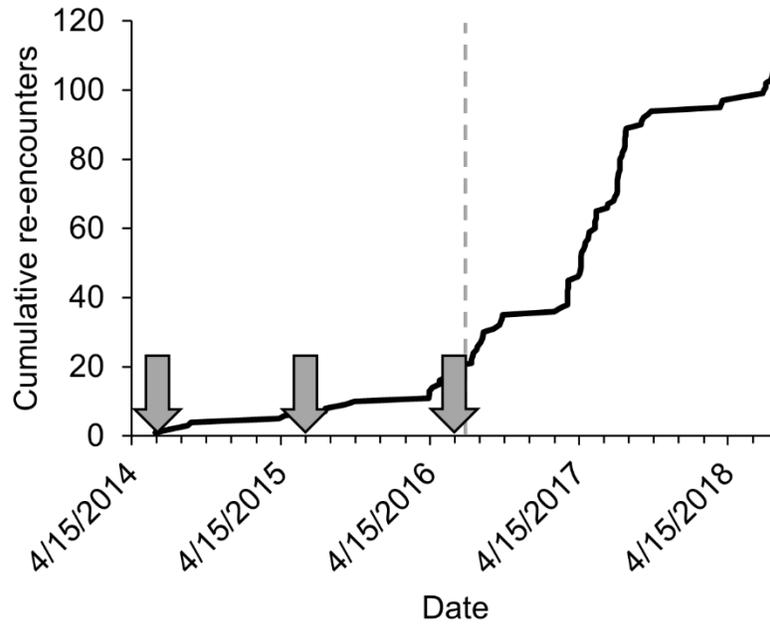


Figure 4.4: Cumulative number of re-encounters ($n = 107$; solid line) outside of the Colorado River Arm (CRA) of Lake Powell. Razorback sucker were captured in the CRA from April through June in 2014-2016 (arrows). A PIT-tag antenna system was constructed at Tusher Diversion weir on the Green River, Utah in May 2016 (dashed line) increasing re-encounters of tagged fish. Records accessed from the STReAMS database included any encounters after the date of translocation through December 13, 2018.

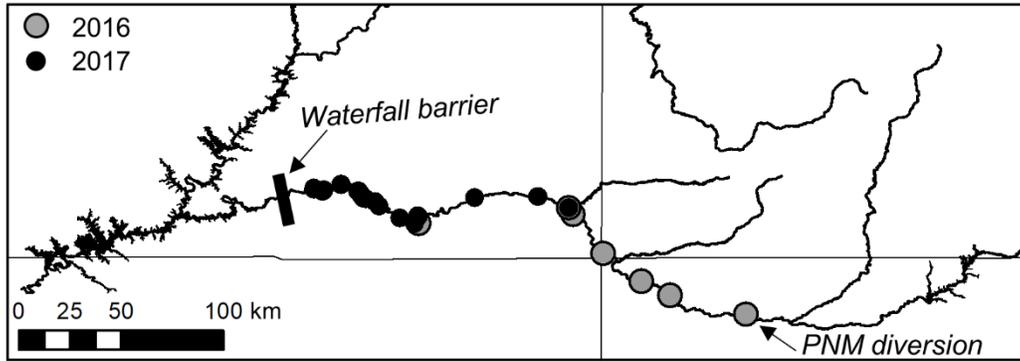


Figure 4.5: Encounter locations (physical captures, PIT-tag detections, or telemetry detections) of razorback sucker that were translocated upstream of the Piute Farms Waterfall and into the San Juan River in 2016-2017. The most upstream encounter occurred at Public Service Company of New Mexico (PNM) Diversion (2016). Records accessed from the STReAMS database included any encounters after the date of translocation through December 13, 2018.

Tables

Table 4.1: Number of razorback sucker originally stocked into rivers of the upper Colorado River system that were subsequently captured in the Colorado River arm of Lake Powell in 2014-2016.

Stocking river (rkm; range)	Year													
	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Colorado River (244-385)	3	1	4	4	3	7	3	2	3	2	2	2	1	
Green River (192-511)		5	18	13	14	42	35	82	106	113	91	46	9	1
Gunnison River (91)						2				1		7	5	
<i>Total</i>	3	6	22	17	17	51	38	84	109	116	93	55	15	1

Table 4.2: Summary of encounters (physical captures, PIT-tag detections, telemetry detections) of razorback sucker captured immediately downstream of the Piute Farms Waterfall in 2016-2017 and subsequently translocated 0.2-3.5 km upstream into the San Juan River. Encounters were assessed via records in the STReaMS database from the date of translocation through December 2018.

Year	Number translocated	Number encountered in river	Minimum distance moved (km; mean, range)	Minimum residence time (days; mean, range)	Number never re-encountered	Number encountered back in Lake Powell
2016	152	9 (6%)	218, 99-307	182, 17-536	27 (18%)	123 (81%)
2017	151	20 (13%)	90, 17-186	39, 13-132	27 (18%)	119 (79%)

Chapter 5 - Conclusions

Conservation efforts have been limited by a complete understanding of multiplicative factors causing the decline of freshwater fishes. I provide new insights and present existing challenges into factors influencing populations of razorback sucker in Chapters 2, 3, and 4 of this dissertation using field studies and assessment of museum-vouchered specimens. Collectively, these studies contribute to an increased understanding of razorback sucker ecology and use of novel ecosystems that can aid conservation efforts. Differences in diets of early life stage fishes might help explain differences in recruitment dynamics observed in co-occurring species and assessing how similar species respond to environmental change. All three species I assessed co-occur with a suite of non-native species, which are hypothesized to cause declines in native fish populations. However, differences in survival of early life stages among species in the face of non-native species occurrence suggests the effects of non-native species might not be generalizable across native fishes (Chapter 2). Knowledge on species distributions along environmental gradients might help assess potential species interactions and habitat requirements (Chapter 3). Connectivity between and movement among habitats is vitally important for fish to complete their life history, and this occurs at multiple spatial and temporal scales. To fully understand a species' spatial ecology, movements need to be assessed over broad-spatial extents (Chapter 4), taking into account the potential for both short- and long-distance movements, which are both important for different ecological reasons (e.g., feeding, spawning, biotic interactions). These studies contribute to the conservation of aquatic biodiversity in novel ecosystems by elucidating potential reasons for differential species responses to environmental change and informing conservation efforts on habitat use and movement that has potential to influence population dynamics of imperiled species.

For currently unknown reasons, seemingly similar species (i.e., within the same family) showcase differential survival in response to water development and non-native species. All three sucker species assessed in my study co-occur with a suite of non-native fishes, yet exhibit widely different levels of recruitment. All have experienced range-wide declines in distribution, but two species have maintained self-sustaining populations while razorback sucker have not (Budy et al. 2015). Thus, there appears to be other factors limiting the success of native populations other than non-native species alone, or potentially differential responses among species to the presence of non-native species. Water development has altered riverine habitats such that flow regimes in mainstem rivers have been decoupled from conditions in which many fishes evolved (Poff et al. 1997). Habitat alteration in the form of altered flow and thermal regimes and fragmentation by dams has occurred on mainstem rivers in the Colorado River basin, while some tributary systems still function under somewhat natural conditions (Laub et al. 2018; Hooley-Underwood et al. 2019). Perhaps this has allowed species such as bluehead sucker and flannelmouth sucker, which are able to use tributary systems for spawning migrations (Fraser et al. 2017; Cathcart 2018), to maintain self-sustaining populations while more mainstem-adapted species such as razorback sucker have declined. Additionally, fragmentation by dams directly impacts freshwater fishes by blocking dispersal corridors, but interactions between species-specific life histories (e.g., dispersal, drifting life stages, tributary spawning) and river fragmentation means species are not impacted equally (Perkin and Gido 2011; Perkin et al. 2015; Troia et al. 2019). Being larger-bodied, razorback sucker might require longer intact river fragments either to find suitable habitat or to allow for mobility of various life stages (e.g., drifting larvae) compared to bluehead or flannelmouth sucker. It is not clear why razorback sucker recruitment to adulthood has not been documented in Lake Powell given it occurs in Lake

Mead (Albrecht et al. 2010; 2018). Vegetative cover and turbidity are both hypothesized to increase survival of early life stages in inflow areas to Lake Mead (Albrecht et al. 2010), but there has not been a direct comparison of these two factors between Lake Mead and Lake Powell. Future efforts quantifying differences in inflow areas in Lake Mead versus Lake Powell could prove fruitful for furthering mechanistic understanding of factors limiting razorback sucker recruitment.

Rivers flowing into reservoirs are now common features across riverscapes around the globe. Fisheries management in reservoirs is typically focused on production of coveted sport fishes, which have been widely introduced (Havel et al. 2005). Conversely, management in rivers commonly occurs to conserve populations of native fish that have suffered declines following habitat alteration and introduction of non-native species (Franssen et al. 2014). Rivers and reservoirs are structurally connected through water flows, but also functionally connected by the movement of aquatic organisms, similar to naturally occurring river-lake systems. Native riverine species are commonly found in reservoir habitats, yet the use of reservoirs by native species and their effects on population dynamics are not well understood. Guy et al. (2015) argued for broadening the regulated-river paradigm by looking upstream when assessing the impacts of dams on riverine fishes. Most research on dam effects on aquatic systems have focused on mitigating or managing downstream impacts through flow prescriptions (Poff et al. 1997; Guy et al. 2015; Poff 2018), and relatively little management occurs at the transition of rivers and reservoirs despite these areas harboring high biodiversity (Buckmeirer et al. 2014; Da Silva 2019).

What can be done to manage fish in river-reservoir inflows? Large reservoirs present management challenges because of their size and multi-purpose uses (Matthews et al. 2004).

However, current management practices used independently in riverine and reservoir habitats including water level management (or flow management), habitat management, predator control, and stocking could also be used to manage fish populations in river-reservoir inflow areas. Species able to utilize lotic and lentic habitats might do well in reservoirs especially near river inflows because of abundant food resources, relatively warm water temperatures during certain times of the year, and a mix of flowing and low-velocity habitats (i.e., habitat complexity). Reservoirs present challenges for some rheophilic species and life stages not conducive to lentic habitats or if habitats have poor water quality (e.g., anoxic sediments; Guy et al. 2015). Reservoirs are commonly stocked with non-native predator species that consume native fishes (e.g., Ehlo et al. 2017). But, that razorback sucker recruit in the inflows to Lake Mead and other native rheophilic species commonly occur in reservoir systems suggests river-reservoir inflows could be directly managed for native species or included in current river and reservoir management schemes. For example, submerged vegetation can be beneficial to recruitment of fishes by providing cover and increased food resources (Strakosh et al. 2009). The cycle of drying and re-wetting that occurs in river-reservoir delta areas as water level fluctuates promotes high levels of native vegetation production (Volke et al. 2015) and inundated low-velocity habitats provide nursery areas for early life stage fishes in river-reservoir inflows (Gilbert and Pease 2019). Consequently, reservoir water level could be managed to provide off-channel habitat at inflow areas during spawning seasons of targeted species to encourage increased production of young-of-the-year fish. Additionally, for species requiring lotic habitats, water level could be reduced at certain times to provide more riverine habitat upstream of reservoirs (Guy et al. 2015; Coulter et al. 2019). Removal of non-native fishes or fish predators is another management strategy that could take place in river-reservoir systems. This would obviously be a

more effective option in water bodies strictly managed for native fish conservation and not sport fishing to avoid conflicts between native species conservation and sport fish production (Clarkson et al. 2005) and also to ensure a greater chance of success of removal efforts from repeated introductions or stocking. Finally, stocking of fishes into turbid river inflows might be a successful strategy to increase local densities of fish where predation by non-native predators is a concern (Albrecht et al. 2010).

Conservation of species in novel ecosystems such as river-reservoir complexes will require creative solutions to balance the complexities of these human-made habitats. More research that includes an upstream perspective to river-reservoir management is needed to fully assess the potential for these systems to be used as places of native fish conservation (Buckmeier et al. 2014; Guy et al. 2015). Since Guy et al. (2015) called for broadening of the regulated river paradigm there has been an increase in studies on fish assemblages in river reservoir inflows, but these have mainly focused on quantifying fish assemblage diversity and structure. Any conservation potential these areas might provide will not be realized until more research is conducted assessing factors promoting success of native fishes, including potential interactions with fish predators, and applying and evaluating management actions directly to river-reservoir inflows. Sport fish managers have traditionally focused management efforts on down-reservoir habitats and native fish managers have largely dismissed reservoirs as native fish habitat. Both have largely ignored the transition zones between rivers and reservoirs. Given the cosmopolitan occurrence of reservoirs, we need to consider using them for conservation and fish production where adequate habitats exist.

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